# TOOTH REPLACEMENT IN A NEW GENUS OF PROCOLOPHONID FROM THE EARLY TRIASSIC OF CHINA

*by* LI JIN LING

ABSTRACT. A new genus of procolophonid, *Eumetabolodon*, from the lower Triassic of Inner Mongolia, China, is described; *E. bathycephalus* (sp. nov.) is the type-species of the new genus and *E. dongshengensis* (sp. nov.) is also referred to that genus. *Eumetabolodon* is characterized by its very deep skull, large orbit, and by the posterior position of the articulation for the lower jaw. The dental morphology, the tooth wear, and the evidence of tooth replacement in this animal are also described in detail. It is suggested that the animal replaced its teeth during growth, for it seems that the conical post-canine teeth of young individuals are replaced by transversely broad, bicuspid teeth, which are themselves replaced in turn by the next generation of teeth. The replacement of individual teeth is discussed; the sequence and rate of replacement are still unknown.

Two previous papers have described procolophonids from China: a single skull from Yushe, Shanxi province, as the new genus *Neoprocolophon* (Young 1957), and three teeth from the lower Er-Ma-Ying Formation (lower Triassic) of Baode county, Shanxi province, as *Paoteodon* (Chow and Sun 1960). (Romer 1966 referred to the latter incorrectly as being of upper Triassic age.) The present paper is based upon a number of incomplete skulls which were collected by two field groups of the IVPP in 1977 and 1979 from the north-eastern part of the Shaan-Gan-Ning Basin, in the border region between Inner Mongolia and Shaanxi province. The distance between the two localities, Zhuengeerqi and Gucheng, is 17·5 km (text-fig. 1). Most of the fossils were found in the upper He-Shang-Gou (He-Shan-Kou in old use) Formation. Three other groups of tetrapods have previously been identified from the same formation: scaloposaurs, pseudosuchians, and labyrinthodonts (Sun 1980). A few procolophonids have also been discovered in the lower Er-Ma-Ying Formation, together with a large number of dicynodonts, some primitive thecodontians, and scaloposaurs.

Because the new specimens show clearly characters different from those of previously described genera, a new genus is erected in this paper. The name *Eumetabolodon* is proposed, from the Greek *εὐμετάβολος* (changeable) and *ὀδούς* (tooth), because there is evidence that it developed replacement teeth during its lifetime. The specimens are in the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing.

## SYSTEMATIC PALAEONTOLOGY

Family PROCOLOPHONIDAE
Genus EUMETABOLODON nov.

*Diagnosis*. Skull generally triangular, relatively deep and broad posteriorly; orbit large, trapezoid; pineal foramen rounded, of medium size, located anterior to the posterior margin of the orbit, bordered anteriorly by the frontals; tabular and squamosal, quadratojugal and quadrate extend slightly obliquely backward; jaw articulation placed far posteriorly, just under the posterior rim of the skull table; otic notch distinct.

### *Eumetabolodon bathycephalus* sp. nov.

*Etymology*. The species name is derived from the Greek *βαθύς* (deep) and *κεφαλή* (head).

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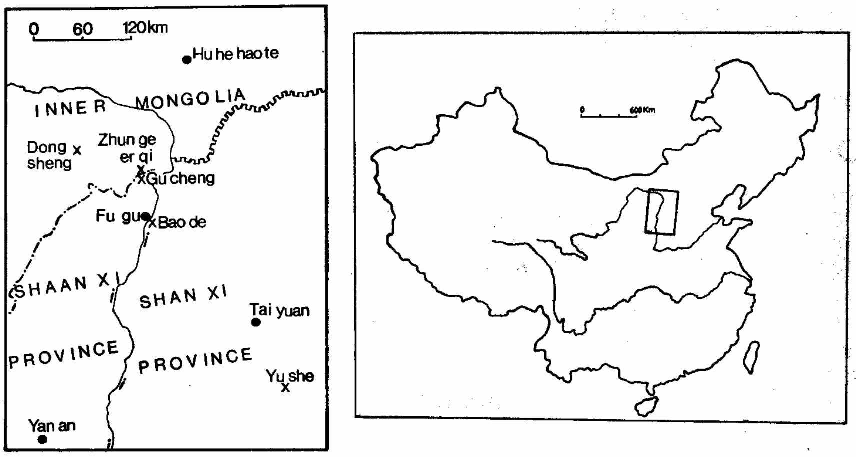



TEXT-FIG. 1. Localities at which procolophonids were found are shown by x in map on left, which is an enlargement of the rectangular area shown in map of China on right.

*Diagnosis.* Maxillary teeth separated by gaps between their bases, relatively short; may be longitudinally elongated in small animals, transversely widened and bicuspid in larger ones.

*Holotype.* V.6064, an almost complete skull and lower jaw.

*Paratypes.* Specimens (all skull material), as listed below.

*Locality and Horizon.* Zhuengeerqi county, Inner Mongolia, China; upper He-Shang-Gou Formation, $T_1$.

*Description.* The holotype is a well-preserved skull with lower jaw interlocked; both stapes are missing. Only the right quadrate, the rear of the right ramus of the lower jaw, and the snout are slightly broken. Thus the whole structure of the skull can be reconstructed with confidence (text-fig. 2).

Dorsal view. The posterior part of the skull is almost parallel-sided but, from a level midway along the orbits, the skull tapers anteriorly to a blunt snout. There is therefore, in dorsal view, a pronounced angulation in the skull profile, in which it is very different from the almost triangular skull of *Procolophon*, with its straight cheek region and postero-laterally directed quadratojugal bones. The large, irregular orbits occupy nearly half of the total skull length. The skull is high, and the orbits are therefore directed dorso-laterally.

Though the skull is well preserved, it is impossible to trace some of the sutures.

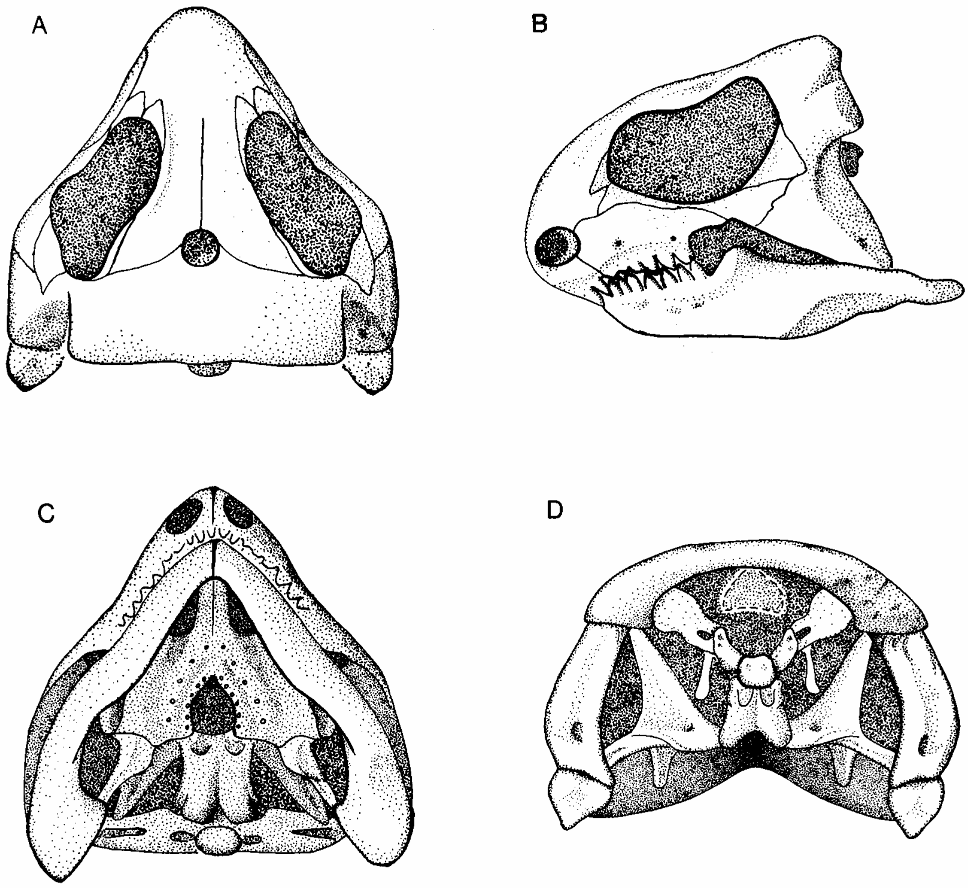
The nasals are badly damaged, only a small piece of the right nasal remaining. The lacrimals are, as usual, short and do not reach the external nares. The frontals are large and are unusual in that they, rather than the parietals, form the anterior border of the pineal foramen.

Side view. The jaws are closed in their natural position, the upper teeth being outside the lower teeth and interlocking with them. Only a few of the upper teeth are broken. This view clearly shows the great depth of the skull, both posteriorly and anteriorly; its maximum depth is 3·5 cm, nearly 70% of the skull length. The jaw articulation is placed very far posteriorly. The jaw symphysis shows a clear gap, which implies there was some mobility between the two rami of the lower jaw during life.

The external naris is large and elliptical. No trace of a septomaxilla could be found. The suture between the maxillae and the jugals is firm, not overlapping as in *Tichvinskia* (Ivachnenko 1973); this suggests that there was no mobility in *Eumetabolodon* at this position.

A longitudinal ridge separates the maxilla into two parts, the lower of which, a curved belt above the dentition, is directed ventro-medially. A noticeable foramen lies above the third maxillary tooth. Ivachnenko, who named this the anterior maxillary foramen, suggested that it transmitted an artery, a nerve, and perhaps also a vein. Another smaller foramen opens at a slightly more ventral level above the sixth maxillary tooth. It is also worth noting that, because of the deeper maxillae of *Eumetabolodon*, the foramen lies further from the tooth row than in *Tichvinskia*.

In having a very posteriorly placed jaw articulation, and consequently an unshortened lower jaw,



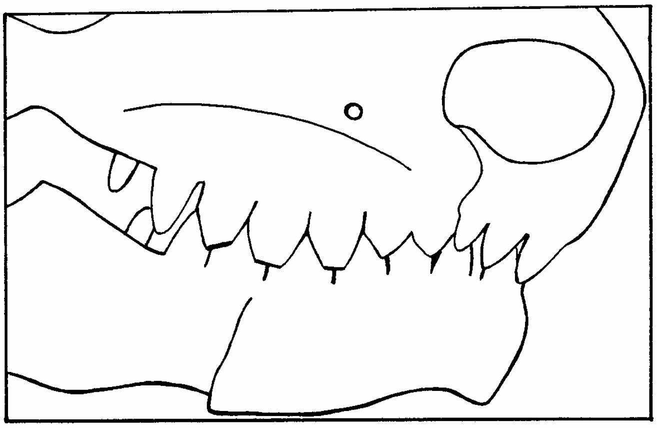

TEXT-FIG. 2. *Eumetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6064, natural size. A, dorsal view; B, lateral view; C, ventral view; D, occipital view.

*Eumetabolodon* appears to be a primitive type of procolophonid. The lower jaw, which has a long retroarticular process, is therefore as long as the skull. The quadrate bears two condyles.

Because the teeth are tightly interlocked, it is difficult to study the details of the structure of the teeth, but several points can be noted. The upper and lower tooth rows are each 19–20 mm long. On the right side there are three premaxillary teeth and seven maxillary teeth, but on the left side there are two premaxillary teeth and six maxillary teeth. The premaxillary teeth are long and conical, and gradually diminish in size posteriorly. Behind the second premaxillary tooth on the left side there is a 1 mm gap, which is not seen in other specimens. The suggestion that the left tooth row is at a slightly earlier stage of development than the right is supported by the fact that its tooth row is also slightly shorter, with one maxillary tooth fewer. The last, seventh maxillary tooth on the right side is small and conical, unlike the larger, more anterior teeth. The last, sixth, maxillary tooth on the left side is large, and it seems unlikely that on this side the small seventh tooth had already been lost and would be replaced. It therefore seems more likely that it had not yet erupted.

The first and second maxillary teeth on both sides are so badly damaged that one can only say that they were small in size; their shape is unknown. The more posterior teeth increase noticeably in size and were apparently transversely widened. The posterior view of the sixth left maxillary tooth shows that it has two cusps, lingual and labial. The teeth are long (*c.* 2·5 mm) relative to the height of the skull. Their crowns are covered with clear brown enamel. In several, the cusps have worn away. The wear facets do not seem to show a similar oblique direction, parallel in each tooth, as in *Hypsognathus* (Colbert 1946), but are irregular (text-fig. 3). The fact that the teeth are only slightly worn suggests that the specimen was a young individual. The dentitions of the two sides of the lower jaw are similar, each bearing eight teeth, of which the last is conical or blunt in shape.

Ventral view. The palate is of normal procolophonid structure, with large pterygoids surrounding a short, wide, heart-shaped interpterygoid vacuity as in *Procolophon*. There are two rows of small conical teeth, one row along the side of the interpterygoid vacuity and the other more lateral. The deep sockets on the pterygoids, which articulate with the parasphenoid, appear to face postero-dorsally rather than postero-medially as in *Procolophon* (Kemp 1974); this may be connected with the fact that the skull of *Eumetabolodon* is much deeper. The transverse palatal flange, formed by the pterygoid, almost touches the medial surface of the lower jaw. There can, therefore, have been little transverse movement of the latter.



TEXT-FIG. 3. *Eumetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6064, ×4. Lateral view to show dentition.

The quadrate ramus of the pterygoid extends horizontally and then twists gradually to suture with the quadrate as usual. Near where the pterygoid meets the parasphenoid, another long, strong spur of the pterygoid rises dorso-laterally to meet the squamosal. The suture between the ectopterygoid and the palatine, though hardly visible, is marked by a long, narrow palatonasal fenestra (Ivachnenko 1973). The vomers are damaged; no teeth can be seen on them.

The para-basisphenoid is very similar to that of *Procolophon*, described very carefully by Kemp (1974), so only a few differences need be mentioned here. The first is that the para-basisphenoid of *Eumetabolodon* extends postero-dorsally to meet the occipital condyle, which is at a higher level than the pterygoid; this makes a distinct angle between the palatal surface and the axis of the para-basisphenoid. Secondly, a very clear suture separates the parasphenoid from the basisphenoid; the former is 9 mm long, the latter 4 mm. The third point worthy of mention is that the contact between the basisphenoid does not rise as a delicate, vertical sheet to contact the anterior end of the prootic, as was described by Kemp (1974). No cultriform process can be seen.

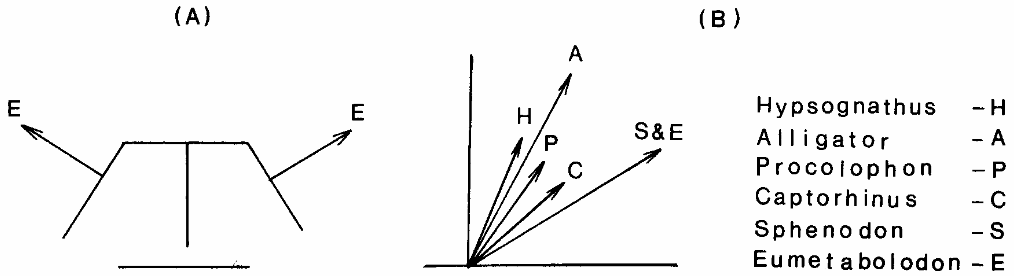
Posterior view. This shows clearly the great height of the skull. It is 15 mm from the upper margin of the occipital condyle to the top of the skull and a similar distance from the lower margin of the condyle to the surface of the quadrate condyle, so that the occipital condyle lies equidistant at the centre of the posterior surface. The basioccipital forms the whole of the condyle. It is small, rounded, and different from that of *Procolophon*, as there is no medial cleft and merely a low convexity on either side (Kemp 1974). The supraoccipital is a small triangular bone, displaced anteriorly. The exoccipitals, making up the lateral walls of the foramen magnum, resemble those of *Procolophon*. As mentioned by Watson (1914, p. 736) 'the bone extends outwards for a little distance with its upper part in contact with the posterior surface of the paraoccipital, from which bone it is separated below by the large, round foramen jugulare'. But in *Eumetabolodon* the dorsal part of the bone is penetrated by two foramina, a larger dorsal foramen and a smaller ventral foramen.

In *Procolophon* the opisthotic described by Kemp (1974) 'runs horizontally and somewhat posteriorly and slightly ventrally as a very well-developed process'. However, in *Eumetabolodon* it extends dorso-laterally to meet the tabular. The situation is more like that in *Nyctiphruretus*. The epipterygoids are very slender.

*Discussion*. The triangular skull, enlarged orbits, and few, apparently transversely widened teeth show that *Eumetabolodon* is a procolophonid. It is not difficult to distinguish *Eumetabolodon* from most other lower Triassic procolophonids, for it shows a number of unique features, notably the short high skull with large orbits and short snout, the anterior position of the pineal foramen so that it is partly bordered by the frontals, and the long lower jaw articulation near the posterior end of the skull. However, it also shows many resemblances to *Procolophon* itself and seems particularly close to *Koiloskiosaurus* (von Huene 1911). *Eumetabolodon* appears to be a smaller form than *Koiloskiosaurus*, though this difference must be treated with caution since we could be dealing with individuals of different ages. A more reliable difference lies in the skull proportions. The skull of *Eumetabolodon* is short and deep, whereas that of *Koiloskiosaurus* has an elongate snout and is more flattened; the skull of *Procolophon* is intermediate in these characters.

Such a change in skull height and width must cause a change in orientation of the orbits. Colbert (1946, p. 242) noticed 'this change in the direction of the orbits was the result primarily of transverse growth in the skull, from the primitive Permian and Lower Triassic procolophonids to the most specialized Upper Triassic genera. As the skull broadened, it flattened out, and with this flattening there was an accompanying change in the pointing of the orbits from a lateral to an almost vertical direction.'

The early representatives of this group, *Nyctiphruretus* (Efremov 1938) and *Owenetta* (Broom 1939), have flattened skulls. From the Permian to the early Triassic, the relative height of the skull increased. Colbert (1946, fig. 8) shows the direction of the orbits of a number of procolophonids and other reptiles in anterior or posterior view. The direction of the orbits of *Eumetabolodon* coincides with that of *Sphenodon*, which has a much narrower head (text-fig. 4). From the early to the late Triassic the procolophonid skull increased more rapidly in width than in height, so that the orbits became gradually more dorsally directed.




TEXT-FIG. 4. Diagrammatic cross-sections of reptilian skulls to show angles of the orbits. A, *Eumetabolodon*. The skull roof is shown by the upper horizontal line, and the arrow is drawn at right angles to the orbit. B, comparison of several reptiles (after Colbert 1946, with *Eumetabolodon* added).

In *Eumetabolodon* the distance between the posterior edge of the orbit and the posterior edge of skull is similar to that in *Procolophon* and *Koiloskiosaurus*. However, in *Eumetabolodon* the pineal foramen has moved anteriorly so that its posterior margin lies a little anterior to the posterior edge of the orbits, whereas it is level with that point in the other two genera.

Though Colbert (1946) suggested that the enlargement of the orbit into an orbito-temporal opening was connected with the shortening of the lower jaw and specialization of the dentition, *Eumetabolodon* has developed a very large orbito-temporal opening but retains a lower jaw of normal length.

The characteristics of its teeth are discussed below.

### *Eumetabolodon dongshengensis* sp. nov.

*Etymology*. Dongsheng is the small town near to where the specimen was collected.

*Diagnosis*. Maxillary teeth closely spaced, with long conical crowns.

*Holotype*. V.6073, a small portion of skull, including right frontal, prefrontal, lacrimal, maxilla with seven teeth, and right ramus of lower jaw.

*Locaity and Horizon*. This specimen is the only one which was not collected by field parties of the IVPP. It was found by Liu Shu ren in 1956 in the Shih-Tien-Feng Formation, which has since been subdivided into the Er-Ma-Ying, He-Shang-Gou, and Liu-Jia-Gou Formations. The locality is Wusilangou, Hantai valley, Dongsheng town, Inner Mongolia, only several dozen kilometres from Zhuengeerqi county, where the other fossils were discovered.

*Description*. The dorsal bones are in poor condition, so it is impossible to describe every element in detail.

The distance from the front edge of the orbit to the back margin of the external narial opening is only 6 mm, indicating that this is a small animal, much smaller than *E. bathycephalus* (V.6064), in which the corresponding distance is 13 mm (text-fig. 5).

There are seven teeth. Six of these are certainly implanted in the maxilla, but the first one is in the area where a thin layer of premaxilla overlies the ventral surface of the maxilla. The base of the tooth is nevertheless implanted in the maxilla, and it is therefore regarded as the first maxillary tooth.

All seven teeth are long and conical. They increase gradually in size from front to back until the sixth; the last one is a small, young tooth. At their bases they almost contact each other, only narrow gaps existing between the fifth, sixth, and seventh.

*Discussion*. Collected from a locality far from those of the remaining specimens of *Eumetabolodon* group 1 (see below for description and discussion), V.6073 has a similar deep skull but shows remarkable differences in its dentition. The cheek teeth are longer than those of other small individuals of *E. bathycephalus*, and are so closely spaced that their bases almost touch. They are also all conical, lacking the cusps and the longitudinal elongation of the base found in some of the cheek teeth of the other specimens. V.6073 may therefore be regarded as the holotype of a new species, *E. dongshengensis*. The distinction might even be generic but, in view of the inadequacy of the material, it seems preferable, at least for the present, to leave V.6073 within the genus *Eumetabolodon*.

## THE DENTITION OF *EUMETABOLODON BATHYCEPHALUS*

The collection includes eighteen incomplete individuals. One specimen (V.6070) was collected in the Er-Ma-Ying Formation at Zhungeerqi, Inner Mongolia. The holotype (V.6064) also was collected at this locality but in the He-Shang-Gou Formation. These two specimens are comparatively well preserved. All the remaining specimens were collected in the He-Shang-Gou Formation, at Gucheng, Shaanxi Province, and are in rather poor condition. Some are seriously damaged, being represented by nothing more than a small piece of jaw-bone with several teeth; some, unfortunately, were broken again during mechanical preparation, for the bone is invariably very soft and embedded in hard red sandstone. The specimens are rather varied in size, tooth shape, and the nature of their occlusal surfaces. It is difficult to compare them in skull structure because of their incompleteness, but they can be divided into four groups, according to their size and to the characters of their maxillary teeth (see also Tables 1 and 2).

GROUP 1. The smallest specimens; the distance between the posterior border of the external naris and the front of the orbit is 7–8 mm. There are three to four premaxillary teeth, six maxillary teeth, and six teeth on the lower jaw. The maxillary teeth have only a single cusp, being conical; some of them are strong and laterally compressed. The teeth are only very slightly worn.

GROUP 2. Medium-sized specimens; the distance between the posterior border of the external naris and the front edge of the orbit is 9–17 mm. There are three to four premaxillary teeth, six to seven maxillary teeth, and eight teeth on the lower jaw. The first maxillary tooth has only a single cusp, but the remainder have an inner and an outer cusp and are transversely broadened. Slight wear has produced shallow occlusal facets.

GROUP 3. Larger specimens; the distance between the posterior border of the external naris and the front edge of the orbit is 20–21 mm. There are three premaxillary teeth and six maxillary teeth; the lower dentition is unknown. All the maxillary teeth are transversely broadened, but wear has removed all the cusps except on the most posterior or replacing teeth.

GROUP 4. A single very large specimen, the distance between the posterior border of the external naris and the front edge of the orbit being 28 mm. There appear to be nine teeth in both upper and lower jaws, but prolonged wear has removed almost all trace of them except for the two most posterior teeth.

The specimens are now described and illustrated (text-figs. 5–30) in order of size.

GROUP 1

*V.6168 (1)*. A broken snout interlocked with the right ramus of its lower jaw, and the separate, seriously damaged left ramus of the lower jaw (text-fig. 6).

All the premaxillary teeth are round in basal cross-section. Pm 1 and left Pm 2 have a horizontal occlusal surface, but right Pm 2 and Pm 3 seem to have oblique occlusal facets on their lingual sides. They may have been cone-like when still unworn. The maxillary teeth, which are stouter and stronger than those on the premaxilla, increase in size backwards along the jaw as far as M5. The shapes of the anterior four teeth are difficult to see, because they are interlocked with the lower jaw. The right M2 appears to have been lost accidentally, for a short portion of it is still ankylosed to the jaw-bone. The left M3 is a conical tooth with a blunt tip. M5 and M6 are of equal length and both are conical; M5, though stouter than M6, is strikingly compressed.

Six dentary teeth are concealed by the upper dentition, in lingual view they are obviously larger than the maxillary teeth. Wide gaps exist between adjacent teeth.

*V.6168 (2)*. A right ramus of lower jaw (text-fig. 7).

There are six teeth. Teeth one to five are the same in height but different in diameter at their bases; the fourth is the stoutest. The first four teeth are compressed and increase gradually in width posteriorly. The fifth, a single-cusped tooth, shows clearly a transversely widened basal portion. The sixth, a small conical tooth is almost in contact with the fifth, whereas obvious gaps exist between the other teeth.

*V.6170*. A damaged snout with the left ramus of the lower jaw (text-fig. 8).

This specimen is unusual in that there are four premaxillary teeth on the left side. There are six maxillary teeth on the right side and five on the left. Six damaged dentary teeth are attached to the lower jaw.

The premaxillary teeth are peg-like. They are different from those of V.6168 in having a pointed tip and an occlusal surface on the lingual side. The maxillary teeth are short; they increase in size along the jaw from the M1 as far as the left M3 and right M4. Most of them have lost their tip, only the posterior three on the left are well preserved. The M3, the largest on the left side, has a longitudinally elongated base and a smooth occlusal surface facing ventro-lingually. The M4 and M5 have complete single tips and are slightly compressed.

The dentary teeth are stouter than the upper teeth. No cusps remain, but their bases exhibit longitudinally elongated cross-sections except the first and the last (text-fig. 9).

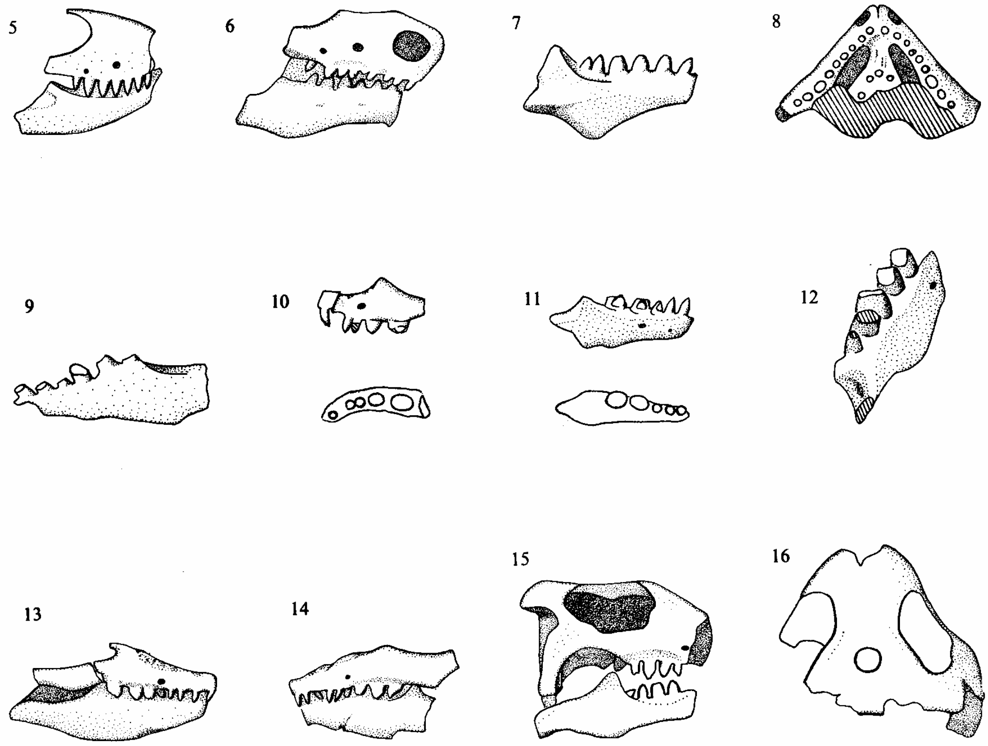
*V.6172*. A piece of the left side of the upper jaw (text-fig. 10) and the right side of the lower jaw (text-fig. 11).

The number of premaxillary teeth is unknown; only one has been left at the posterior end of the left premaxilla. Along the suture with the premaxilla, the maxilla has been pushed downwards a little. Associated with this, a small piece of the maxilla at the antero-ventral corner has been lost, causing a 1·5 mm gap between the last premaxillary tooth and the first maxillary tooth preserved; thus it is possible that the first maxillary tooth proper has been lost accidentally. Behind this gap, four teeth are borne on the maxilla. There are five dentary teeth. The premaxillary tooth, the second maxillary tooth, and the first two dentary teeth are all long, sharp, and peg-like. But the others are short, stout, laterally compressed, and increase in diameter posteriorly. Their crowns are incomplete but the pulp cavities, filled with matrix, show clearly that there was only a single cusp. At the bases of M4 and M5, there are clear sutures between the teeth and the bone; this suggests that the teeth have just erupted and have not yet fused to the jaw-bone.

GROUP 2

*V.6171*. A damaged snout with interlocked lower jaw (text-figs. 13, 14).

There are two premaxillary teeth on the right, three on the left, and six maxillary teeth on each side; the lower



TEXT-FIGS. 5–16. 5, *Eumetabolodon dongshengensis* (sp. nov.), specimen V.6073, right lateral view of snout. 6–16, *E. bathycephalus* (gen. et sp. nov.). 6, specimen V.6168 (1), right, lateral view of snout; 7, specimen V.6168 (2), right lateral view of lower jaw; 8, specimen V.6170, palatal view of snout; 9, specimen V.6170, left lateral view of lower jaw; 10, specimen V.6172, lateral and occlusal views of left upper jaw; 11, specimen V.6172, lateral and occlusal views of right lower jaw; 12, specimen V.6065, postero-ventro-lateral view of left upper jaw; 13, specimen V.6171, right lateral view of snout; 14, specimen V.6171, left lateral view of snout; 15, specimen V.6065, right lateral view of skull; 16, specimen V.6065, dorsal view of skull. Figs. 15 and 16, two-thirds natural size, remainder × 1⅓.

teeth cannot be seen. M1 is long, thin, sharp, and conical. M2 has become transversely widened but longitudinally very narrow; the tip of the tooth on the left has a rounded profile in anterior view. It is difficult to establish the shape of M3 because it lies more medially. M4, M5, and M6 are stout.

*V.6064*. The holotype; see description above (p. 567).

*V.6065*. An incomplete skull and lower jaw (text-figs. 12, 15, 16).

As the anterior end of the skull and the symphyseal region of the lower jaw are missing, the dental formula is unknown. Only four maxillary teeth can be seen on the right side, and five on the left, and there are four dentary teeth on each side.

The maxillary teeth on the right are different from one another. The first tooth preserved, just under the anterior maxillary foramen, is short, transversely broad, and chisel-like. The main occlusal surface of the tooth is inclined steeply postero-ventrally, so that it makes a large angle with the flattened end. The second tooth preserved, also transversely broad, is larger than the first; it has an oblique occlusal surface and a horizontal end facet. The third, the biggest, is twice as high as the first; it has a wide base, an expanded middle part, and a narrow, contracted end. The fourth preserved is a small, thin bicuspid tooth, with the long axis of its cross-section not parallel to that of the others; this suggests that, before it became a functional tooth, a rotation around the vertical axis would have taken place; which in turn, means that the tooth could not have been ankylosed to the bone at the time of death. The characteristics of the four right maxillary teeth are similar to those of the left side.

On the right lower jaw ramus, the first and second teeth preserved are broken, but it is clear that they were transversely broad. The third preserved is thinner than the second and its cross-section seems to be rounder. A small and obtuse tooth had just erupted at the end of the tooth row; it is transversely widened but has only one rounded cusp.

The last four teeth in the lower jaw are recognizable on the left ramus. The broken cross-section of the first tooth preserved suggests that it was compressed. The second tooth preserved, the largest, has an oblique occlusal surface facing antero-labially; its lingual margin is much higher than the labial. The third of these teeth is damaged; only the basal part remains, showing a longitudinally elongated contour and the pulp cavity. It is possible that this is a new tooth, not yet ankylosed. The last tooth is obviously smaller than its neighbour; it is transversely broad, with its long axis perpendicular to the margin of the jaw-bone. On both jaw rami the last tooth is too immature to show whether or not it would have been bicuspid.

*V.6068*. A small piece of right maxilla, right jugal, quadratojugal, quadrate, squamosal and right ramus of lower jaw (text-fig. 17).

Two teeth, one large, one small, are at the hind end of the upper jaw. The large one is very wide, with a horizontal occlusal surface. The small tooth has not been used, for it clearly shows two cusps.

There should have been seven teeth on the dentary, but the second is missing. They decrease in size from D1 to D3, then increase along the jaw until D6. D1-D4 are broken, D5 and D6 have an oblique occlusal surface facing labio-dorsally.

*V.6069*. A piece of left upper jaw and a piece of left lower jaw (text-fig. 18).

There are five upper teeth and three lower teeth, but the dental formula is unknown. The upper teeth are transversely widened, except the last which is irregular in shape. The first, fourth and fifth of those preserved have lost their crowns. The third, which is the largest, has a narrow end surface running labio-lingually, which separates an oblique anteriorly directed facet from a similar facet directed posteriorly. The second tooth preserved is obviously different from the third, having an almost horizontal end surface, but the postero-lingual part forms a curved depression. The dentary teeth are transversely broad; their lingual margins are higher than the labial, and their occlusal surfaces decline steeply.

*V.6166 (1)*. An incomplete upper jaw and lower jaw of the left side (text-fig. 19).

Four premaxillary teeth and four maxillary teeth can be seen. The original number of teeth in the upper dentition is unknown, for the maxilla is broken posteriorly. There are very wide gaps on either side of M1. The last tooth M4 was large and transversely widened, but is broken too. There are two dentary teeth posterior to M4, which suggests that at least M5 had erupted and occupied the gap between D7 and D8. There are eight teeth in the lower jaw.

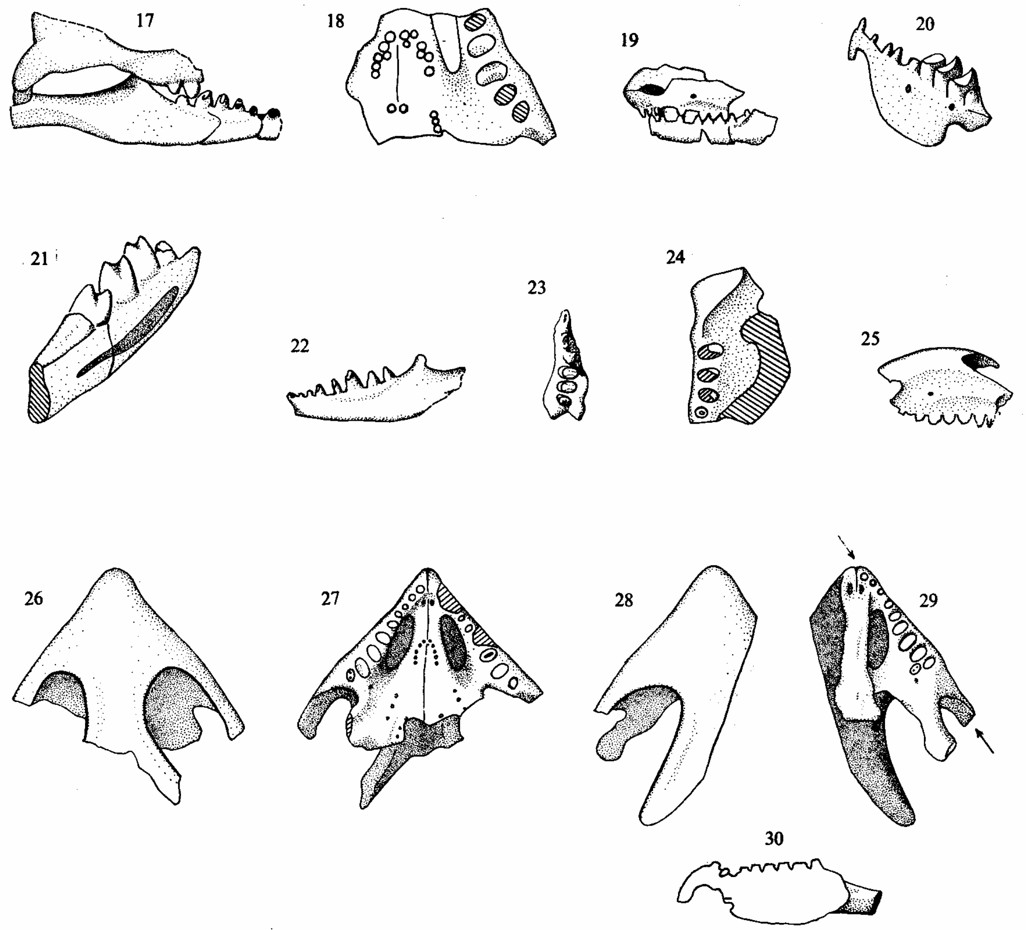
The premaxillary teeth are peg-like, decreasing in size from front to back. All had been used heavily, so obvious wear facets have formed on their lingual sides. A noticeable feature is that Pm1 and Pm2 are almost touching. D1-3 and D8 are conical; M1-4 and D4-7 are transversely widened and bicuspid. An interesting phenomenon is that there are very wide gaps between the teeth on the anterior part of the maxilla and those in the opposing region of the dentary, but neither new tooth buds nor broken tooth bases could be found in those gaps. The number of dentary teeth also proves that no teeth have been lost from the lower jaw. A possible explanation is that the gaps were formed by the growth of the jaw-bone and would be filled by the larger new teeth of the next generation, due to replace the older teeth.

*V.6166 (2)*. The anterior part of a skull and a small section of the left lower jaw ramus (text-fig. 20).

On the right side there are three premaxillary teeth and six maxillary teeth. The number of dentary teeth is unknown. The teeth are strong and broad. Most of the premaxillary teeth are damaged, but the first is well preserved. They are widened in the direction of the tooth row. The lingual parts have been worn away and left a steep occlusal surface, so that the teeth are chisel-like. The maxillary teeth (except M1) are bicuspid, high, and very wide. M4 and M5 on the right show a very clear occlusal surface; on M4 this is curved and faces postero-ventrally, on M5 a transverse ridge separates the tooth crown into two parts, an anterior curved surface and a posterior surface. The last tooth on the right maxilla is small, round in the cross-section and has a blunt tip.

*V.6169*. A small piece of right lower jaw ramus (text-fig. 21).

The last four dentary teeth are present, increasing in size posteriorly as far as the penultimate. The anterior




TEXT-FIGS. 17–30. *Eumetabolodon bathycephalus* (gen. et sp. nov). 17, specimen V.6068, left lateral view; 18, specimen V.6069, palatal view; 19, specimen V.6166 (1), left lateral view of snout; 20, specimen V.6166 (2), postero-ventro-lateral view of right upper jaw; 21, specimen V.6169, postero-dorso-lateral view of lower jaw; 22, specimen V.6167, left lateral view of lower jaw; 23, specimen V.6173, palatal view of right upper jaw; 24, specimen V.6174, palatal view of right upper jaw; 25, specimen V.6175, lateral view of left upper jaw, 26, 27, specimen V.6066, snout in dorsal and palatal view; 28, 29, specimen V.6067 incomplete snout in dorsal and palatal view; 30, specimen V.6067, section through snout in plane of arrows shown in fig. 29. Figs. 18, 20, 21, and 24 $\times 1\frac{1}{3}$, remainder $\times \frac{2}{3}$.

tooth has lost its tip; its width and length are equal on the cross-section of the basal portion. The second to fourth are bicuspid, with a sharp ridge connecting the two cusps; on both sides of the ridge there are deep and narrow concave facets, so that no occlusal surface could be seen.

*V.6167*. A left lower jaw ramus (text-fig. 22).

The first eight teeth are present, decreasing in size from D1 to D3, then increasing to D6 and decreasing again to D8 D1–D3 are conical, the others are transversely broad and bicuspid, but their length and width seems to be equal at the basal cross-section. The occlusal surfaces of D5 and D6 are at their tips; they are labially oblique, so that the lingual margins of the teeth are higher than the labial.

*V.6173.* A piece of right upper jaw (text-fig. 23).

The last four teeth are preserved, of which the second is the largest. They decrease in size anteriorly and posteriorly, and are transversely broad, but only the last is clearly bicuspid. On the second and third teeth the occlusal surfaces are basically horizontal, but small, shallow oblique facets exist on the front of the second tooth and the back of the third.

*V.6174.* A piece of right upper jaw (text-fig. 24).

The last four teeth are preserved; they increase in size from the first to the third but the fourth is the smallest. The anterior three are transversely broad, but unfortunately, their occlusal surfaces are damaged. The last tooth is rounded in its basal cross-section, but it has a blunt and slightly widened tip.

*V.6175.* An incomplete snout (text-fig. 25).

One premaxillary tooth and seven maxillary teeth are preserved on the left side. The premaxillary tooth is small and rounded in basal cross-section. The maxillary teeth increase in size from the M1 to M5, then decrease to M7. They are transversely broad and bicuspid; the distance between the two cusps depends upon tooth size (i.e. the wider the tooth, the longer the distance). Most of the teeth are damaged, but the curved occlusal surfaces facing postero-ventrally appear on the posterior side of the teeth from M4 to M7.

GROUP 3

*V.6066.* A damaged anterior part of a skull (text-figs. 26, 27).

There are three premaxillary teeth and six maxillary teeth on the right side. The premaxillary teeth are round in cross-section and decrease in size from front to back. The maxillary teeth increase in size from the first to the fifth; they have horizontal, flattened occlusal surfaces. The sixth, a small new tooth which had not yet ankylosed to the jaw-bone, clearly shows two cusps.

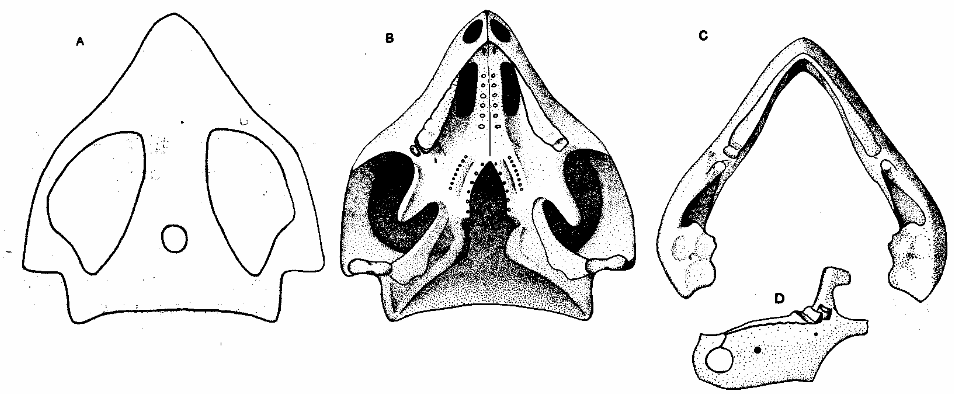
*V.6067.* A damaged anterior part of a skull (text-figs. 28–30).

This specimen is very similar to V.6066 in nearly every respect. However, the sixth maxillary tooth has been used and lost the tips of its cusps. Further, a new tooth has erupted from the inner side of the dentition between the fifth and sixth maxillary teeth; it is transversely broad and bicuspid, with a crown approximately the same height as the others. Finally, the third premaxillary tooth is very small, with only a short crown; a cross-sectional view shows that it inserts obliquely into the premaxilla.

GROUP 4

*V.6070.* An incomplete skull and lower jaw; some dorsal bones are missing, but traces of them show clearly the structure in dorsal view. The brain-case is missing (text-fig. 31).

All the teeth have been worn away on the premaxilla and the anterior part of the maxilla; no trace remains, so that it is impossible to count their exact number. Behind a point just under the anterior maxillary foramen, the




TEXT-FIG. 31. *Eumetabolodon bathycephalus* (gen. et sp. nov.), specimen V.6070, × ½. A, dorsal outline of skull; B, ventral view of skull; C, dorsal view of lower jaw; D, antero-ventro-lateral view of right upper jaw.

maxilla suddenly becomes wider; the teeth in this region have also been worn away except for the last two on both sides, but the number of the teeth can be counted because traces can be seen. On the right side there were evidently seven teeth. The last tooth but one is the widest. The last one is small, bicuspid, and lies parallel to the others. The condition in the lower jaw is the same as in the upper jaw; only two teeth remain at the posterior end. The ventral part of the left maxilla forms a longitudinal curved surface. It is depressed in the middle, but a little raised on the lingual and labial sides. On the right side of the upper jaw the lingual ridge has been lost so that the wearing surfaces occur ventro-lingually. The wear facets on both sides are remarkably asymmetrical. These toothless margins of the jaws were doubtless used to crush the animal's food (text-fig. 26).

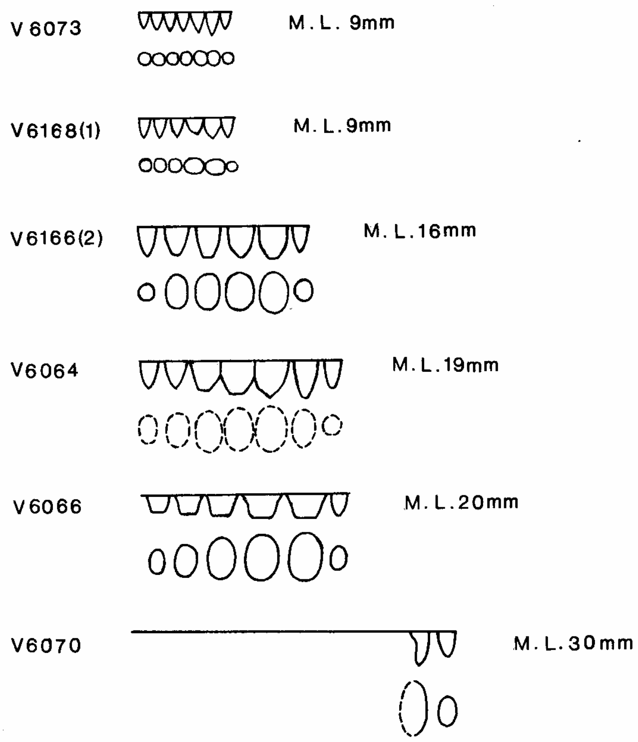
*Discussion. One species or two?* It is clear from the above description that the specimens of the second, third, and fourth groups share certain similarities. They have transversely widened cheek teeth and a similar dental formula, the number of teeth being two to four in the premaxilla, six to seven in the maxilla (except V.6070, see below), and seven to eight in the dentary (see Table 1). The differences between them in skull size and the degree of tooth wear are also evident, and are probably due to differences in ages.

TABLE 1. Dimensions of the dentitions, and tooth formulae (all lengths in millimetres)

| Specimen number | Distance between anterior margin of orbit and posterior margin of external naris | Length of premaxillary tooth row | Length of maxillary tooth row | Length of dentary tooth row | Average length of one maxillary tooth | Average length of each dentary tooth | Maximum height of maxillary tooth crown | Tooth formula | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Pmx. | Mx. | Dent. |
| V.6168 (1) | 8 | 4 | 9 | 10 | 1·5 | 1·7 | 2 | 3 | 6 | 6 |
| V.6168 (2) | — | — | — | 12 | — | 2·0 | — | — | — | 6 |
| V.6170 | 8 | 3 | 9 | 13 | 1·5 | 2·1 | 1·7 | 3 (4) | 6 (5) | 6 |
| V.6172 | — | — | 8 | 9 | 1·6 | 1·8 | 2·0 | — | 5 | 5 |
| V.6171 | — | 4 | 10 | — | 1·6 | — | 1·7 | 2 (3) | 6 | — |
| V.6064 l. | 13 | 5 | 14 | 20 | 2·3 | 2·5 | 3·0 | 2 | 6 | 8 |
| V.6064 r. | 13 | 5 | 19 | 20 | 2·7 | 2·5 | 3·0 | 3 | 7 | 8 |
| V.6065 | 13 | — | — | — | 2·8 | 2·7 | 3·5 | — | — | — |
| V.6068 | — | — | — | 24 | — | 3·4 | 3 | — | — | 7 |
| V.6069 | — | — | — | — | 2·6 | 3·0 | 2·5 | — | — | — |
| V.6166 (1) | 14 | — | — | 22 | 3·0 | 2·8 | 2·5 | 4 | 5? | 8 |
| V.6166 (2) | 15 | 8 | 16 | — | 2·7 | — | 3·5 | 3 | 6 | — |
| V.6167 | — | — | — | — | — | 2·9 | — | — | — | — |
| V.6169 | — | — | — | 24 | — | 3·0 | — | — | — | 8 |
| V.6173 | 14 | — | — | — | 3·0 | — | 2·5 | — | — | — |
| V.6174 | — | — | — | — | 2·2 | — | 2·0 | — | — | — |
| V.6175 | — | — | 20 | — | 2·9 | — | 2·5 | — | 7 | — |
| V.6066 | 20 | 7 | 20 | — | 3·3 | — | 1·8 | 3 | 6 | — |
| V.6067 | 21 | 8 | 19 | — | 3·2 | — | 1·5 | 3 | 6 (7) | — |
| V.6070 | 28 | 8 | 30 | 32 | — | — | — | — | ≥9 | — |

The members of the first group, however, are small animals with fewer teeth. Their important characteristic is that their cheek teeth have but a single cusp. Some of the teeth are typically cone-shaped, some are expanded at the base, but no bicuspid teeth can be seen. For this interesting difference between the large and the small animals there are two possible explanations. The first is that they belong to different species, the smaller species with simple cheek teeth and the larger with bicuspid teeth. A similar phenomenon has been reported from South Africa; *Spondylolestes* (Broom 1937) is small with conical teeth and *Procolophon* is bigger with bicuspid teeth. The other explanation is that they all belong to the same species, which in early life had simple conical teeth, adapted to an insectivorous diet, but which later became herbivorous with transversely widened, bicuspid teeth. A similar ontogenetic change occurs in the living lizard *Varanus niloticus* (Edmund 1969).

The second interpretation seems preferable, for the following reasons. All twenty fossils (except V.6073 described here as *E. dongshengensis*) were discovered in one small area. There are fifteen individuals with transversely broad teeth, their sizes ranging from medium to very large; the smallest of specimens with transversely broad, bicuspid teeth, V.6171, is slightly larger than the members of the first group. It would be very surprising if this group included none of the juveniles of one species but, by chance, several specimens of a second, smaller species. The second reason for viewing all of these specimens as members of one species is that tooth replacement could be clearly observed occasionally. For example, on the left maxilla of V.6067 a new bicuspid tooth has erupted which will




TEXT-FIG. 32. Diagrammatic representation of maxillary tooth rows of six specimens of *Eumetabolodon bathycephalus* in lateral and occlusal view. M.L., length of maxillary tooth row.

apparently replace an earlier, transversely broad tooth. The teeth of procolophonids, being either acrodont or protothecodont, fuse on to the dentigerous bone. Our fossils show clearly that the width of each tooth is almost equal to that of the jaw-bone at any developing stage. As the skull increased in size, the jaw-bone became stronger and the teeth became wider, especially behind the level of the anterior maxillary foramen on the upper jaw and the corresponding position on the lower jaw. It is reasonable to suggest that, in order to adopt a different habit of life and obtain enough food, a conical cheek tooth would be replaced by a transversely widened one as the animal grew.

It is worthy of note that there is an argument against this suggestion. For, lacking direct evidence of a conical tooth being replaced by a bicuspid tooth, V.6171 can be treated as the only juvenile of *E. bathycephalus* instead of as a representative of an intermediate type. In that case, the specimens in the first group (V.6168, V.6170, V.6172) would belong to another species, which remained small throughout life, bore single-cusped teeth, and shared the same habitat with *E. bathycephalus*. In order to resolve this problem, further fossil collection should be carried out. Meanwhile, however, all these specimens are provisionally referred to the species *E. bathycephalus*.

*The process of replacement of an individual tooth.* The evidence of tooth replacement in procolophonids was given by Ivachnenko (1974). Gow (1977) studied *Procolophon trigoniceps* and suggested a model of molar succession. It is clear that a replacing tooth germ developed initially from the dental lamina posterior and lingual to the tooth being replaced. The new tooth erupted from the jaw-bone and grew bigger and bigger until reaching the height of its predecessor. At this stage no pit or groove could be detected from the surface of the bone, as shown in *Ericiolacerta* (Crompton 1962). The actual replacement of an old tooth by a new one has never been seen, which suggests that the process of tooth replacement must have taken place very quickly. It is unlikely that an old tooth was shed, and that a new one then took its place. The present study does not confirm Gow's suggestion that teeth were lost at the front of the maxilla and dentary and that new ones were added at the rear of the tooth row.

*The sequence of tooth replacement.* The tooth shape of all of the specimens is shown diagrammatically in Table 2. Because of the incompleteness of the fossils, it is difficult to determine the exact sequence of their replacement, but the replacement tendency reflected by different groups seems to be more reliable.

In discussing *Contritosaurus simus* Ivachnenko (1974) stated: 'In connection with the appreciable differentiation of the teeth, replacement is occasionally observed only on the front teeth of the maxillary and the dentary. Replacement is hardly ever observed in the rear "quasicheek" teeth.' But the situation seems to be more complicated in another specimen. For example, it can be seen in *Phaanthosaurus ignatjevi* (Ivachnenko, 1974, fig. 1) that a new tooth has erupted behind and labial to the eighth dentary tooth (itself not preserved). Our fossils provide further evidence of tooth replacement, and suggest that it occurs not only in the front of the maxilla and dentary, but also at the rear of the maxillary tooth row (as in V.6067).

From Table 2 it can be seen that, at an early stage, the conical teeth on the maxilla and dentary appear to be replaced by another generation of single-cusped teeth, which are stronger and have a longitudinal elongated basal portion. This took place first in the maxillary teeth 3–5 and their counterparts in the dentary.

When the animals reached medium size, most of the cheek teeth had been replaced by transversely broad bicuspid teeth. This change seems to start in the second maxillary tooth. The first is often damaged but in a few instances is still preserved as a small conical tooth; at a later stage it would be replaced by a small widened tooth. Table 2 also shows that the biggest cheek teeth often appear at the fifth and sixth maxillary tooth positions, anterior to a small tooth. In some cases the fourth maxillary tooth is the biggest tooth on the upper jaw, there being two smaller teeth behind it.

At present there is not enough information about the exact sequence and rate of tooth replacement. Reptiles grow throughout life; but V.6070, a very old animal, which had worn away the teeth on most of its jaw, demonstrates that tooth replacement appears to cease after a certain growth stage is reached. No further teeth were produced and the animal probably crushed its food with the margin of its jaw-bone.

A characteristic of V.6070 worthy of mention is its large number of maxillary teeth. That might have been produced by adding new teeth to the back end of the jaws: the older the animal, the higher the tooth count. Another possibility is that the dental formula evolved a little with time; V.6070 is the only good specimen obtained from the bottom of the Er-Ma-Ying Formation which, though also lower Triassic in age, lies several dozen metres above the layer of the He-Shang-Gou Formation in which the other *Eumetabolodon* were found.

*Tooth wear.* The fossils clearly show regular correlation between the height of the teeth, the direction of the occlusal surfaces, and the age of the animals. When the animals were young, the crowns of the teeth were short, and generally the occlusal surfaces were not evident. When the animals reached medium size, their teeth attained maximum height (see Table 1 and text-fig. 32), but the occlusal surfaces seem to be irregular. In some cases, curved occluding facets appear on the posterior side of the upper teeth and the anterior side of the lower teeth (as in V.6065, V.6175). In other cases, occlusal facets lie obliquely at the end of the teeth. They face ventro-lingually on the upper teeth and dorso-labially on the lower teeth. At this stage the formation of occluding surfaces depends

TABLE 2

| | Left ramus of upper jaw | | | | | | | | | | | | | Right ramus of upper jaw | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mx | | | | | | | | | Pmx | | | | Pmx | | | | Mx | | | | | | | | |
| | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 4 | 3 | 2 | 1 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| V.6073 | | | | | | | | | | | | | | | | | | ▲ | ▲ | ▲ | ▲ | ▲ | ▲ | ▲\| | | |
| V.6168 (1) | | | | | | | ▲ | △ | ▲ | | \|▲ | ▲ | ▲ | ▲ | ▲ | ▲\| | | ▲ | △ | ● | ● | ● | ▲\| | | | |
| V.6170 | | | | | \|▲ | ▲ | ● | △ | △ | \|▲ | ▲ | ▲ | ▲ | ▲ | ▲ | △\| | | △ | △ | △ | ● | ▲ | ▲\| | | | |
| V.6172 | | | | | \|● | ● | ▲ | ▲ | | | \|▲ | | | | | | | | | | | | | | | |
| V.6171 | | | | \|■ | ■ | ■ | ■ | ■ | ▲ | | \|▲ | ▲ | ▲ | ▲ | ▲\| | | | ▲ | ■ | ■ | ■ | ■ | ■\| | | | |
| V.6064 | | | | \|■ | ■ | ■ | ■ | □ | □ | | | \|▲ | ▲ | ▲ | ▲ | ▲\| | | □ | □ | ■ | ■ | ■ | ■ | ◆\| | | |
| V.6065 | | | | \|◆ | □ | ■ | ■ | ■ | | | | | | | | | | | | ■ | ■ | ■ | ■\| | | | |
| V.6069 | | | | \|□ | □ | ■ | ■ | □ | | | | | | | | | | | | | | | | | | |
| V.6166 (1) | | | | | | □ | ■ | ■ | □ | \|▲ | ▲ | ▲ | ▲ | | | | | | | | | | | | | |
| V.6166 (2) | | | | | □ | □ | ■ | ■ | ▲ | | \|▲ | ▲ | ▲ | ▲ | ▲ | ▲\| | | △ | □ | ■ | ■ | ■ | ◆\| | | | |
| V.6174 | | | | | | | | | | | | | | | | | | | | □ | □ | □ | ◆\| | | | |
| V.6173 | | | | | | | | | | | | | | | | | | | □ | ■ | ■ | ■ | ■\| | | | |
| V.6175 | | | \|■ | ■ | ■ | ■ | ■ | ■ | □ | | \|▲ | | | | | | | | | | | | | | | |
| V.6068 | | | | | | | | | | | | | | | | | | | | | | ■ | ■\| | | | |
| V.6066 | | | | \|□ | □ | □ | | | | | | | | ▲ | ▲ | ▲\| | | ? | ■ | ■ | ■ | ■ | ■\| | | | |
| V.6067 | | | | \|■ | ▟ | ■ | ■ | ■ | ■ | | \|▲ | ▲ | ▲ | | | | | | | | | | | | | |
| V.6070 | \|■ | ■ | | | | | | | | | | | | | | | | | | | | | | | ■ | ■\| |

| | Left ramus of lower jaw | | | | | | | | | | | | | Right ramus of lower jaw | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | | | |
| V.6168 (1) | | | | | | | | | | | | | | ▲ | ▲ | ▲ | ● | ● | ●\| | | | | | | |
| V.6168 (2) | | | | | | | | | | | | | | ▲ | ▲ | ● | ● | ● | ▲\| | | | | | | |
| V.6170 | | | | | | | | \|△ | △ | ● | ● | ● | △ | | | | | | | | | | | | | |
| V.6172 | | | | | | | | | | | | | | ▲ | ▲ | ● | ● | ●\| | | | | | | | |
| V.6064 | | | | | | \|◆ | ■ | ■ | ■ | ■ | ▲ | ▲ | ▲ | ▲ | ▲ | ▲ | ■ | ■ | ■ | ■ | ▲\| | | | | |
| V.6065 | | | | | | | \|◆ | □ | ■ | □ | | | | | | | ■ | □ | ■ | ◆\| | | | | | |
| V.6068 | | | | | | | | | | | | | | △ | △ | △ | □ | ■ | ■ | ■\| | | | | | |
| V.6069 | | | | | | | \|□ | □ | □ | | | | | | | | | | | | | | | | | |
| V.6166 (1) | | | | | | \|△ | ■ | ■ | ■ | ■ | ▲ | ▲ | ▲ | | | | | | | | | | | | | |
| V.6167 | | | | | | \|■ | ■ | ■ | ■ | ■ | △ | △ | △ | | | | | | | | | | | | | |
| V.6169 | | | | | | | | | | | | | | | | | □ | ■ | ■ | ■\| | | | | | |
| V.6070 | | | | | \|■ | ■ | | | | | | | | | | | | | | | | | | | | |

▲ Conical tooth.

● Enlarged and longitudinally extended tooth.

■ Transversely broad tooth.

◆ Small blunt tooth.

△ ○ □ Broken teeth.

▲ ● ■ The biggest teeth.

▟ Replacing teeth.

| The end of premaxillary, maxillary, or dentary tooth row.

on the relationship of adjacent upper and lower teeth. At the beginning, because they had two cusps and a very narrow crest, the teeth could not make stable contact with each other at their tips. The posterior surface of the distal part of the upper teeth often contacted the anterior surface of the distal part of the lower teeth. As mentioned above, the two rami of the lower jaw were only loosely connected at the symphysis; this makes complex movement of the lower jaw possible and could thus result in a variety of shapes and directions of the occluding surfaces.

In large animals, represented by V.6066 and V.6067, the teeth have lost their tips and have flattened occlusal surfaces. This suggests that the animals needed a great deal of food and used their teeth heavily. At this stage tooth replacement continued; but, as any new tooth would have been worn down on reaching the height of the old ones, it could not be recognized after migrating into its position.

The last stage of tooth wear is clearly shown in V.6070. The wear surfaces are on the jaw-bone, and only two teeth remain at the posterior end of the row. This phenomenon appears also in some living reptiles. In *Uromastyx* (as described by Robinson 1976) the anterior sectors of maxillae and dentaries are so heavily worn that the teeth have been abraded away entirely and the bony jaw margins are used in feeding. In V.6070 a special point worthy of notice (see above description) is that the occlusal surfaces are asymmetrical (text-fig. 27).

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LI JIN LING

Institute of
Vertebrate Palaeontology and Palaeoanthropology
P.O. Box 643
Beijing, China

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