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CONTRIBUIÇÃO PARA O CONHECIMENTO DA FAUNA DO KIMERIDGIANO DA MINA DE LIGNITO GUIMAROTA (LEIRIA, PORTUGAL)

IV PARTE

HALDANODON EXSPECTATUS KÜHNE & KRUSAT 1972
(Mammalia, Docodonta)

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1. PREFACE

Of the three mammalian groups found during paleontological excavations in the Upper Jurassic coal of the Guimarota mine (Leiria/Middle Portugal) so far only the multituberculates have been described comprehensively and in detail (HAHN 1969, 1971). KREBS (1969, 1971) had commented on a few of the problems pertaining to the Pantotheres. The docodonts were given to me for study in the spring of 1971. The results of my studies have already been printed as a doctoral thesis at the end of 1973 and are here published in English translation with additional plates. The text was translated mainly by Mr. J. Fairbank. The remains of the skull skeleton and the dentition of the species Haldanodon expectatus KÜHNE & KRUSAT 1972 (Order Docodonta) are described and figured. Haldanodon is compared to related forms and integrated into the mammalian phylogeny. From the morphology an attempt is made to aquire data about the ontogeny and living habits of the animal.

2. INTRODUCTION

The fossil-deposit in the Guimarota coalmine was discovered by W. G. Kühne and W. Frey in 1959. Systematic excavations followed between 1960 and 1962 under the directions of W. G. Kühne and later S. Henkel. The recovery of larger fossil remains was accomplished by manually splitting coal lumps, while isolated teeth and small fragments of bone were obtained by washing and screening slack. HENKEL (1966) and KÜHNE (1968) have given full accounts of the history of these excavations and the methods used, so that further remarks are not necessary here.

The geological age of fossil-bearing strata in the Guimarota mine has been determined by HELMDACH (1968), by use of ostracods and charophyta gyrogonites as Lower Kimmeridgian. The strata belong to the so-called Lusitanien, a succession of mainly nonmarine sediments of the Middle and Upper Jurassic common in Portugal. Publications of HELMDACH (1966, 1968) and SEIFFERT (1970) contain geological-stratigraphical descriptions of the Lusitanien in the vicinity of the Guimarota coalmine together with maps and profiles.

The material described in this paper consists of the fossil remains of a mammalian species belonging to the order Docodonta. The docodonts had first obtained their systematic position as an order in 1946 by KRETZOI. Before that they had generally been considered as an aberrand family of the order Pantotheria (SIMPSON 1925; 1929). Nevertheless KRETZOI's arguments for the separate position of the docodonts have proven wrong (SIMPSON 1961). Thus priority belongs to him after the rules of nomenclature, however, the present generally accepted diagnosis and definition of the new order came from PATTERSON (1956).

There are still disagreements between authorities about the systematic subdivision of the order. Consensus is found in the acknowledgement of the family Docodontidae SIMPSON 1929, which includes the four presently known genera of the Middle and Upper Jurassic. Abundant fossil remains of the first genus were found at the end of the last century during the well-known excavations for dinosaurs in the late-jurassic Morrison-formation of Wyoming and Colorado (USA). MARSH (1880; 1881; 1887) described them as three genera (*Diplocynodon*, *Docodon* and *Enneodon*).

Because the first and the third of these names were preoccupied, MARSH (1888; 1890) changed them to *Dicrocynodon* and *Ennacodon*. SIMPSON (1929) in his monograph about the mesozoic mammals of North America established the three genera as being synonymous. He united them under the eldest valid genus *Docodon* basing the four species *Docodon striatus* MARSH 1881, *Docodon victor* (MARSH 1880), *Docodon affinis* (MARSH 1887) and *Docodon crassus* (MARSH 1887) on lower jaws and *Docodon superus* SIMPSON 1929 on upper jaw dentitions (Fig. 1 B). SIMPSON (1929) himself expressed the opinion that there was a certain possibility of these «species» being morphological variations of the same species. JENKINS (1969) later confirmed this assumption. Although a revision of the genus *Docodon* has not occurred yet, I have generally disregarded the separate species names.

SIMPSON (1928 a) in his extensive catalogue of British Mesozoic mammals described a lower jaw fragment of a docodont, which he named *Peraiocynodon inexpectatus* (Fig. 1 C). *Peraiocynodon* comes from the Purbeckian of Southern England and is about the same age as *Docodon*.

The third genus to be noted here is *Borealestes serendipitus* WALDMAN & SAVAGE 1972 taken from the Middle Bathonien on the Isle of

Skye (Scotland) (Fig. 1 A). The hypodigma consists of two uncompletely conserved mandibulae.

Finally the fourth genus, *Haldanodon exspectatus* KÜHNE & KRUSAT 1972 is the theme of this thesis. KÜHNE (1968) named and illustrated

Haldanodon for the first time in a short report about the discoveries of Mesozoic mammals in Portugal. As KÜHNE had neglected to appoint a species to the genus-name *Haldanodon*, legalisation after the rules of nomenclature was necessary. At this
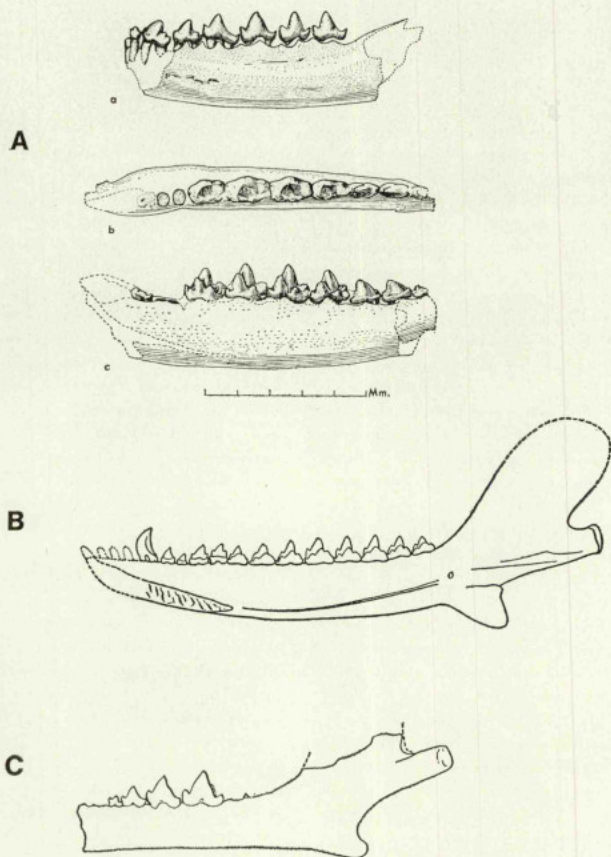

FIG. 1 — A: *Borealestes serendipitus*, left mandibula (from WALDMANN & SAVAGE 1972). a: Lateral view. b: Dorsal view. c: Medial view.
B: *Docodon sp.*, right mandibula (from SIMPSON 1929). Medial view, without scale.
C: *Peraiocynodon inexpectatus*, left mandibula (from SIMPSON 1928 a). Lateral view, without scale.

time the material was not yet completely prepared and examined. Thus in formulating the diagnosis and additional remarks, some mistakes and inaccuracies resulted which shall be resolved here.

The report, that at least two more taxa other than *Haldanodon* can be deduced from the docodont-material of Guimarota-coal, is erroneous. Contrarily it will be shown that *Haldanodon exspectatus* is dimorphous and to be divided in two morphologically differing forms. The buccal cingulum of the lower premolars is not present in all individuals. A further (fifth) incisive tooth has been identified in the upper dentitions.

For the present this work accepts the opinion expressed by HOPSON (1970) that the docodonts are to be united in a subclass Prototheria GILL 1872 together with the triconodonts, multituberculates and monotremes, whereas all other known fossil and recent mammals have to be included in the subclass Theria. Of the Prototheria the orders Triconodonta and Docodonta are put in an infraclass Eotheria (KERMACK & MUSSETT 1958, HOPSON 1970). Here the classification of the family Morganucodontidae KÜHNE 1958 is debatable. It has been assigned by some authors (especially PARRINGTON 1967 and 1971, CROMPTON & JENKINS 1968, HOPSON & CROMPTON 1969) to the Triconodonta being based particularily on dental anatomy, while among others PATTERSON (1956), KERMACK & MUSSETT (1958) and KERMACK (1967) emphazise the close relationship to the Docodonta.

The derivation of the family Docodontidae from members of the family Morganucodontidae can now be considered as a certainty (CROMPTON & JENKINS 1968). The latter constitute, after the multituberculates, probably the best known group of Mesozoic mammals and have been found up to now in the Upper Triassic of Europe, East Asia and Southern Africa. The relationships of the Morganucodontidae are discussed in detail by CROMPTON & JENKINS (1968), HOPSON & CROMPTON (1969) and MILLS (1971).

The present paper also investigates the relationships between the Docodontidae and the Morganucodontidae. Thus, a comment is appropriate to the priority dispute of *Morganucodon* versus *Eozostrodon*.

In 1941 PARRINGTON gave the names *Eozostrodon parvus* and *Eozostrodon problematicus* to two isolated teeth from rhaetic fissure-fillings in Somerset (England), which he had bought from W. G. Kühne, who was interned at this time in England. The importance of the two teeth at this time was that they were the first remains of Triassic mammals, which could be proven as such. A short time later similar teeth were found, in greater numbers, by B. Peyer in the rhaetic of Schaffhausen (Switzerland). After the war, Kühne was able to continue his diggings in England. He discovered in Glamorgan (Wales) another site containing isolated parts of vertebrate fossils, among them a nearly completely preserved molar tooth of a mammal, which he published in 1949 under the name of *Morganucodon watsoni*. In the following twenty years, many other finds of *Morganucodon* and related forms were reported (KÜHNE 1958, PEYER 1956, CROMPTON 1964, PATTERSON & OLSON 1961, CROMPTON & JENKINS 1968, KERMACK & MUSSETT 1958 and others). In 1967 PARRINGTON went back to the half forgotten genus *Eozostrodon*, trying to prove it a synonym to *Morganucodon* and thus holding priority over the younger genus. He held this point of view also in the following years (PARRINGTON 1971). PARRINGTON was supported, in this respect, especially by CROMPTON & JENKINS (1968), while KERMACK & KERMACK & MUSSETT (1968) and MILLS (1971) emphasized that the two types of the genus *Eozostrodon* don't allow a definite systematic assignment because of their position in the tooth row and their poor degree of preservation. The holotype of *Eozostrodon parvus* is probably an upper premolar and as such not very informative, whereas *Eozostrodon problematicus* is a broken molariform tooth with a large portion missing.

The arguments PARRINGTON (1971) uses to defend his claim of priority are, from my standpoint, unsatisfactory. Nevertheless, this superfluous nomenclatory quarrel will probably go on undecided. For my part, I prefer the better established genus *Morganucodon*. Under this designation are understood teeth, jaws, and skull parts as described by KÜHNE (1958), KERMACK & MUSSETT (1958), PARRINGTON (1971) and MILLS

(1971), but not necessarily the two types of the genus *Eozostrodon* sensu PARRINGTON (1941).

Progress in Mesozoic mammal study is also documented by the fact that the quality of recent finds reflect better collecting methods. Today it it is no longer necessary to fall back on isolated and damaged teeth to provide a genus or species diagnosis. This in turn reduces the number of errors and inexactitudes.

One will also have to get used to the idea of giving Mesozoic mammal teeth a lesser importance in determining phylogenetic connections than in the past. Rather, greater importance will be given to comparative anatomy, especially of the cranial skeleton. As tools for processing food, teeth seem to adapt quickly to ecological changes. So for example, parallel developments can appear between animal groups favouring the same food.

3. BIOSTRATONOMY

The sedimentology and facies of the Guimarota deposit have already been studied in detail by HELMDACH (1966). According to him, deposition occured in a coastal brackish lagoon which was occasionally exposed to small marine transgressions. Low relief energy between the lagoon and the surrounding mainland resulted in the complete absence of coarse clastic rock components. The sediment consists of two «seams» of very impure coal divided by an approximately 10 m thick intermedium of limestone and marl. The findings discussed here were taken from the lower seam, the so-called «Fundflöz». The coal is heavily mixed with marl and bitumenous clay, and can be considered, in its degree of coalification, as gas coal. Root horizons do not occur in the coal. On the other hand, there is a great deal of probable driftwood on hand, whereby also pieces of larger logs can be found. Also in large numbers fruit cuticulae and charophyte gyrogonites have been found. The plants have not yet been identified, however, it can be assumed that among them are the typical Upper Jurassic ferns, cycadeas, bennettideas, nilssonias, conifers and gingko types.

An extensive fauna-list was published by KÜHNE (1968 a). Other than mammals it contained in each case several genera of selachians, holosteans, urodeles, anurans, pterosaurs, turtles, ornithischians, saurischians, crocodiles and lizards. Other than these many ostracodes, mussels, snails and foraminifers along with the more rare remains of echinoids and cirripeds were registred.

It can be assumed, because of the very heterogeneous makeup of this hypodigma, that the area of sedimentation of the Guimarota coal was for part of the fauna, to which the mammals belong, not their actual environment. The large number of discarded crocodile teeth and coproliths show, on the other hand, that it was not a pure taphocoenosis. Other indicators of this sort are doublevalved pelycopod shells that have not been drifted, ostracodes in successive ontogenetic development stages (HELMDACH 1968) and juvenile snails next to the adult animals.

Thus the water body of the deposition area was inhabited by aquatic and semiaquatic animals such as the mentioned invertebrates, fish, amphibians and crocodiles. A portion of these organisms can be considered strays (for instance the crocodilian *Machimosaurus* after KREBS 1967) or were able to live there only for a relatively short period of marine flooding. Together with the remains of this biocoenosis were also found fossils of life forms that had entered the lagoon post-mortem. These were animals that had lived either in the thickly grown, probably swampy, terrestrial area surrounding the lagoon or had inhabited the air above it. The first group were the various dinosaurs, mammals and lizards, whereas the second group consists of pterosaurs and possibly also prehistoric birds.

Interesting is the condition of the vertebrate fossils. Practically no complete fossil aggregates were found but for the most part only isolated bones, teeth, scales and the like. Even the turtle shells are dismembered. Also, the remains of large animals are almost completely absent. The only such findings were the fragments of a skeleton of *Machimosaurus*, that can be estimated of having a body length of about 9 m (KREBS 1967) and the scales and teeth of two types of fish, which could have reached from 1 to 2 m (KÜHNE 1968 a). Almost all the remains of large reptiles came from small and young animals. In general, the bones are incomplete and show signs of having been damaged before burial. The joint ends of limb bones are often missing.

With the exception of four skull remains, the mammalian material consists of dentition fragments as well as undescribed parts of the post-cranial skeleton. These were also often broken before burial. For the most part, in the docodont mandibules these fractures are behind the canines between the Pars alveolaris and the Ramus mandibulae as well as in the region of the Processus coronoideus. Often deformations are also present, particularly in the mammalian skulls. The cause of this phenomenon was due to the loss of water from the coal-mud during diagenesis resulting in a substantial shrinking of the sediments. This put a mechanical stress particularly on those fossils being partially or entirely hollow.

The question how the damages occured on the vertebrate remains is related to how the terrestrial animals came into the lagoon. Apart from post-mortem drifting in the slightly flowing water, both occurences are to a great extent probably due to the numerous crocodiles. Excepting the marine *Machimosaurus*, these preyed on their own species as well as on other vertebrates or their corpses. As is seen by the size spectrum of the crocodile remains in the Guimarota coal (above all from isolated teeth and skin ossifications) these animals were capable of catching prey of very small to middle size. Fully grown dinosaurs or adult crocodiles were probably seldom victims and are thus relatively rare. The presence of invertebrate scavengers is also assumed, can however not be proven. The snails, that probably made up a portion of these, have not yet been identified. It is very probable that most of the vertebrate fossils contained in Guimarota coal are the food rests of crocodiles; these were discharged in the water as «pellets», thus becoming so scattered throughout the sediment.

A further influence on the condition of the fossils happened after burial and was of a chemical nature. In the deposition of coal sediments, humic acids are set free, which react with calcium carbonate and calcium phosphate, so that only plant fossils remain. The large percentage of lime in Guimarota coal caused, however, that the acids were buffered and thus made ineffective. Occasionally bones and teeth showing signs of corrosion turn up that were deposited in places of lime deficiency.

4. *HALDANODON EXSPECTATUS* KÜHNE & KRUSAT 1972

Class Mammalia.
Order Docodonta (KRETZOI 1946) PATTERSON 1956.
Family Docodontidae SIMPSON 1929.
Haldanodon KÜHNE & KRUSAT 1972.

Derivatio nominis: Derived from Haldane — in honor of the British geneticist J. B. S. Haldane (1892-1964), and odon — Greek for tooth.

Diagnosis: A genus of the family Docodontidae with the dental formula

$$\frac{5\,I:C:3\,P:5\,M}{+\,2\,I:C:3\,P:5\,M}$$

The I^5 is rooted in the maxilla. The interior side of the dentary has a wide trough-like sulcus, which contained ossicles of the reptilian mandibula. Below, reaching as far as the symphysis, is an «internal groove», which combined both the functions of a Sulcus primordialis and a Sulcus mylohyoideus. The depression for the rudimentary coronoid-bone is situated medially behind the tooth row.

Lower premolars can also have a buccal cingulum. The lower molars, looking in the occlusal view like rounded rectangles, have the same cusps as the corresponding teeth of the other Upper Jurassic docodonts but in differing proportions. The upper molars in the occlusal view resemble a distorted figure eight. The lingual half of an upper molar occludes directly with two adjacent lower molars, whereas the buccal half comes to rest next to their buccal side. *Haldanodon*'s tooth-change is diphyodont or nearly so.

Relations: It is difficult to establish the conformities and diversities in morphology with those of the three other genera now known to be in the family Docodontidae. To an extent, the material is inadequately described *(Docodon)*, also due to the nature and state of preservation, many specimens don't allow extensive comparison *(Borealestes* and *Peraiocynodon)*. The most distinct difference to Haldanodon is revealed in the dental formulae. The genus *Docodon* has the dental formula:

$$\frac{?\,I:C:\quad 3\,P:+6?\,M}{+\,3\,I:C:3\text{-}4\,P:\quad 7\text{-}8\,M}$$

(SIMPSON 1929). The dental formula of the lower jaw in *Borealestes* is +3? P : 6 M (WALDMAN & SAVAGE 1972). The type of *Peraiocynodon* is represented only by one known specimen (the mandibula of a young animal with a probable dental formula of +3? P (1 P and 2 Pd): + 2 M and thus is not very descriptive. Comparative teeth of the three genera are constructed in the same manner.

In all probability, ossicles of the primary mandibular joint were present also in the lower jaws of the other Docodontidae.

Occurence: Lower Kimmeridgian of Portugal.

Type species: *Haldanodon exspectatus* KÜHNE & KRUSAT 1972.

Derivatio nominis: exspectatus — latin for expected. A docodont mammal, less advanced than *Docodon* but with similar anatomical features, was to be expected in the Kimmeridgian.

Holotype: The mandibula, illustrated in KÜHNE (1968), Page 115, Fig. 3 (here specimen VJ 1001-155, Fig. 2 and 14).

Locus typicus: «Fundflöz» (= the lower coalseam, which yielded the mammalian remains) in the Guimarota mine near Leiria, Portugal.

Stratum typicum: Lower Kimmeridgian, based on the occurrence of the ostracod *Oertliana kimmeridgensis* KILENY 1965 and the Charophyta gyrogonites *Porochara raskyae* MÄDLER 1952 and *Porochara westerbeckensis* MÄDLER 1952.

Diagnosis: Presently the only known species with the characteristics of the genus. The lower jaws of adult individuals show morphologic variations, which can be partially ascribed to sexual (?) dimorphism.

4.1 Material

The fossil material used in this paper consists of fragments of seven mandibulae, a maxilla, an anterior skull and 43 isolated teeth and teeth fragments. Other teeth fragments were disregarded because of their poor condition. The specimens being used have been provided with continuous catalogue numbers corresponding to an agreement with the Serviços Geológicos de Portugal. They
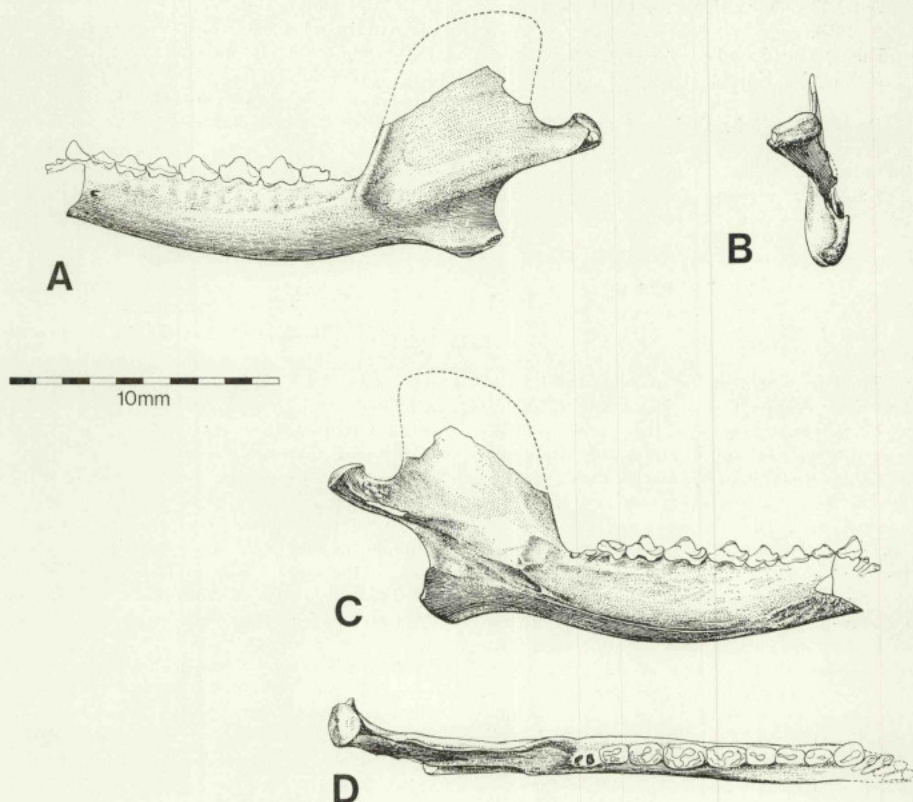

FIG. 2 — Left lower jaw VJ 1001 - 155 (holotype).
A: Lateral view.
B: Caudal view.
C: Medial view.
D: Dorsal view.

will be cataloged and filed in the museum of this institution in Lisbon under the numbers refered to in the text. A short description of the individual cataloged specimens is given, in preparation for the following analysis and interpretation of the anatomy and functional morphology of *Haldanodon*.

A) MANDIBULAE

1) *VJ 1001 - 155* (= *Haldanodon sp.* in KÜHNE 1968, = holotype of *Haldanodon exspectatus* KÜHNE & KRUSAT 1972) (2 fragments). Fig. 2 and 14, Plate II A, B, C.

Left mandibula in very good preservation. Only the most anterior part of the Pars alveolaris and the upper half of the Processus coronoideus are lacking. In the tooth row the most anterior incisors and the last molar are lacking. There is a fracture between the canine and the first premolar. As both fracture surfaces are covered with artificial matrix (*), the original condition of the mandibula can not be really reconstructed. Thus the drawing of the VJ 1001-155 fracture assembly must be regarded as an interpretation.

Fragment 1:

Fragment of the anterior of Pars alv. with two incisors (presumably I_3 and I_4) and the canine. Of the jaw bone only part of the labial alveolar margin is visible. On the lingual side the roots of the incisors are exposed. On both canine roots only the vestiges are visible. The posterior root is broken off.

Fragment 2:

The mandibula and teeth have been fully exposed and are visible from all sides. The post-canine tooth row is complete except for the discarded M_5. Between the P_3 and the M_1 there is rather intense imbrication. In contrast to the premolars, which show here a buccal and lingual cingulum, the molars are relatively worn. There is no recognizable tooth replacement.

(*) During preparation of fragile bones an artificial matrix has often be used for stabilisation. This matrix is a yellow resin powder called Palavit M, which polymerizes after being mixed with a special fluid. It is normally used by dentists for making casts of teeth. (KÜHNE 1968 b).

Dental formula: $+2$ I : C : 3 P : 5 M (M_5 = alveola).

Measurements:

a) *Jaw bone.*

Fragment 1: not measurable

Fragment 2: distance between fracture and condyle = 19,5 mm; distance between Foramen mandibulae and condyle = 8,7 mm; height under M_4 = 2,9 mm; height of condyle = 2,0 mm; width of condyle = 2,0 mm.

b) *Dentition*

Fragment 1:	length in mm	width in mm
I_3?	0,7	0,6
I_4?	0,6	0,5
C	1,2	0,8

Fragment 2:	length in mm	width in mm
P_1	1,0	0,5
P_2	1,2	0,7
P_3	1,2	0,8
M_1	1,6	1,0
M_2	1,8	1,2
M_3	1,6	1,1
M_4	1,1	0,8

length of the postcanine dentition = 9,1 mm

2) *VJ 1002 - 155* (2 fragments). Fig. 3 and 17, Plate II D, E, F.

Left mandibula in incomplete preservation. Both the anterior part of Pars. alv. as well as most of Ramus mandibulae were broken off before burial and are thus not present. That which remains has an almost complete postcanine tooth row and is broken between the second and third premolar. The fractured area is covered with artificial matrix. Nevertheless, the original condition can be easily reconstructed from tooth impressions.

Fragment 1:

Fragment of the anterior of Pars alv. with the posterior end of the canine alveola and complete P_1 and P_2, whereby the main cusp is broken off. The jaw bone is visible only from the buccal side showing that the canine did not follow the postcanine tooth row but was buccally out of place. This is illustrated in the reconstruction scetch of the mandibula (Fig. 5).

Fragment 2:

The complete exposed main part of Pars alv. with the beginning of Ramus mand. The posterior fracture lies caudal to the Foramen mandibulae. As the anterior fracture follows the lingual margin of P_1 and P_2, the lingual part of the mandibula of fragment 1 is present here. The bone surface is in excellent condition with weakly pronounced «youth striae» and a relatively open internal groove extending to the prominent symphysis. Only the last (fifth) molar is missing in the tooth row. There is a rather large margin between its alveola and the M_4. The reason for this is probably to be understood in that the alveola of the discarded M_5 had already begun to be plugged with bony material, thereby reducing the periphery and enlarging the space to the neighbouring tooth. Imbrication is evident between the teeth, whereby it is particularly developed between the P_3 and M_1. The degree of wear on the teeth increases successively from front to back. Whereas the P_1 shows no apparent wear, the cusps of the M_4 are already completely worn away. The premolars have no buccal cingulum. Evidence of tooth replacement is not present.

Dental formula: C : 3 P : 5 M (C und M_5 = alveolae)

Measurements:

a) Jaw bone

Fragment 1: length = ca. 2,9 — 3,5 mm.
Fragment 2: length = 14,3 mm;
height below M_4 = 3,4 mm;
width below M_4 = 2,0 mm.

b) Dentition

Fragment 1:	length in mm	width in mm
P_1	0,8	0,7
P_2	1,1	0,8

Fragment 2:

P_3	1,2	0,8
M_1	1,7	0,9
M_2	1,8	1,0
M_3	1,8	1,1
M_4	1,5	0,9

total length of the dentition of Fragment 1 = = 1,9 mm
total length of the dentition of Fragment 2 = = 7,5 mm

3) *VJ 1003 - 155* (2 fragments) Fig. 4 and 19, Plates I and III A, B.

The posterior part of a left mandibula. Of Ramus mand. only the upper half or the Proc. coronoideus is missing, which was already broken off before burial. On the other hand, excepting a jaw fragment with a badly damaged double--rooted tooth, the part of Pars alv. before the third last molar ($M_{3?}$) was lost during excavation. Because of the poor condition this fragment was not further examined. Particularly striking in the size of the jaw bone, the major fragment has been fully exposed and is in very good condition. The bone surface allows particularly good study of the masticatory muscle insertions and of the rudimentary bones of the primary jaw joint. Pathological changes on the foremost section of the jaw fragment seem to have caused a profound upward curve of the ventral side of Pars alv.

The two remaining molars show relatively light but obvious wear. The last molar has been discarded. Its alveola is linked directly to the preceding molar ($M_{4?}$). Imbrication between the two molars is weakly apparent. In front of the foremost molar ($M_{3?}$) the impressions of the roots of a further M_+ are evident.

Dental formula: 4 M ($M_{2?}$ and $M_{5?}$ = alveolae).

Measurements:

a) Jaw bones

Length condyle — anterior fracture $= 19,7$ mm; height below $M_{4?} = 4,2$ mm; width below $M_{4?} = 2,6$ mm; distance Foramen mandibulae — condyle $= 11,2$ mm; height of condyle $= 2,1$ mm; width of condyle $= 3,2$ mm.

b) Dentition

	length in mm	width in mm
$M_{3?}$	2,1	1,4
$M_{4?}$	1,6	1,2

total length of dentition $= 3,6$ mm

4) *VJ 1004-155* (2 fragments). Fig. 6 and 24, Plate III C, D, E, F.

Part of a right mandibula whereby the foremost section was already broken before burial and also damaged in excavation. Missing is the anterior of the Pars alv. in front of P_1 and the upper half of Proc. coronoideus. The jaw is broken about halfway between the transition of Pars alv. and Ramus mand. diagonally through the alveola of M_2. Impressions in the artificial matrix allowed both fragments to be reassembled without a seam in the reconstruction drawing. The mandibula is of a young animal and thus rather small.

Fragment 1:

A fragment of Pars alv. in artificial matrix with the posterior end of the canine (?) alveola, the anterior root in situ and the alveola of the posterior root of $P_{1?}$, the erupting $P_{2?}$, the Pd_3, the M_1 and M_2 and the alveola base of M_3.

The jaw bone is missing below the internal groove and in the area of P_1 and P_2 also broken off at the alveolas. The bone is further limited on the buccal side by a covering of artificial matrix. Of the three molars the Pd_3 shows the most wear. M_1 and M_2 show only light wear on the main cusps. The main cusp of the erupting

P_2 lies still under the alveolar margin and is therefore not used in the chewing process.

The lingual side of fragment 2 is preserved as an impression in artificial matrix. Included as bone rests in the impression are parts of Proc. coronoideus and Crista pterygoidea.

Fragment 2:

The posterior of Pars alv. and the practically complete Ramus mand. have been exposed on all sides and are visible. Here the jaw bone is present under the wide open internal groove. The bone surface is covered with numerous youthstriae. Above the Foramen mand. is an open cavity containing the bud of M_4. The bud of M_5 had not yet left a trace on the bone. The M_3 together with the lingual wall of its alveola was already broken off before embedding.

Only light imbrication had developed between the two molars.

Dental formula: C (alveola); 2 P ($P_1 = $ rest of root, $P_2 = $ erupting);
Pd_3 (in situ); 4 M (M_1 and M_2 in situ, $M_3 = $ alveola, $M_4 = $ tooth bud)

Measurements:

a) Jaw bone

Fragment 1: distance between fracture surfaces $= 10,2$ mm.
Fragment 2: distance fracture area — condyle $= 11,2$ mm; distance foramen mandibulae — condyle $= 7,1$ mm; height below M_3 $= 2,4$ mm; width below $M_3 = 1,3$ mm; height of condyle $= 1,7$ mm; width of condyle $= 1,6$ mm

b) Dentition

Fragment 1:

	length in mm	width in mm
P_1	not measurable	
P_2	not measurable	
Pd_3	1,1	0,7
M_1	1,6	1,0
M_2	2,0	1,3

length of dentition (anterior root of P_1 — distal end of M_2) $= 4,6$ mm

5) *V J 1005 - 155* (2 fragments). Fig. 19 and 23, Plate IV A, B, C.

A fragment of Pars alv. from a right mandible. During excavation the jaw was broken along the alveolae in a buccal and a lingual half. The anterior and posterior parts of the mandible were broken off before embedding, leaving only the piece between the canine and the M_3. The jaw fragment belonged to a young animal. This is apparent from the youth-striae on the bone surface, the wide open internal groove and the development stage of the dentition.

Fragment 1:

The buccal half of Pars alv. Visible are the buccal alveolar walls and a small part of the outer side of the jaw below the alveolar margin. Furthermore, underneath the fractured alveolae is a piece of the jaw's inner side showing the internal groove. The buccal surface is almost entirely covered with artificial matrix. The damage on the jaw-bone has uncovered two erupting teeth; these being the P_1, whereby only the main cusp is visible, and the M_2, which has been partly broken off on the lingual side. In the case of both teeth the main cusps have barely cut above the alveolar margin and are thus completely unworn.

Fragment 2:

The lingual half of Pars alv. whereby the fractured alveolae are covered with artificial matrix and the lingual bone surface above the internal groove is exposed. Preserved are parts of the alveola of the already discarded Pd_1, the completely worn Pd_2, the Pd_3, particularly worn on the distal part, and the already fully erupted M_1, showing only slight wear on the cusps. The teeth have been exposed on all sides.
Dental formula: 1 P (erupting): 2 Pd (in situ): 2 M (in situ and erupting)

Measurements:

a) Jaw bone

Fragment 1: length = 5,5 mm; height = 1,9 mm.

b) Dentition

Fragment 1: length in mm   width in mm
P_1 not measurable   not measurable

Fragment 2:

	length in mm	width in mm
Pd_2	0,8	0,3
Pd_3	1,2	0,6
M_1	1,5	0,8

6) *V J 1006 - 155* (1 fragment). Fig. 7

A small fragment of Pars alv. from a right mandible with a somewhat corroded, yet practically unworn premolar (probably P_3) and the posterior half of the completely worn down following tooth (probably M_1) in situ. The unstriated bone surface is visible only on the buccal side beneath the teeth. At least the posterior part of the jaw and the anterior of the questionable M_1 were broken away before excavation. The premolar has also an outer cingulum.

Dentition:	length in mm	width in mm
P_3?	1,2	0,7

7) *V J 1007 - 155* (2 fragments). Fig. 8 and 31, Plates IV D, E, F and V A.

A fragment of a right mandible. Missing are the anterior of Pars alv. in front of P_3, the greater portion of the Pars alv. ventral to the internal groove as well as practically the entire Ramus mand., excepting a portion of the Proc. coronoideus. This damage seems to have taken place before burial. During excavation the jaw was broken into two pieces. The oblique break runs from the anterior outside to the posterior inside vertically through M_3. Both fracture surfaces are covered with artificial matrix.

Fragment 1:

A fragment of Pars alv. with the posterior half of P_3, the M_1 and M_2 and the mesio-lingual portion

of M_3. The anterior break runs diagonally through the alveola of the front root of P_3. The premolar sits lower than the molars and is entirely unworn. The molars, on the other hand, are completely worn down. The degree of wear increases successively from front to back. Because of the damaged alveolar margin, the roots of the teeth are partially exposed.

On the anterior part of the fragment the Canalis mandibulae can be seen in cross-section.

Fragment 2:

A fragment of the posterior portion of Pars alv. with a part of the anterior of Proc. corocoideus. The bone under the internal groove is broken away, longitudinally exposing the Canalis mand. The muscle impressions on the Proc. coronoideus are well marked. The fragment contains the disto-buccal portion of M_3 and the mesial half of M_4. The distal half of the crown of this tooth in broken off, so that the root in the alveola is exposed. A M_5 is missing and can not be proved by an empty alveola.

Dental formula: 1 P, 5 M (M_5 is discarded, its alveola is secondarily plugged).

Measurements:

a) *Jaw bone*

Fragment 1: not measurable.
Fragment 2: not measurable.

b) *Dentition*

Fragment 1:	length in mm	width in mm
P_3	not measurable	0,8
M_1	1,6	0,8
M_2	1,8	1,0
M_3	1,9	1,0

Fragment 2:

M_4	not measurable	0,9

B) MAXILLA

V J 1008 - 155 (2 fragments). Fig. 20.

Left upper jaw, flattened and badly corroded. The posterior tooth row is complete from the last I^+ to the last M^+. Of the bones only the Proc. alveolaris of the left maxilla including a part of the inner nasal wall remains. The fracture runs in an acute angle to the tooth row and breaks the jaw in such a manner that of the P^3 and M^1 the buccal halves remain on the first fragment and the lingual halves on the second. In Fig. 20 A the two fragments are reassembled.

Fragment 1:

a) Maxilla: A portion of the corpus and the Pars alv. is visible. The inner side of the jaw is covered with artificial matrix. The corpus of the maxilla is so badly flattened that the tip of the posterior root of C^+ has broken through to the other side. The alveola margins are broken away so that the root necks of the teeth are exposed. Conspicuous is a pronounced scarring of the bone surface. This is probably due to the corrosive effects of humic acids (see the chapter on biostratinomy). The Sutura praemaxillaris can be detected only above the $I^{5?}$.

b) Teeth. Present are: $I^{5?}$ (root), C^+ (cusps are broken off), P^2, P^3, M^1 (buccal halves) and M^2 (impression of the buccal side). The alveola margin of the postcanine teeth lies higher in the dorsal direction than that of the incisives and canine. The teeth have lost almost all their enamel and appear badly corroded.

Fragment 2:

a) Maxilla. A part of the Proc. alv. and the nasal passage is visible. The corpus is laterally masked with artificial matrix. A part of the palate has been bent under and pressed against the teeth. The nasal passage is so well exposed that the interior of a part of the Canalis infraorbitale can be seen.

b) Teeth. Present are P^3 and M^1 (the lingual halves), M^2, M^3, M^4 and M^5. Through pressure

from the caudal direction the M^5 has been turned and pushed against the M^4, thus breaking it in two. The condition of the teeth is equivalent to those of the other fragment.

Dental formula: 1 I^+ ($I^{5?}$ = in the maxilla): C: 3 P (P^1 = alveola): 5 M.

Measurements:

a) *Jaw bone*

Fragment 1: not measurable
Fragment 2: not measurable

b) *Dentition*

Fragment 1:	length in mm	width in mm
$I^{5?}$	not measurable	not measurable
C	1,4	1,1
P^2	1,0	not measurable
P^3	1,1	not measurable
M^1	1,6	not measurable
M^2	1,8	1,9

Fragment 2:

M^3	1,5	1,7
M^4	not measurable	not measurable
M^5	1,1	1,4

The overall length of the dentition of fragment 1 (including $I^{5?}$ and M^2) = 8.3 mm

Because of the tilted teeth, the overall length of the dentition of fragment 2 is not measurable.

c) SKULL

V J 1009 - 155 (5 fragments, 5 isolated teeth and teeth fragments (identifiable); in addition to this various unidentifiable bone and teeth fragments), Fig. 11, 12, 13, 15, 16 and 20, Plate V D, E, F.

Anterior skull severely deformed diagenetically and broken in excavation. The rear cranium was not saved. The left tooth row is complete to the M^3, the right has been proved to the M^4, partially through impressions and roots. The premaxilla and both maxillae and nasals are

relatively complete. The anteriors of both jugales are identifiable. Parts of the left palatine and lacrimal are probably present, however, because of poor condition they cannot be identified.

Fragment 1: The left and part of the right anterior skull with the nasal cavity.

a) Premaxilla. Of the left premaxilla, present are the anterior portion, isolated and shoved forward and upward (visible from the outside, the inside and from below) and the posterior portion, in situ resting on the Sutura praemax. (visible from the outside and the inside). In the space between the two portions, the root of the broken off I^1 and the root ends of the I^2 and the I^3 are visible. The anterior portion of the right premaxilla lies flattened in front of the left (visible is a portion of the Proc. alv. with the alveola of the right I^1 broken open and the root end of the right I^2 in its alveola).

b) Maxilla: The anterior portion of the left maxilla is preserved as bone as far as the tilted P^2. The corpus is complete in this region. The Proc. alv. is missing behind the C^+; due to the flattened condition, Proc. pal. is quite incomplete.

c) Nasal: The left nasal is raised and pushed into the nasal cavity. The anterior is complete and visible from the outside. The left nasal is tilted about 90° and shoved foreward. The anterior portion is broken away. A portion of the interior is visible.

d) Teeth: The left tooth row: I^1 (root), I^2, I^3, I^4, I^5, C^+, P^1 are completely in situ. P^2 is broken and tilted to the outside. P^3, M^1 and M^2 are preserved as an impression of the buccal side.

Fragment 2: The right wall of the front part of the skull.

a) Premaxilla: Visible is the posterior portion of the corpus with the right margin of the nasal opening as far as the Sut. praemax. The anterior portion is broken away.

b) Maxilla: The corpus near the teeth is in bone, otherwise, it is preserved primarily as an impression. It is badly bent above the P².

c) Jugal: The anterior portion (?) dorsal to the maxilla is in situ. The Sut. zygomaticomaxillaris to the maxilla is in situ. The bones in the caudal direction are present only as an impression.

d) Teeth: The right P³ and M¹ are complete. The M² is partly preserved as an impression. I³, I⁴, I⁵, C⁺, P¹, P² and M³ are visible only as impressions from the outside.

Fragment 3: Left upper jaw, directly connecting to fragment 1.

a) Maxilla: Only a portion of the Proc. alv. adjoining directly to the teeth is preserved.

b) Teeth: The dislocated right P², the left P³ in situ and the lingual halves of P² and M¹ are present.

Fragment 4: The posterior portion of the left anterior skull continuing from fragments 1 and 3. No direct connection preserved. Because of intense flattening and a partial masking with artificial matrix, the identification of some portions is very difficult.

a) Maxilla: The posterior part of the left maxilla at the beginning of the zygomatic arch (visible from the outside and from underneath).

b) Jugal: The anterior portion in contact with the maxilla is partially visible.

c) An unidentified bone lies in the posterior portion of the orbit or in the anterior of the temporal depression. Pressure from the side has pushed the zygomatic arch against the skull and a portion of the palate has been folded down.

d) Teeth: Only the left M³ is present completely in situ.

Fragment 5: The beginning of the right zygomatic arch continuing from fragment 2. The connection ist not direct.

Present are parts of the maxilla and jugal including a few tooth roots. The bone suture is difficult to recognize.

Isolated teeth: Present are, on the left, the I³ and C⁺, and on the right, molar fragments (two buccal halves and a non-corresponding lingual half).

Dental formula of the left half of the jaw:
5 I (I¹ = root, I⁵ = in the maxilla) : C : 3 P : : 3 M (M₁ = lingual half, M² = impression).

Dental formula of the right half of the jaw:
5 I (I¹ and I² = alveolas, I⁴ = broken off and isolated, I⁵ = impression) : C (= broken off and isolated) : 3 P (P¹ = impression) : 3 M (M² = buccal half, M³ = impression).

Measurements of the left jaw half:

a) Jaw bone = not measurable

b) Dentition

Fragment 1:	length in mm	width in mm
I¹	not measurable	not measurable
I²	0,6	0,5
I³	0,8	0,6
I⁴	0,8	0,6
I⁵	0,5	0,5
C⁺	1,3	0,8
P¹	0,5	0,4
Fragment 3:		
P²	1,2	not measurable
P³	1,4	1,0
M¹	not measurable	not measurable
M²	not measurable	not measurable
Fragment 4:		
M³	1,6	1,6

Total length of the dentition on fragment 1, including I¹ and P³ = 6,3 mm.

Measurements of the right jaw half:

a) Jaw bone = not measurable

b) Dentition

Fragment 2:	length in mm	width in mm
I³	not measurable	not measurable
I⁴	0,7	0,5
I⁵	not measurable	not measurable
C⁺	1,3	0,8

Fragment 3:

P²	0,9	not measurable

Fragment 2:

P³	1,3	0,9
M¹	1,7	1,7
M²	1,8	not measurable
M³	not measurable	not measurable

Total length of the dentition on fragment 2: anterior dentition (including I³ and P¹) = 4,7 mm; posterior dentition (P³, M¹ and M²) = 4,8 mm.

D) ISOLATED PREMOLARS

1) VJ 1011-155

Right P², crown complete, roots broken off, no wear.
length = 1,3 mm   width = 0,8 mm

2) VJ 1012-155, Plate VII A, B, C, D, E.

Right P³, crown complete, roots broken off, no wear.
length = 1,5 mm   width = 1,1 mm

3) VJ 1013-155, Plate VI I, K.

Left P², crown complete, root broken off, no wear.
length = 1,2 mm   width = 0,8 mm

4) VJ 1029-155

Right P², crown complete, without roots, pulp cavity wide open, no wear. Young, not yet fully erupted tooth.
length = 1,2 mm   width = 1,0 mm

5) VJ 1032-155, Plate VII F, G.

Left P³, crown complete, anterior root complete, about half the length of the posterior root is broken off (here both posterior roots are connected together and possess the same canal, which lies in the mesial and distally tapered area of contact, having a drawn out oval cross-section), slight wear. The root necks are constricted bordering the crown.
length = 1,3 mm   width = 1,0 mm

6) VJ 1035-155, Plate VI C, D, E.

Left P₂ or P₃, crown complete, roots broken off, no wear, no external cingulum.
length = 1,3 mm   width = 0,8 mm

7) VJ 1036-155

Left P₂ or P₃, crown complete, roots broken off, very slight wear on the cusps, external cingulum.
length = 1,2 mm   width = 0,8 mm

8) VJ 1037-155

Right P₂ or P₃, crown complete, roots broken off, no wear, external cingulum.
length = 1,2 mm   width = 0,7 mm

9) VJ 1038-155, Plate VI F, G, H.

Left P₂ or P₃, crown complete, roots broken off, no wear, external cingulum.
length = 1,3 mm   width = 0,7 mm

10) VJ 1039-155, Plate VI A, B.

Left P₁, crown complete, anterior root complete, half of the posterior root broken off, no wear, no external cingulum.
length = 0,8 mm   width = 0,6 mm

11) VJ 1040-155

Left P₁, crown sightly damaged, roots broken off, no wear, no external cingulum.
length = 1,0 mm   width = 0,6 mm

E) ISOLATED MILK MOLARS

1) *VJ 1030-155*, Plate VIII F, G, H.

Right Pd$^+$, crown complete, roots resorbed, pulp chamber wide open with resorbtion pits, tooth slightly worn.
length = 1,4 mm   width = 1,3 mm

2) *VJ 1031-155*

Right Pd$^+$, crown complete, root resorbed, pulp chamber wide open with resorbtion pits, tooth slightly worn.
length = 1,1 mm   width = 0,9 mm

3) *VJ 1033-155*

Right Pd$_+$, anterior of the crown broken away, roots resorbed, pulp chamber wide open with resorbtion pits, tooth slightly worn.
length not measurable   width = 0,8 mm

4) *VJ 1041-155*, Plate VIII I, K.

Right Pd$_+$, crown complete, roots resorbed, pulp chamber wide open with resorbtion pits, tooth slightly worn.
length = 1,5 mm   width = 0,8 mm

5) *VJ 1042-155*

Left Pd$_+$, crown complete, roots resorbed, pulp chamber wide open, tooth heavily worn.
length = 1,2 mm   width = 0,7 mm

6) *VJ 1043-155*, Plate VII H, I.

Right Pd$_+$, crown complete, roots resorbed, pulp chamber wide open with resorbtion pits, tooth slightly worn.
length = 1,5 mm   width = 0,7 mm

7) *VJ 1044-155*

Right Pd$_+$, crown complete, roots not yet completely resorbed, resorbtion pits, tooth strongly worn.
length = 1,4 mm   width = 0,7 mm

8) *VJ 1028-155*, Plate VIII A, B, C, D, E.

Left Pd$_+$, crown complete, roots broken off, slight wear on the cusps. Root canals wide open. Tooth is not discarded but broken off.
length = 1,2 mm   width = 0,6 mm

F) ISOLATED MOLARS

1) *VJ 1010-155*, Plate IX A, B.

Right M$_+$, crown complete with a damaged accessory cusp «h», roots not yet developed, pulp chamber wide open, no wear. Newly formed, not yet erupted tooth.
length = 1,6 mm   width = 1,2 mm

2) *VJ 1025-125*

Right M$_+$, crown complete, anterior root completely, posterior root partially broken off, extensive wear.
length = 1,5 mm   width = 1,0 mm

3) *VJ 1019-155*

Right M$_+$, crown complete, roots broken off, wear beginning on the tooth flanks.
length = 1,9 mm   width = 1,3 mm

4) *VJ 1018-155*, Plate X F, G.

Left M$_+$, crown complete, roots broken off, extensive wear on the anterior accessory cusp «b». Aberrant molar with a comperatively small main cusp «a» and sturdily formed accessory cusps. The largest cusp is here the accessory cusp «b».
length = 1,5 mm   width = 1,1 mm

5) *VJ 1020-155*

Right M$_+$, crown complete, roots broken off, cusps worn, wear beginning on the tooth flanks.
length = 1,8 mm   width = 1,2 mm

6) *VJ 1016-155* Plate X A.

Left M$_+$, crown slightly damaged distally, anterior root complete, posterior root

broken off, wear particulary in the mesio-lingual portion.

length = 1,8 mm   width = 1,1 mm

height of the root = 2,1 mm

7) *VJ 1023 - 155*

Right M_+, anterior third of the crown broken off, roots broken off, very slight wear on the cusps, pulp chamber still open.

length = not measurable   width = 1,1 mm

8) *VJ 1026 - 155*, Plate X C, D.

Right M_+, main cusp «a» broken off, buccal margin damaged, roots broken off, slight wear, pulp chamber still open. Several cingulum buds developed lingually and mesially. No accessory cusp «h».

length = 1,7 mm   width = not measurable

9) *VJ 1017 - 155*, Plate X C, D.

Right $M_{5?}$, crown slightly damaged, roots broken off, very slight wear on the cusps, pulp chamber open. The tooth is relatively small and roundened. Its appearance shows that it came from the posterior end of the tooth row and is probably a newly erupted M_5. Such molars have not been found in situ in the mandibles of *Halda-nodon*.

length = 1,3 mm   width = 0,9 mm

10) *VJ 1022 - 155*

Right M_+, posterior fourth of the crown is broken off, the anterior root is to a third, the posterior root completely broken off, wear is particulary mesio-lingual.

length = not measurable   width = 1,2 mm

11) *VJ 1027 - 155*

Right M_+, crown complete, no roots, very slight wear on the cusps, pulp chamber wide open with smooth edges. A young molar yet without developed roots, in the state of eruption.

length = 1,8 mm   width = 1,0 mm

12) *VJ 1021 - 155*, Plate IX C, D.

Right M_+, crown complete, roots broken off; broad root canals, slight wear.

length = 2,0 mm   width = 1,2 mm

13) *VJ 1024 - 155*

Left M_+, crown slightly damaged mesio-buccally, anterior root completely and two thirds of the posterior root broken off, slight wear, root canals wide open.

length = 1,6 mm   width = 1,0 mm

14) *VJ 1035 - 155*

Right M_+, posterior end of the crown broken off, roots broken off, slight wear.

length = not measurable   width = 1,0 mm

15) *VJ 1045 - 155*, Plate XI A, B.

Right M_+, posterior end of the crown slightly damaged, anterior root completely, posterior root half broken off, intensive wear especially on the posterior portion of the tooth.

length = 1,8 mm   width = 1,3 mm

16) *VJ 1046 - 155*, Plate X B.

Left $M_{5?}$, crown complete, roots complete, intensive wear. The tooth likens VJ 1017--155.

length = 1,4 mm   width = 1,0 mm

17) *VJ 1015 - 155*, Plate IX E, F, G, H, I, K.

Right M_+, crown complete, anterior root two thirds broken off. Posterior roots completely broken off, very slight wear on the tooth cusps, pulp chamber and root canal wide open.

length = 2,0 mm   width = 1,3 mm

18) *VJ 1047 - 155*, Plate X H, I, K.

Left M_+, crown complete, anterior root completely broken off; posterior root three quarters broken off, tooth almost completely worn down. M_4 or M_5 shortly before being discarded.

length = 1,2 mm   width = 0,8 mm

19) *VJ 1048-155*, Plate XI C, D, E.

Right M$^+$, crown complete, roots broken off, wear on the cusps, pulp chamber still somewhat open. M^4 or M^5.
length = 1,0 mm   width = 1,2 mm

20) *VJ 1014-155*, Plates XI F, G, H and XIII A.
Right M$^+$, crown slightly damaged mesially, roots broken off, cusps and flanks worn.
length = 1,6 mm   width = 1,7 mm

21) *VJ 1034-155*

Right M$^+$, lingual half of the crown broken off, roots broken off, very slight wear on the cusps.
length = 1,6 mm   width = not measurable

22) *VJ 1049-155*

Left M$^+$, buccal half of the crown broken off, slight wear. No measurements.

23) *VJ 1050-155*, Plate XII B, C, D.

Right M$^+$, buccal half broken off, no wear. No measurements.

24) *VJ 1051-155*, Plate XII E, F.

Left M$^+$, buccal half broken off, very slightly worn. No measurements.

4.2 Comparative Anatomy of the Lower Jaw

4.2.1 Dentary

The mandible of the genus *Haldanodon* is made up of several bones, of which the dentary is by far the most important. It has the docodont's typical form and consists of the teethcarrying Pars alveolaris and the Ramus mandibulae, which terminates in its three processes, Processus coronoideus, Processus condylaris and Processus pseudangularis (see below). On the inner side of the ramus are places of attachment for other bones of the primary mandible; that will be discussed later.

The Pars alveolaris of the dentary consists of a long, thin, straight bone shaft, whereby the ventral part is convexly formed. The bulge reaches its maximum under the central molars. In the alveolar region of the teeth, the bone thins down to a width more narrow than that of the teeths' crowns. Thus, on the inside of the jaw bone, a shelf is formed tapering off to the front. The alveolar margin has about the same height on the inside as well as the outside.

Both mandibles of *Haldanodon* are connected by a long symphysis, reaching to the first and perhaps even as far as the third molar. The surface of the symphysal region is grooved and wrinkled. It can be assumed that when the animal was alive both dentaries were connected by an elastic layer of cartilage, the anterior part of the Meckelian cartilage, allowing a certain amount of movement between the two halves of the lower jaw. Correspondingly, an unusually long symphysis of a similar form is also found in *Docodon* (SIMPSON 1929).

An X-ray of *Haldanodon* shows a Canalis mandibulae, beginning on the inside of the ramus with the Foramen mandibulae, running under the teeth roots and ending in a Foramen mentale, which lies on the outside of Pars alveolaris underneath the anterior root of the first premolar.

According to SIMPSON (1929), *Docodon victor* (MARSH 1880), *Docodon striatus* (MARSH 1881) and *Docodon crassus* (MARSH 1887) have a corresponding Foramen mentale underneath the P$_3$, and *Docodon affinis* (MARSH 1887) has two of them under the P$_1$ and P$_2$. As in most Jurassic mammals (excepting the multituberculates) the docodonts have running along the inside of the Pars alveolaris a deep groove, called in english written literature the «internal groove» (SIMPSON 1928 b). In *Haldanodon*, the groove begins on the ramus, runs along the lower part of Pars alveolaris about parallel to its undermost border and ends by merging into the symphysis region. In the adult, the groove, etched deep in the jaw bone, is closed, whereby in younger subjects it lies open. In the more completely preserved specimens branches of the groove can be observed running diagonally towards the lower front. VJ 1002-155 possesses such a branch under the M$_2$; VJ 1001-155 has

two lying under the M_2 and the M_1. After such a branching the lumen of the groove narrows. In the area directly around the groove blood vessel impressions are more plentiful than anywhere else on the mandible.

Iberian peninsula. In contrast to their more later evolved kin, the Jurassic dryolestids, also found in the Guimarota diggings, possess a well developed internal groove. KREBS's interpretation of the features of his material points to a probable
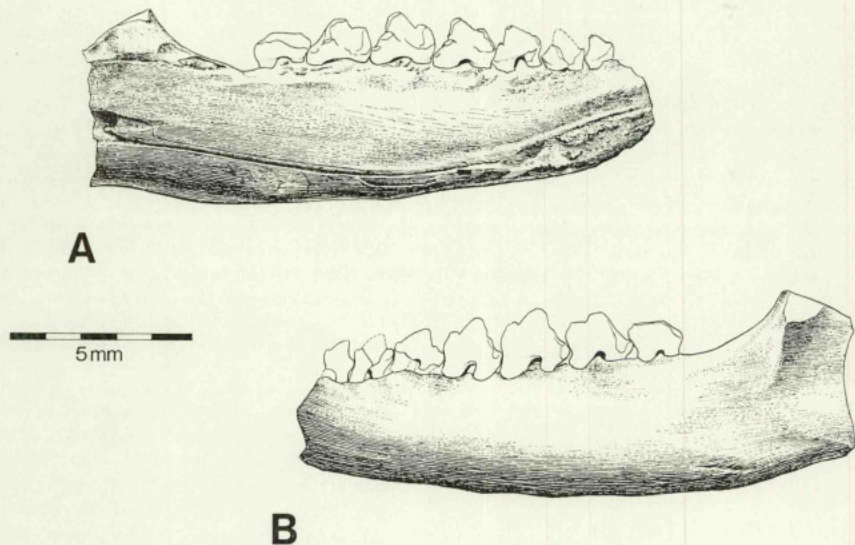

FIG. 3 — Left lower jaw VJ 1002 - 155.
A: Medial view.
B: Lateral view.

The function of the internal groove had been argued for a long time. BENSLEY (1902) thought he was able to prove it to be a Sulcus primordialis which held only a persistent Meckelian cartilage. SIMPSON (1928 b), who also studied the groove development on the lower jaw of recent and fossil mammals, tried to disprove this theory. He came to the conclusion that the internal groove had principally the function of a Sulcus mylohyoideus, as do similar structures in recent mammals; that is to say, it held the artery and nerve supplying the mouth floor. Recently KREBS (1971) published a paper specifically covering this subject based on dryolestids out of the Upper Jurassic and Lower Cretaceous of the

synthesis of both above mentioned hypotheses. The following considerations seem important.

1) In recent mammals the Arteria and Nervus mylohyoideus, serving the Musculus mylohyoideus and the anterior belly of M. digastricus, branch off from the Arteria and Nervus alveolaris inf. just before entering in the Foramen mandibulae. Both muscles form a portion of the mouth floor. The Foramen mandibulae and the internal groove lie close on one another. It can thus be assumed from SIMPSON (1928 b) that in Mesozoic mammals the Arteria and Nervus mylohyoideus ran along the lower jaw, in or on the internal groove.

2) The internal groove follows through as far as the symphysis. This is not necessary for simply supplying the mouth floor. It corresponds, however, to the extention of the Meckelian cartilage in the embryos of recent mammals.

3) Persistence of the Meckelian cartilage can be drawn from the fact that, also in the jaws of unmistakably adult animals, the internal groove has not fully been filled in as, for example, is the case with the alveolas of discarded teeth.

4) In some cases, the internal groove is divided into two parallel running grooves. Probably the one serves as Sulcus mylohyoideus and the other as Sulcus primordialis. This correlates also with embryological evidence.

The opinion held by KREBS (1971) for dryolestids — that the internal groove held the persistent Meckelian cartilage as well as the Arteria and Nervus mylohyoideus — can be applied also to *Haldanodon* and the other docodonts. The posterior part of the mammalian mandible, the so-called Ramus mandibulae, serves the insertion of the jaw-closing muscles as well as to connect the lower jaw to the skull. In *Haldanodon* and other Mesozoic mammals, it further contained rudimentary bones of the primary mandible. This took place, similar to *Morganucodon* and *Docodon*, for the most part, in a wide, deep, triangular sulcus which, extending the internal groove, continually widens in the posterior direction, until it finally openes underneath the projection of the condyles. Incorporated in the sulcus and broken by a weak ridge running diagonally in the upper posterior direction, a groove forms the projection of the Foramen mandibulae. Its form and position indicates that the Arteria and Nervus alv. were led in it from the upper posterior to the foramen. The direct extention of the internal groove runs, in a similar yet smaller groove, parallel to the lower edge of the sulcus, finally running into it. One can assume that the Meckelian cartilage, before entering the internal groove, was situated on the lower edge of the sulcus.

There it went into a synchondrotic connection with the dermal bones of the reptilian lower jaw and ossified in its posterior part as an articulary.

Above, the sulcus is bordered against the Proc. coronoideus by an edge that, towards the posterior, developes to a distinct ledge, the Crista pterygoidea. Also in the lower direction, the sulcus ends with a sharp border. This is particularly distinct as the lower portion is curved inward like a gutter, thus forming an obtuse angle to the ramus. Above the Foramen mandibulae, the sulcus borders on a well developed Lingula mandibulae, that posteriorly merges into the mentioned Crista pter. In front of the sulcus is a triangular area, bordered above by an indentation on the Lingula mand. and below by the, in this region particularly wide, internal groove. The anterior tip runs into the internal groove; posteriorly there is no noticeable border.

Above the Lingula mand., in about the height of an imaginary continuation of the teeth roots, lies a distinctly defined concavity with an irregular, usually lozenge shaped outline, which probably contained the rudimentary coronoid. The sulcus itself has an irregular, striated surface, of which can be inferred the location of earlier attached bones. Particularly noticeable is a bow shaped depression, bordering the posterior of the sulcus. The presence of bones of the primary mandible on the dentary of *Haldanodon* can be postulated from recent knowledge of mammal-like reptiles and mammals of the Upper Triassic and Jurassic.

Regretfully, the Proc. coronoideus is not completely preserved in the present mandibles of *Haldanodon*. Thus the reconstruction of its outer contour is hypothetical and follows here more or less the form that MARSH (1881) and SIMPSON (1929) asserted to *Docodon*. The outward curve of Proc. coronoideus begins very abrupt and steep on the outside of the posterior alveolar margin, so that the buccal side of the last molar is already partially covered. The angle between the alveolar margin and the front edge of the Proc. coronoideus is about 110-120°. Thus, the Proc. coronoideus rises somewhat steeper than it does in *Morganucodon*, where the angle is about 130-140° and in *Docodon*, where it is about 120-130° (measurements are taken from illustrations in SIMPSON 1929, KERMACK & MUSSETT 1958 and PARRINGTON 1971).

On the lateral side, the anterior edge of the Proc. coronoideus is bulged and thickened. A further, even broader bulge runs along the outside of the ramus, from the Pars alveolaris to the Proc. condylaris and divides the Proc. coronoideus from the ventro-caudal process (Proc. pseudoangularis, see below). The two bulges meet at an angle of about 50° forming a distinct depression, which served the attachment of masticatory muscles. A further, less pronounced insertion area is present on the medial surface of the Proc. coronoideus. Above all, however, the swelled anterior edge was the point of attachment for a strong jaw-closing muscle.

To the posterior, the Proc. coronoideus passes over to the long-stemmed Proc. condylaris. Both processes share a mutual component: the Crista pter. and an overlaying deep groove. The Crista pter. developes out of the edge that divides the sulcus from the Proc. coronoideus. In the posterior of the sulcus it emerges as a sturdy ledge, that is almost at right angles to the surface of the ramus.

Because of damage, the angle cannot be exactly determined. In *Docodon* the Crista pter. points diagonally in a dorsomedial direction (SIMPSON 1929). The Crista pter. joins the underside of the condyle stem and prevents the sulcus from continuing to the Caput mand. Other than in *Morganucodon* and the reptiles *Oligokyphus* and *Diarthrognathus*, the sulcus ends here already at the beginning of the condyle. As can be seen in stereo photos from SIMPSON (1929) and KERMACK & MUSSETT (1958), *Docodon striatus* MARSH (1881) seems to be similar in this respect. Next, the Crista pter. runs along with the condyle stem posteriorly and curves finally — again reduced to an edge-like thickening — upwards to the inside of the Caput mand.

Above the Crista pter. lies a deep, elongated depression, which takes in practically the entire inner side of the Proc. condylaris, with its longitudinal axis running parallel to it. The undermost portion of the depression is set in deepest where it veers in a sharp angle into the Crista pter. The purpose of the depression was to enlarge the dorsal surface of the Crista pter. and so obtain a more effective attachment surface for a pterygoid muscle. An equivalent structure is not developed in *Morga-*

nucodon, however, it seems to be present in *Docodon striatus* MARSH 1881 (stereo photo in KERMACK & MUSSETT 1958).

The Proc. condylaris consists of a curved stem and a strong condyle ball. The stem curves out in a dorso-lateral direction so that the condyle ball lies above the level of the teeth cusps. Thus, the Caput mandibulae sits higher than it does in *Morganucodon* and *Docodon*, where it is located at about the level of the alveolar margin. In a cross-section, the stem of the condyle has a triangular shape. The base of the triangle is formed by the convex underside, projecting on both sides into a reinforcing ridge. On the inside, this is the already mentioned Crista pter. and its extension. On the outside, the ridge developes out of the bulge deviding the Proc. coronoideus and the ventrocaudal continuation of the Ramus mand. This outer ridge continues posteriorly in a hook-shaped body, lying laterally next to the condyle ball, which served as insertion-place of a Ligamentum laterale to reinforce the articular capsule.

The concave side surfaces of the stem join above to form a ridge, running in an arch between the condyle ball and the ascending Proc. coronoideus. Posteriorly, towards the articular part the stem becomes wider. The articular facet of the Caput mand. has the form of a lightly faceted and flattened segment of a parabola. Its width is about the same as its height (VJ 1001-155, Fig. 2) or a fraction larger (VJ 1003-155, Fig. 4). The two facets lie one above the other and are divided by a feeble horizontal line. The articular facet is not at a right angle to the axis of the stem but is bend more or less upward.

According to STARCK (1967), the jaw joint of *Haldanodon* has a form that is typical for the articulation in omnivorous animals (such as bunodont ungulates, ursids, primates); namely a universal type that because of its flattened and oval form allows a great deal of freedom of movement.

Located underneath the Proc. coronoideus is a process that occurs homologous in *Morganucodon* and *Docodon*. Its naming and its anatomical value are uncertain and have been debated by several authors. Here at first is given a descrip-
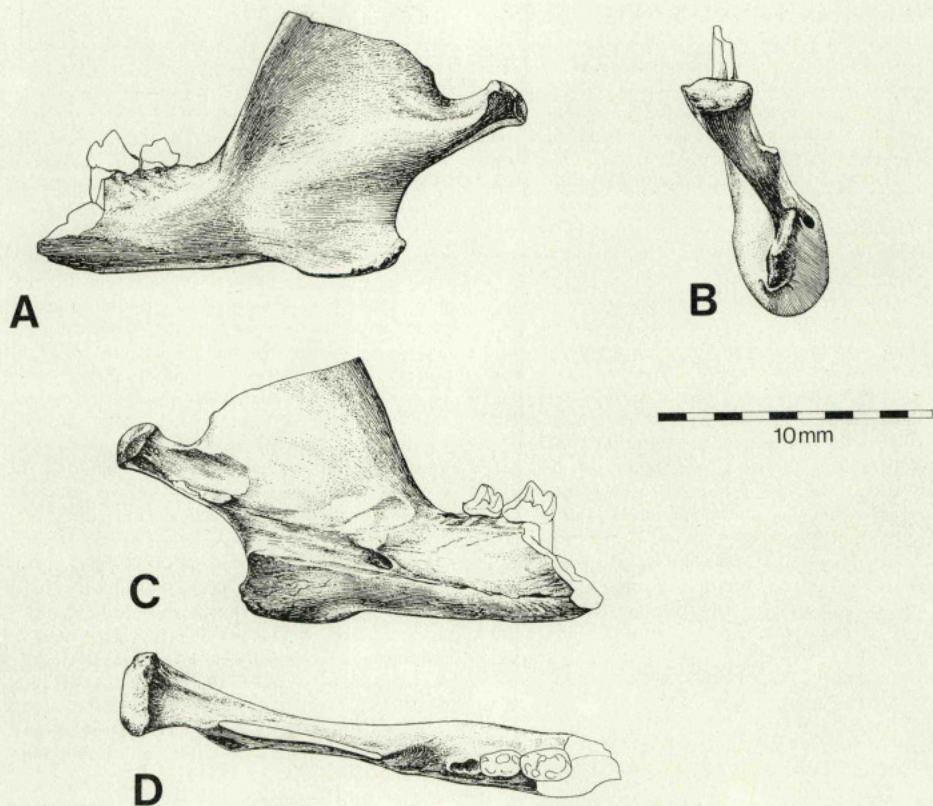
FIG. 4 — Left lower jaw   VJ 1003 - 155.
A: Lateral view.   C: Medial view.
B: Caudal view.   D: Dorsal view.

tion, while a functional analysis will be delt with in the chapter about jaw musculature.

The very sturdy developed process can be compared with the Proc. angularis of the theria. Similarly, it served the attachment of muscles, however it differs in position and direction. In *Haldanodon*, the process curves away from the Corpus mand., and forms a more or less trapazoidal body, aligned diagonally and ventro-caudal to the mandibular axis. The process ends in a concave arch, terminating the sulcus in the posterior and finally merging into the underside of the condyle.

The surface of the process is curved to the outside, and has a bulge-like swelling on its lateral edge. Thus on the outside a shallow depression is formed, in which a muscle was attached. At the posterior part of the bulge are striking wart-like projections, on which probably a jaw-opening muscle inserted. On the convex medial surface

of the process another weakly developed muscle attachment can be seen. The medial side of the process forms, along with the deep-set under-edge of the sulcus, on its ventro-caudal end a sharp projection, where possibly a ligamentum was attached, connecting the jaw and the back of the skull.

The here given general description of the lower jaw morphology is based on the holotype of *Haldanodon exspectatus* (VJ 1001-155). The deviations found in the paratypes are to be supplemented here.

The seven mandible fragments are of differing ontogenetic stages of development. VJ 1004-155 (Fig. 6) was the mandible of a young animal, and did not yet possess a complete tooth-row (the M_4 is present as a bud in an open crypt on the inner side of the ramus). Other indications point to the relatively young age of the individual. Noticeable is the small size of the jaw bone in relation to the size of the teeth and to the other, regarded here as adult, specimens. Further, it can be seen that the surface of the bone has «youth-striae», that the lumen of the internal groove is very wide and that the muscle insertions appear faint and are little pronounced.
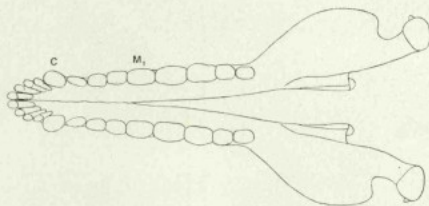

FIG. 5 — Reconstruction of the lower jaw of *Haldanodon* (Dorsal view).

The bony substance is not as well preserved as in the other mandibles, which can be attributed to the fact that the ossification was not so far advanced. This condition is also responsible for the development of the condyle ball, that does not have the well-rounded, even form and surface as do specimens VJ 1001-155 and VJ 1003-155. It can be assumed that in young animals

the Caput mand. was of cartilage substance and ossified with increasing age. On a whole, mandible VJ 1004-155 gives an «unfinished», and in the frontal-caudal direction compressed impression. The bud of the last molar lies underneath the impression for the coronoid. On the other hand, in adult animals the last molar lies at the same height as the coronoid impression and in front of it. The Proc. coronoideus is small and low, merging directly into the condyle which had not yet developed a stem. Thus, here the sulcus reaches relatively further caudally than in the adult subjects of *Haldanodon* indicating an area of persisting bones nearer to the secondary jaw joint as in this case. The angle between the alveolar margin and the anterior edge of the Proc. coronoideus is in adult animals about 15° steeper than in the young subject. Specimen VJ 1005-155, because of its heavily striated bone surface, its very broad internal groove and the fact that it was just undergoing tooth replacement is also regarded as the remains of a young animal.

Otherwise, the specimens VJ 1001-155, VJ 1002-155 and VJ 1003-155 are all mandible-remains of adult individuals. Deviations occur in these that cannot be ontogenetically explained. As in VJ 1002-155 only the Pars alveolaris remained, attention is centered on a comparison of the other two specimens. Particularly noticeable is, above all, the enormous variation in size. The jaw bones and teeth of VJ 1003-155 are of a size about 1/3 larger than those of VJ 1001-155 (see measurements).

The other differences are found particularly in the form and proportion of Proc. coronoideus and the ventro-caudal mandible process. In the first specimen, the condylus is provided with a sturdy, straight stem. In the other specimen (the holotype of *Haldanodon exspectatus*), the stem is bow-shaped and bent upward, so that the articular facet appears to be directed more dorsally than caudally. In the first specimen, the ventro-caudal mandible process is substantially longer and closer to the ramus.

Thus, from lower jaws of adult subjects of *Haldanodon* we can prove a (sexual?) — dimorphism with a form A, based on VJ 1003-155, and a form B, based on VJ 1001-155.
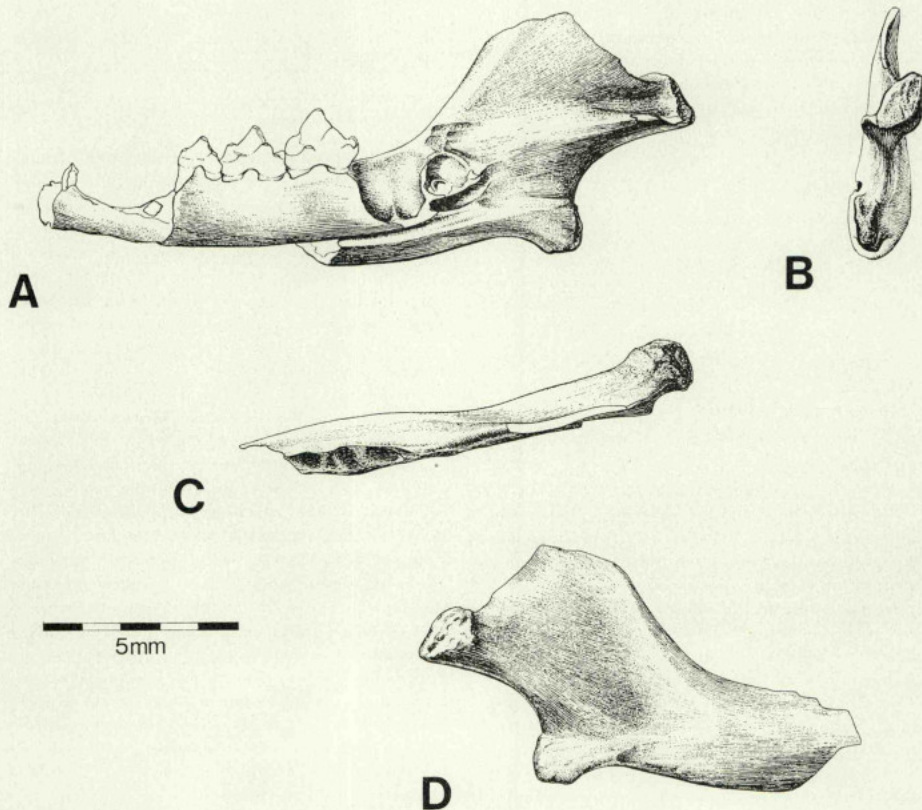
FIG. 6 — Right lower jaw VJ 1004 - 155.
A: Medial view.   C: Dorsal view.
B: Caudal view.   D: Lateral view.

Because of its similar size, VJ 1002-155 can be considered the Pars alveolaris of form A. In this case, the dimorphism would also effect the form of the premolars, which in this fragment do not have an external cingulum. From its proportions it is likely that VJ 1004-155 is a young subject of form B. Also because of their proportions, the upper jaws VJ 1008-155 and VJ 1009-155 could be assigned to form B. On the other hand, VJ 1006-155 (Fig. 7) is representative of form B, because its permolar is provided with an external cingulum.

Because of the limited number of jaw fragments available of *Haldanodon*, these assertions must be viewed with some caution. It must be expected that Mesozoic mammals, trying for new living space and under strong selective pressure, had a high rate of mutation, which possibly contri-

buted to the morphological variations of the jaw parts. Interesting in conjunction with this are PARRINGTON's (1971) observations, who with a very abundant collection of jaw fragments of *Morganucodon* was able to prove dimorphism and perhaps even polymorphism.
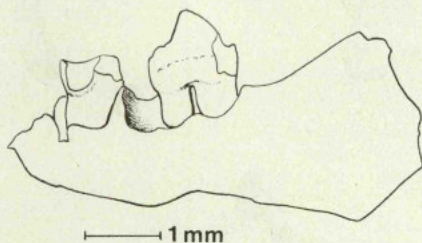

FIG. 7 — Right lower jaw VJ 1006 - 155.
Lateral view.

At this point, another specimen that must be noted is VJ 1007-155 (Fig. 8). In this fragment the posterior portion of the last premolar and the four molars are preserved. The molars are worn practically to the roots. On the other hand, the premolar, lying somewhat lower than the molars, is completely untouched. Between the posterior molars and the anterior edge of the Proc. coronoideus, there is a broad gap. The dorsal surface of the Pars alveolaris is indented in this gap. Impressions of the rudimentary coronoid and muscle insertions are deep and distinct. Without a doubt, the specimen can be classified as the mandible fragment of an individual still fit for life, however at the end of its ontogenetical development and showing signs of old age. The absence of an external cingulum on the premolars and the size of the jaw groups it also with form A of *Haldanodon*. From its features, the following can also be assumed: At least the last premolar can be replaced also at an advanced age. The molars are still functional when worn down. The last molar was discarded and its alveola filled with bony substance. (In the three mandibles of adult individuals present, although the last molar is missing, the alveolas are open). The loss of the postcanine molars without replacement

and the filling-in of the alveolas is, to a very large degree, characteristic in *Morganucodon* (MILLS 1971, PARRINGTON 1971).

4.2.2 Accessory bones

It is well known that in advanced therapsids together with the transformation of the jaw musculature and the development of the heterodont denture the dentary was considerably enlarged. The remaining bones of the lower jaw (splenial, coronoid, prearticular, articular, angular and supraangular bone) lose, in differing degrees, their function and are slowly degenerated. This process results in their final, more or less, rudimentary deposition on the inner side of the posterior part of the dentary (WATSON 1912, BARGHUSEN & HOPSON 1970, CROMPTON 1963 a). Eventually, with the development of the condyle the dentary also took over the function of hinging the lower jaw to the skull. The other bones had, according to the Reichert-Gauppian theory, at least by the end of the Middle Jurassic a new function in the middle ear or were lost (splenial, coronoid, supraangular). The exception to this development is seen in the docodonts, where, the secondary jaw joint being fully functional, the mammalian middle ear was not established. In the forerunners of the theria, this phenomenon is present as a development stage in the Upper Triassic (KERMACK & MUSSETT 1967, PARRINGTON 1971) which was resolved, however, in the course of evolution. Specially examined for reptilian characteristics, the dryolestids of the Kimmeridgian show only a rudimentary coronoid and splenial. In similar forms of the Lower Cretaceous, these bones also have disappeared (KREBS 1971).

Identifying the contact surface of bones of the reptilian lower jaw on the dentary of *Haldanodon* is rather difficult, as none of these rudiments are preserved and impressions are not distinct. Help in solving this problem is found in works on mammals and mammal-like reptiles of the Triassic, as well as in a monograph by KUHN (1971) concerning the early ontogenetic development of the skull in the monotreme genus *Tachyglossus*.
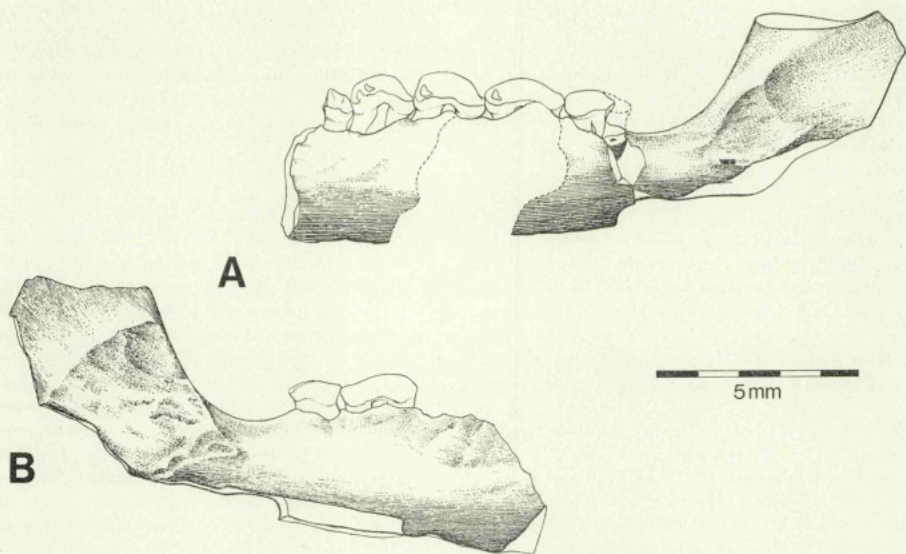
FIG. 8 — Right lower jaw VJ 1007 - 155.
A: Medial view.
B: Lateral view.

KÜHNE (1958) described isolated teeth of *Morganucodon watsoni*, and, on a mandible fragment, studied its correlation to *Docodon* and to the tritylodont *Oligokyphus*. He noticed that the therapsid as well as the mammal had as a common structural element a deep groove on the inner side of the dentary. KÜHNE named this groove «sulcus cartilaginis meckeli», because he assumed that, in both cases, it served to accomodate the Meckelian cartilage, which was ossified as articular at its proximal end. This proved to KÜHNE that *Docodon* still possessed a primary jaw joint located medially from the secondary one, having an identical axis of rotation. KÜHNE was further able to prove that a lower jaw fragment of *Morganucodon* also possessed the same sulcus. This led him to postulate that, for these mammals (which he believed to be triconodonts) also both a primary and a secondary jaw joint were present.

At practically the same time, KERMACK & MUSSETT (1958) published a work on *Morganu-codon*-material from a neighbouring excavation of approximately the same age, also containing well preserved mandibular and cranial fragments. Both authors judged the function of the sulcus as had KÜHNE, and with their extensive material were able to make further remarks. They succeeded in reconstructing the posterior portion of the mandible, and compared it with *Docodon* and *Peraiocynodon* as well as *Oligokyphus*. They concluded that, for the three mammals as well as the therapsid, along with the other bones of the primary joint also the articular was located in the sulcus. While in *Oligokyphus* the articular alone functioned as a joint, in the mammals also a condyle, developed at the dentary, served this purpose. According to KERMACK & MUSSETT, in the living animal the articular would have been located in the posterior end of the sulcus on the condylus, where it still partially retained its original function as a part of the jaw joint. In one specimen of *Morganucodon* an accessory

bone is preserved, covering medially the anterior part of the sulcus. Encouraged by D. M. Watson, KERMACK & MUSSETT indicated this bone as prearticular or angular.

PARRINGTON published in 1971 a comprehensive account on Upper Triassic mammals. Along with considerations as to the phylogeny, which will be discussed later, he introduced the most up-to-date reconstruction of the lower jaw of *Morganucodon* (Fig. 9) based on new material. Included were interesting remarks about persistent bones of the primary lower jaw, as both the splenial as well as the coronoid could be detected in situ. Also small isolated bones were found, which PARRINGTON supposed to be the articular and quadrate. As a long thin splinter the splenial covered a good portion of the «internal groove». In the front, it reached as far as under the first or second molar, whereas in the back it ended just inside the sulcus. Probably PARRINGTON's splenial is identical to the bone fragment that KERMACK & MUSSETT (1958) interpreted, in their mandible, as prearticular or angular. The coronoid

lies above the sulcus on a flat bulge («coronoid boss») which was recessed to accommodate it. Its base is thin with an irregular outline, and forms a kidney-shaped swelling in the middle. PARRINGTON remarks about the small, isolated bones:

«Two specimen of what are probably the articulars and their associated bones have been found. These tiny fragments comprise the articulars, which form articulating condyles, together with the prearticulars and, possibly, the angulars and surangulars, but they are imperfectly preserved. No retroarticular process has been seen. I am indebted to Dr. J. A. Hopson, who is familiar with the postdentary of the tritylodonts, for his opinion of these difficult fragments. He informs me that 'the similarity is amazing considering the phylogenetic distance between the two'. A very small bone which lacks marked features may be the quadrate. It is a slightly tapered bone with the larger end forming a somewhat screw-shaped but cylindrical articulating con-
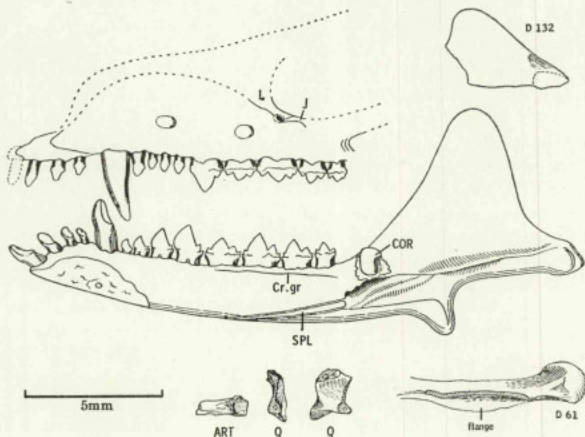

FIG. 9 — Reconstruction of the right lower jaw (medial view) and the left upper jaw (lateral view) of *Morganucodon* (from PARRINGTON 1971). Abbreviations: COR = coronoid, Cr. gr. = Crompton's groove, J = jugal, L = lacrimal, SPL = splenial. In addition are shown the apex of a Proc. coronoideus (medial view), a Proc. condylaris (dorsal view), an articular (dorsal view) and suspected quadrata (outer and frontal view).

dyle, separated from the thinner dorsal component by a slight neck. This bone has some resemblance to the quadrate of such a cynodont as *Thrinaxodon liorhinus* PARRINGTON 1946».

Thus, PARRINGTON acknowledged the assumption of KÜHNE (1958) and KERMACK & MUSSETT (1958) that *Morganucodon* possessed two jaw joints functioning of the same time.

The sulcus of *Morganucodon* is, except for the different proportions, very similar to that of *Haldanodon*. It differs however, in one important aspect. As in *Haldanodon*, here also the upper border is formed by the heavy ridge-like Crista pter. («medial ridge»), running posteriorly as far as the condyle. However, other than in *Haldanodon* and also *Docodon*, the ridge lies noticably higher on the Proc. coronoideus, and ends about half way up of the Caput mand. (illustration in PARRINGTON 1971). In this manner, the sulcus in *Morganucodon* is extended posteriorly as far as the caudal end of the condyle. Only so, is it possible that persistent bones of the primary lower jaw could fasten on the Crista pter. and the Proc. condylaris and that the articular could find a place next to the condyle of the dentary. Through the medial attachment on the Caput mand., as will be shortly seen is similarly the case in *Diarthrognathus*, the articular could fullfill a part of the function of the jaw articulation.

Whereas *Morganucodon* is known to be a mammal equipped with both jaw joints, *Diarthrognathus* (CROMPTON 1958, 1963) is a reptile, of about the same period, also possessing this characteristic. (The problem in definition, reptile — mammal, will be discussed later). *Diarthrognathus* is particularly important as many of the bones of the primary lower jaw are found in situ.

Here also a deep trough-like sulcus is present, stretching to the anterior, beyond the Foramen mand., and merging into an «internal groove». Above, similar to *Morganucodon*, the sulcus is bordered by a strong horizontal ridge, running as far as the condyle formed at the posterior end of the dentary. Thus the sulcus is here also extended far to the posterior. In the posterior part of the sulcus, connected only dorso-laterally with the dentary, lie the prearticular, the supraangular

and the angular as well as the articular. Whereas in *Oligokyphus* and the advanced cynodonts, these four bones are fused into one unity, in *Diarthrognathus* the articular is formed as an individual component, connected loosely caudal to the others. The posterior position of the articular nestles against the condyle of the dentary, building with it a funcional unit. Thereby, the dentary already possesses by far the larger portion of the articulary plane. Unique in comparison to all the therapsids and also *Morganucodon* is the fact that in *Diarthrognathus* the articular is connected with a convex surface to the concave surface of the quadrate. (Normally the articular has the concave surface and the quadrate the convex one). KERMACK (1967), on noticing this, did not exclude the possibility that CROMPTON (1963) had made a false interpretation. It is possible that CROMPTON's articular is in reality the quadrate, and that the real articular is fused in the prearticular - angular - supraangular - complex.

CROMPTON & JENKINS (1968) remarked in a footnote:

«It is, however, pertinent to state that recently discovered material has confirmed Kermack's (1967) observation that CROMPTON (1958, 1963) incorrectly identified the quadrate and the articular in *Diarthrognathus*».

There is, however, no further explanation on how the jaw joint of *Diarthrognathus* is actually constructed. Another criticism of CROMPTON's (1958) interpretation comes from FRICK & STRARCK (1963):

«Bordering the angular, which is connected in the rostral direction to the articular covering its posterior end to a slight degree ventrally, lies on the medio-dorsal periphery a small bone splinter, which CROMPTON termed a probable supraangular. As far as the somewhat rough scetch and short text allow a judgement at all, we consider this bone splinter a prearticular (gonial). In our opinion a supraangular would be expected laterally not medially to the angular. The bone piece bordering the

angular rostrally is certainly not a prearticular as CROMPTON termed it. In the text he discusses it also as a splenial; it could, however, also very well be considered as ossified Meckelian cartilage».

The possibility is not to be discarded, that the posterior end of the lower jaw of *Diarthrognathus* is more similar to corresponding conditions in other advanced therapsids and Upper Triassic mammals than CROMPTON had originally thought.

Diarthrognathus originated from the Upper Triassic — a time in which «real» mammals are known to have existed — and can be considered as member of a specialized side line of mammal-like reptiles. On the other hand, recently with *Probainognathus*, out of the Middle Triassic of South America, a cynodont therapsid was introduced also having a joint connection between the dentary and the squamosum (ROMER 1969). Whereas closely related forms possess only a reduced primary jaw joint between a rod-like connection from the angular, surangular, prearticular and caudal articular and a movable quadrate, in *Probainognathus* on the squamosum a depression is formed, that accommodated the enlarged posterior end of the dentary. In this manner, here for the first time a secondary jaw joint is formed and namely in a group of therapsids that, according to present knowledge, is the most probable forerunner of the mammals.

From the described characteristics of *Haldanodon* and the discussed literature the following can be concluded:

1) Bones of the primary lower jaw are present in the structure of *Haldanodon's* mandible. In the living animal, these were attached only syndesmoticly in the sulcus of the dentary and its surrounding area, which eased post-mortem detachment.

2) The coronoid was located as a thin bone scale on the rostro-ventral area of the Proc. coronoideus. The form and extent of the faceted area of attachment differ in the various individuals of *Haldanodon*. Besides by PARRINGTON (1971) for *Morganucodon*, the coronoid could be proved for

the Upper Triassic symmetrodont *Kueneotherium* by KERMACK & KERMACK & MUSSETT (1967) and in paurodonts and dryolestids from the Kimmeridgian by KREBS (1969). The area of attachment is found there in practically the same place.

3) The splenial lay as a thin triangular bone chip on the anterior part of the sulcus and covered the area medially in front and above the opening of the Foramen mand.. Outside the sulcus, the splenial ran with its small anterior portion on the «internal groove», thus building a short Canalis primordialis. From the insertion facet the rostral limit of the splenial is hard to perceive. The splenial can also be proved in dryolestids of the Kimmeridgian (KREBS 1971). The possession of a coronoid and a splenial as well as a persisting Meckelian cartilage was probably the normal case in Jurassic mammals (with exception of the multituberculates). At about the turn of the Jurassic-Triassic, these reptilian relics were then lost in triconodonts, symmetrodonts and pantotherians.

4) The angular, supraangular and prearticular were grown together, and lay as a functionless unit inside the sulcus, dorso-medially to the persistent Meckelian cartilage.

5) The caudal end of the Meckelian cartilage was ossified as an articular. The articular lay in the posterior part of the sulcus, far removed from the condyle of the dentary, and no longer had a function in articulation. Attachment to the condyle as in *Morganucodon* or *Diarthrognathus* was not possible, as in *Haldanodon* the sulcus ends because of the low lying Crista pter. already under the rostral end of the stem of the condyle.

6) The primary jaw articulation no longer functioned in *Haldanodon*. The corresponding bones were present, however, because of the enlargement and strengthening of the dentary-condyle, they had become unnecessary and thus degenerated.

7) The development of the middle ear in *Haldanodon* probably remained at the level of

Triassic mammals and advanced therapsids, as the bones of the primary lower jaw were not moved over in the sound-conveying apparatus.

A modification of the results 4) through 7) leaves the possibility open that *Haldanodon* did indeed possess a mammalian middle ear. In this case the articular, prearticular and angular would have to have been disconnected from the lower jaw in order to take over their new function. Only the supraangular would have remained as a functionless rudiment in the sulcus of the dentary. It is, however, improbable that the size of this bone alone was capable of filling the extensive lumen of the sulcus. Also, the sulcus would certainly — as in other Jurassic mammal groups — have disappeared as soon as its function, namely accommodating the accessory bones, had become superfluous.

4.2.3 Jaw musculature

A reconstruction of the jaw musculature of *Haldanodon* must remain hypothetical as the cranial skeleton is not yet known. However, an attempt will be made to form a picture of the muscle apparatus from the insertion marks on the mandible, as in this manner the pylogenetic relationships between Mesozoic mammals can be discerned. The following scetch (Fig. 10) was made from mandible VJ 1003-155, and supplemented with the other mandibles. Regrettably, the borders of the insertion areas are to a degree indistinctly preserved and can be more suggested than recognized through movement and reflection of the mandible under the binocular microscope. For this reason, the depicted form of the individual marks cannot be considered as fully conclusive. The assignment of the individual muscles to the insertion marks was accomplished with the help of literature on the anatomy of mammalian jaw musculature, and that of mammal-like reptiles, especially LUBOSCH (1938), SABAN (1968 and 1971), TURNBULL (1970) and BARGHUSEN (1968).

Before the jaw musculature of *Haldanodon* can be discussed, one must enter on the problem of the ventro-caudal mandible process in the

docodonts. Noticeable is the fixed position of the process far to the anterior. Compared with this, the Proc. angularis of the theria lies much further caudal, often even on the end of the mandible, ventral or ventro-caudal to the Caput mand., and is not pointed so strongly downward. Its function lies therein, that it serves exclusively the attachment of jaw-closing muscles. On its lateral side insert muscles of the masseter group, and on its medial side, above all, the M. pterygoideus internus. Processes, whose position corresponds to that of the docodonts, are found in some insectivores and carnivores. They serve only the attachment of the jaw-opening M. digastricus, and are relatively smaller and weaker. TOLDT (1905) gave them the name Processus marginis mandibulae.

A third type of ventro-caudal mandible process, that PATTERSON (1956) called the «echidna-angle», is developed in the Tachyglossidae (Monotremata). Here, fastened on the lateral side is the M. massetericus and on the medial side a part of the M. temporalis. The M. pter, int. is missing in the Monotremata. It is only present in the embryo stage and disappears later along with its innervation (SABAN 1971). The most interesting characteristic of the «echidna-angle» is, however, that its apex serves additionally the fastening of the jaw-opening M. detrahens mandibulae. This muscle is a speciality of Monotremata. which were not provided with the depressor muscle of the theria, the Venter caudalis of the M. digastricus. The ontogenetical development of the M. detrahens mandibulae was described thus by SABAN (1971): The muscle is a bundle of fibers separating from the outside of the embryonal M. levator mand. ext.. After the young animal acquired the secondary jaw joint, the muscle transfered its insertion surface from the posterior end of the Meckelian cartilage to the ventro-caudal edge of the dentary. In this way, it is changed from an adductor of the Meckelian cartilage to a depressor of the mandible. In the adult animal it begins on the squamosum *(Ornithorhynchus)* or the petrososqamosal suture *(Tachyglossus)*, runs around the condyle and inserts finally on the (in *Ornithorhynchus* only suggested) «echidna-angle».

It is remarkable that the Tachyglossidae as well as the, in life form and feeding habits, completely different specialised Ornithorhynchidae have these almost identical masticatory muscles, even though the rest of the anatomy is in many important aspects very different. The deviations, which are not only confined to the various adaptive characteristics but also include, for example, the brain structure, point to an early separation of the two monotreme groups (THENIUS 1969). The special jaw musculature and corresponding lower jaw must have been already present at this time, in other words before the withdrawal to vacant ecological niches. Thus, they are an early characteristic in the biogenesis of Monotremata.

The Proc. angularis and the Proc. marginis mandibulae in the theria and the «echidna-angle» in the monotremes are unequivalent structures, that cannot be homologized and show only slight functional analogies (KUHN 1971).

The discussion of the function of the ventro-caudal mandible process in the docodonts was opened by PATTERSON (1956). In the same work, he was the first to give conclusive evidence as to the special position of this mammal group. Before this SIMPSON (1929), who at this time still placed *Docodon* with the Pantotheria, homologized the ventro-caudal mandible process with the Proc. angularis and had an M. pterygoideus int. inserted on its medial surface. PATTERSON, in comparing the lower jaw of *Docodon* with those of the other mammals, came to a different opinion. He concluded that, by means of the anatomical characteristics of the Monotremata and the Theria, it was proven that in the mastigatory apparatus of mammals at least two different bone-muscle systems were developed during the change-over from reptile status and that the «echidna-angle» and the Proc. angularis had developed independently from one another. Nevertheless, the «echidna-angle» and the ventro-caudal process of *Docodon* show many morphological and functional similarities. The relatively large difference in size can be easily explained by the fact that *Docodon* possesses a functional heterodont set of teeth with correspondingly strong mastigatory muscles, whereas the Tachyglossidae take in their food with the tongue and by means of

horny ledges and points crush it between the tongue and palate.

As HOPSON & CROMPTON (1969) and above all recently KERMACK & KIELAN-JAWOROWSKA (1971) have proved, the docodonts are substantially more similar to the recent monotremes than the theria. The anatomical similarities, detectable in the structure of the skull, the brain and the teeth, point to the probability that also the mastigatory apparates of the two related groups were basically homologous in structure.

PIVETEAU (1961, p. 525) and, possibly based on this assumption, KUHN (1971, p. 167) write, that PATTERSON correlates the ventral-caudal mandible process of *Docodon* with the Proc. marg. mand. for the M. digastricus. This is a false interpretation of PATTERSON's text.

SIMPSON (1961) and PATTERSON & OLSON (1961) introduced at the same time the term «pseudangular process» for the ventro-caudal mandible process of *Docodon*, *Peraiocynodon*, *Morganucodon* and *Sinocodon*. According to PATTERSON & OLSON (1961), *Sinoconodon*, a primitive triconodont, possesses a «pseudangular process» on about the same place, although relatively smaller than does *Morganucodon* of approximately the same period.

According to PATTERSON & OLSON, insertion attachment markings of a strong depressor muscle can be seen on the process. They do not, however, give any evidence that on its lateral side adductor muscles inserted.

The most detailed criticism of PATTERSON's interpretation of the bone — muscle relationships on the lower jaw of the docodonts was published by PARRINGTON (1971). PARRINGTON's criticism is failing however, as he didn't use PATTERSON's (1956) complete text on page 75 and 76 in founding his argument. At this point the paragraph pertaining to the «pseudangular process» of the docodonts from PARRINGTON (1971, p. 233) shall be quoted and corrected sentence for sentence:

«He (PATTERSON) accepted *Eozostrodon* as a triconodont and *Morganucodon* as a docodont, but he put forward a new interpretation of the angular process in this form.» (PATTERSON advanced his theory based on

the lower jaw of the genus *Docodon*. The genus *Morganucodon* KÜHNE 1949, which he considered, however, as a pre-docodont or perhaps even a docodont, was known to him only from isolated molars. Only later (KERMACK 1958) were the lower jaws of both forms shown to be basically the same). «Because it is situated further forward than the similar processes in such forms as pantotheres, he suggests that it was not a true angular process but a «pseudangular» process for the attachment of depressor muscles, possibly the monotreme detrahens muscle». (PATTERSON did not view the «pseudangular process» of Docodon as merely the insertion attachment of a depressor muscle, but also considered a homology with the «echidna-angle» of the tachyglossidae as most probable, on whose side surface also adductor muscles insert). «But there are reasons for rejecting this interpretation. First, no mammals are known which have processes of at all comparable size for the attachment of jaw-opening muscles, the forms mentioned by PATTERSON *(Tachyglossus, Solenodon)* having structures which are trivial by comparisation.» (PATTERSON himself rejected a homology with the Proc. marg. mand. of *Solenodon* and *Melursus* as the insertion attachment for M. digastricus and mentioned also the relatively large difference in size. For the rather small size of the «echidna-angle» he gives a plausible explanation which has already been mentioned here). «Secondly, there is no satisfactory functional explanation available for this interpretation, since there would be no obvious mechanical advantage obtained by the provision of such a process». (Contrary to PARRINGTON's view there is a mechanical advantage, as in this manner the lever for the depressor muscles is lengthened, allowing them to be less strongly built). «On the contrary it is a common happening for adductor muscles (masseter, pterygoideus) to be provided with such an angular process for which a

sound mechanical explanation is available, a suitable process allowing the maximum biting force to be achieved when the teeth are about to be clenched rather than when the jaws were agape (PARRINGTON 1960)». (PARRINGTON's view can be followed here, as adductor muscles are fastened to the «pseudangular process» and the homologous «echidna-angle», thus attaining the described effect). «Moreover, a convincing mechanical explanation is available to account for the forward position of the process in very primitive mammals in that it tranfers the biting force on to the teeth and off the (weakened) articulation (CROMPTON 1963)». (The lower jaw of the docodonts is from a functional view difficult to compare with that of the advanced therapsids, to which CROMPTON (1963) referred. Even the two side by side functioning jaw joints of *Morganucodon* cannot be termed as weakened. In no way does this apply to *Haldanodon* and *Docodon*, both which have a very sturdy Proc. condylaris). «Furthermore, this interpretation is consistent with the other data, the retention of the double articulation in the Upper Jurassic docodonts (inferred by the presence of the large mandibular trough) requiring the retention of the forward position of the process, while evidence for the backward movement of the process elsewere is given by *Peramus*, a pantothere now sometimes held to be ancestral to the theria in general. Here the process is about intermediate between the anterior position and the normal posterior position and in this Upper Jurassic form the full mammalian jaw articulation appears to have been achieved». (*Haldanodon* and *Docodon* have no longer the double jaw articulation; they retain, however, their «pseudangular process» on the same site as *Morganucodon*. Also following PARRINGTON's logic, the tachyglossidae, whose lower jaw consists of only the dentary, should not have retained their «echidna-angle» lying in the far anterior position.

The relation of *Peramus* in respect to the later Theria is at least doubtful (CLEMENS & MILLS 1971). It is more likely that *Peramus*, which likens therian main line of development in its teeth structure, is part of an isolated and specialized collateral line. At any rate, its lower jaw is at about the same stage of development as that of the similarly aged paurodontids and dryolestids. That is to say, that the secondary jaw joint is fully developed, though however, a rudimentary coronoid and splenial were probably present. *Peramus* ist not at all comparable with the Docodonta, to which it has no near relationship)».

To repeat once again: PATTERSON is of the opinion that on the «pseudangular process« laterally an M. massetericus and medially an M. temporalis is inserted. In addition to this, fastened to the apex of the process is a jaw-opening muscle; probably the M. detrahens mandibulae of the Monotremata. Thus the process served, as distinguished from the Proc. angularis of the Theria, the fastening of jaw-opening as well as jaw-closing muscles.

This theory is not discredited through PARRINGTON's criticism. As the evidence found for *Haldanodon* also coinsides with PATTERSON's considerations, the term Proc. pseudangularis is also adopted for the ventro-caudal mandible process of this genus. In its functional effect on the adductor muscles fastened to it, the Proc. pseudangularis of the docodonts compares somewhat to the Proc. angularis of the Theria. For the operation of the angular process, PARRINGTON (1960) has given a plausible explanation. He starts out from the fact that the muscles fastened at the lower part of the mandible, as for example the M. massetericus, reach their point of maximum efficiency in that moment when the fibres are at a right angle to the length of the jaw. In forms that do not possess a ventro-caudal mandible process — in Mesozoic mammals theses are the triconodonts, multituberculates and the symmetrodonts—this is the case when the jaw is wide open. This favors a fast, snap-closing of the jaw or the grasping of large food pieces. Thus, for example,

the triconodonts, as their dentition shows, were definitely carnivorous and perhaps even piscivorous (SLAUGHTER 1969) and could seize their prey and kill with one fast bite. It was then not processed with the help of a carnassial dentition, as is with recent animals of prey, but cut in crude chunks and swallowed. The multituberculates, which fed on conifer seeds, fruit, etc. (SIMPSON 1927 b), had to free their food from stalks, seedhusks and cones, thus opening their mouths wide.

If a Proc. angularis or Proc. pseudangularis is present, then the thereon attached jaw-closing muscles are in the most effective position when the jaw is almost closed. The most strength is therefore given to the chewing processing of the food. This applies also to the pantotherians and the docodonts.

It is also important in a taxonomical sense if a mammalian lower jaw possesses a ventro-caudal process. Just as important is the type of muscles fastened to the process, if it be present, as thus familiar relationship between the individual groups can be ascertained. The muscles themselves can be identified from the position and size of the mandible processes, the anatomy of the skull and the thereon located insertion marks. However, so long as all of these mentioned characteristics are not completely known, postulations must be made with a more or lesser degree of uncertainty.

An interpretation of the insertion marks on the mandible of *Haldanodon* gives the following picture: The insertion surfaces for the adductor and detraction muscles lie on the three processes of the Ramus mand. On the Pars alveolaris are insertion marks for the musculature of the mouth floor and the cheeks.

On the outer and inner surfaces of the Proc. coronideus and the Proc. pseudangularis lie the insertions of the muscles of the masseter-temporal-complex (defined after SABAN 1968). These occupy each on both sides of the ramus three separate fields. By far the largest part of the area is taken by the insertion surface of the M. temporalis, which alone accounted for approximately half to two thirds of the bulk of the entire adduction musculature. Thus it was the most effective mastigatory muscle of *Haldanodon*. Because of

damages of the Proc. coronoideus, the entire extent of its insertion surface cannot be identified; it can, however, with relative certainty be reconstructed. The M. temporalis pars superfic. took in the upper portion of the lateral side of the Proc. coronoideus. The swollen anterior edge of the process served to fasten the muscle tendons.

The medial side the Proc. coronoideus was completely occupied by M. temporalis pars prof.. Noticeable here, located on the under the portion of the process is a somewhat triangular field in which a particular portion of the muscle engaged. The Proc. pseudangularis is on its lateral side concavely bent. Here was the point of attachment
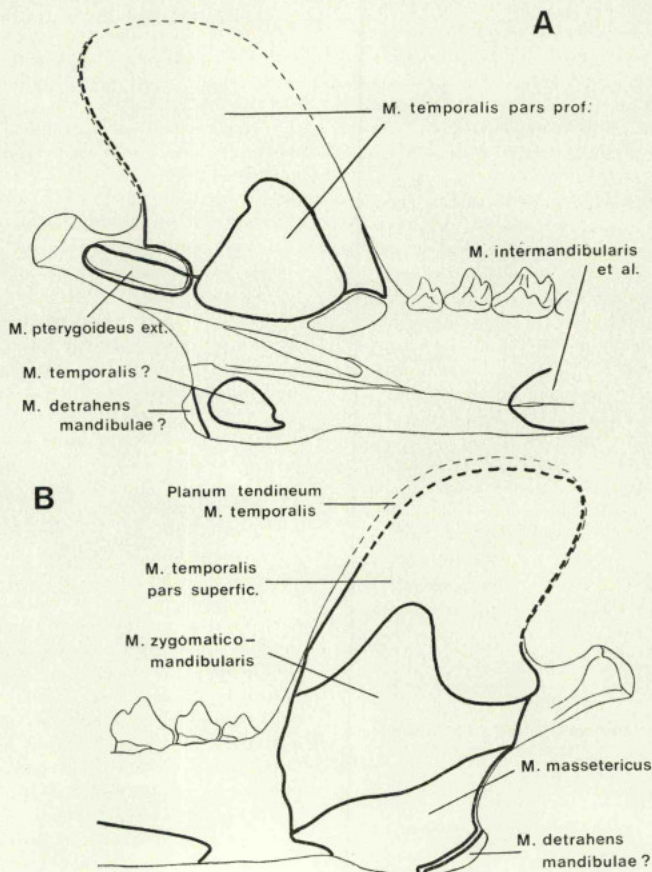
FIG. 10 — Reconstruction of the muscle insertions on the posterior part of the dentary of *Haldanodon*
A: Medial view.   B: Lateral view.

of an M. massetericus. A division into individual muscle layers cannot be detected on the bone. The swollen underedge of the process probably served the fastening of a tendon. The space between the insertion marks of the M. temporalis pars superfic. and the M. massetericus, namely the bulge-like swelling on the outer surface of the ramus and, connected to it, a slight upward indented depression, was occupied by a intermediary muscle. This was probably the M. zygomatico-mandibularis, also present in the Monotremata.

The inner side of the Proc. coronoideus is also furnished whith an insertion area, where probably a portion of the M. temporalis was fastened, thus acting as an antagonist of M. massetericus.

Above the Crista pterygoidea lies the mentioned groove, wherein, in the lower portion, the M. pterygoideus ext. inserts. As a Proc. angularis is missing in *Haldanodon*, the M. pterygoideus int. which would have inserted on it is also missing. Probably to compensate for this, the insertion surface of the existing pterygoid muscle is enlarged, so that the muscle could be more strongly built.

On the inner, outer and under sides of the Pars alveolaris lies a large insertion mark, beginning underneath the last molars and running as far as the symphysis. Here were fastened muscles and ligaments of the mouth floor and above all probably the M. intermandibularis, which was supplied and innerved from the «internal groove».

An analysis of the chewing process and feeding habits of *Haldanodon* is covered in a special chapter in connection with the tooth occlusion.

4.3 Comparative anatomy of the visceral skeleton

With the present material (VJ 1008-155 and VJ 1009-155), the anterior portion of the skull of *Haldanodon exspectatus* can be reconstructed from the front of the muzzle to as far as approximately the end of the tooth row. At first the individual elements will be discussed, in order to prepare from this a synthesis.

4.3.1 Maxilla

The flat, narrow form of the viscerocranium in *Haldanodon* is primarily determined by the maxillae. The corpus of these two bones is pictured as a massive flat plate, that builds the greater part of the side wall of the anterior part of the skull. The lateral surface (Facies facialis) stands at its lower part at first fairly vertical and curves then in the dorsal direction slightly to a contact with the nasal bone. The height of the bone is rather small; it protrudes only slightly over the root apex of C^x. In the frontal-caudal direction the maxilla is more curved, running namely around the canine strongly to the outside in order to finally pull in concavely above the anterior premolars. As with the lower jaw, the two tooth rows are not parallel, but increase the distance from one another in the caudal direction. The alveolar margin of the maxilla lies in its anterior portion lower than over the P^x and M^x.

The Proc. palatinus is not preserved. As far as is discernible from the incomplete material, it can be assumed from some bone rests folded down on the teeth that the palate was of a very thin substance. From the strongly squeezed state of the two jaw halves it can be assumed that they were perforated by many large palatal openings, as is the case, for example, in the recent long snouted insectivore *Elephantulus*.

Between the last precanine and the canine a deep pit is formed which served to take in the lower canine. Above this pit, about half the height of the maxilla is located a large foramen. Two further substantially smaller foramens lie under this, one behind the other. Above the P^1, however not at the same height, are two foramens of equivalent diameter. The outlet of the Canalis infraorbitale, the large Foramen infraorbitale, lies just above the P^3. The foramen opens diagonally to the anterior, as the canal continues in a dorsocaudal direction to the orbita. A further foramen, continuing in a canal running in the same direction, is located on a suture dividing the maxilla and a narrow dorsal bone (jugal or lacrimal, see below).

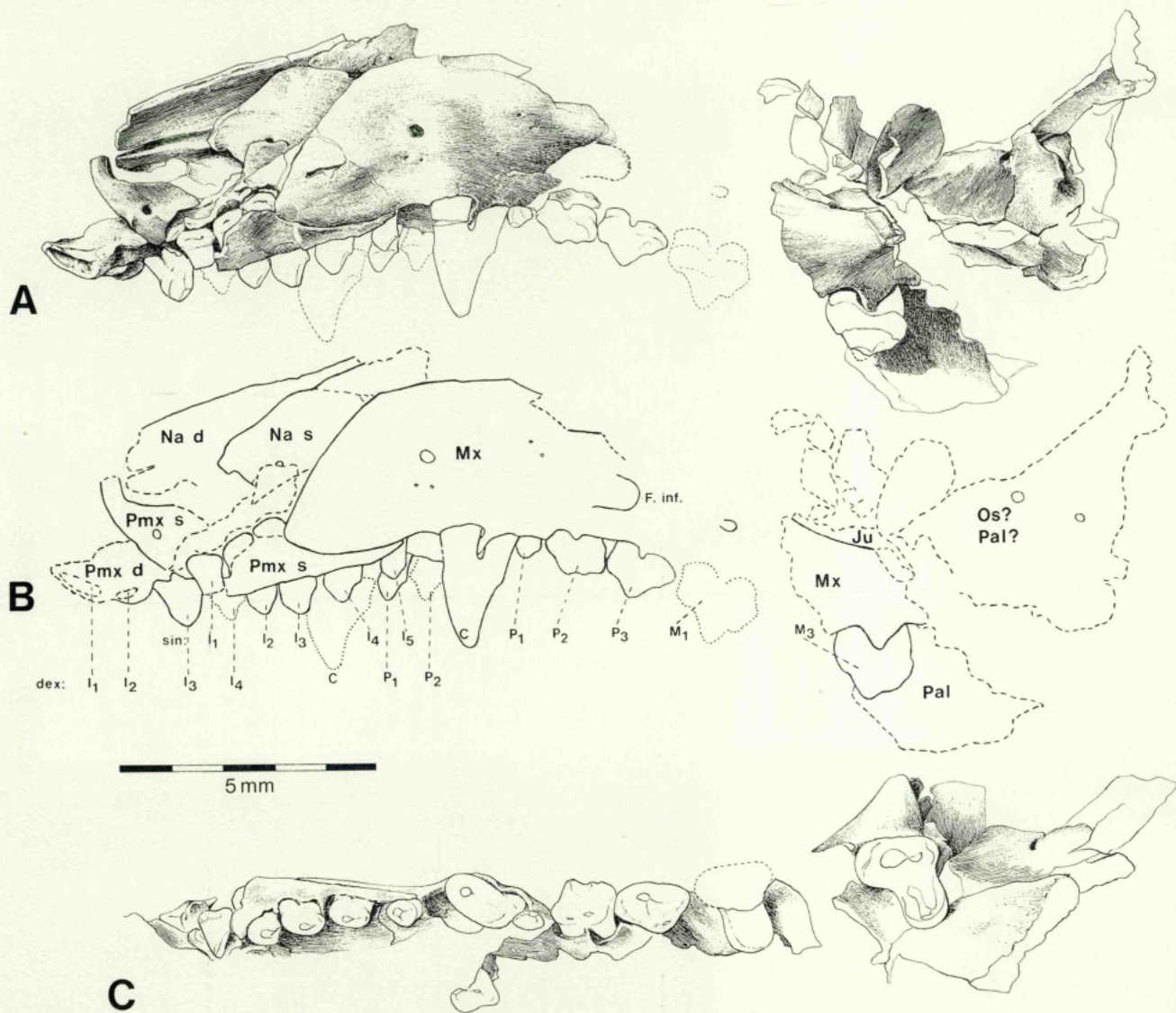Between the alveolar margin and the last mentioned suture runs horizontally a slightly

FIG. 11 — Anterior skull VJ 1009 - 155.
The drawing is a combination of fragments 1, 3 and 4.
A: Lateral view.
B: Location plan of the visceral bones and teeth. (Abbreviations: F. inf. = foramen infraorbi-
    tale, Ju = jugal, Mx = maxilla, Na d = right nasal bone, Na s = left nasal bone, Os =
    orbitosphenoid, Pal = palatinium, Pmx d = right premaxilla, Pmx s = left premaxilla,
    dex = right tooth row, sin = left tooth row). Bone sutures are represented by a solid line and
    fractures by a broken line.
C: Ventral view.

curved longish depression that extends in the caudal direction to a dead-end hole (Fig. 12). Here must have been the location of a gland with its principal mass lying in the gum and secreting into the mouth.

then empty into these. Bolk and Woerdemann termed these glands as Glandulae dentales. Besides these «tooth glands» occur regularly in the same animal other lip glands, emerging from individual epi-

5 mm

Fig. 12 — Anterior skull VJ 1009 - 155. Fragment 2.
Lateral view of the rigth premaxilla and maxilla.

The necessary data in understanding this gland are contained in an article on the glands of the mouth cavity by FAHRENHOLZ (1937). FAHRENHOLZ summarizes from works of various authors (p. 116-117):

«Many reptiles develop certain lip glands ontogenetically out of a continuous epithelial ledge emerging from the labial side of the tooth ledge or yet from the same area of the surface epithel as this and then connectes to it with a thickened epithelian strip. These glands open in their finished state always right next to the teeth and show, according to their number and position, fixed relationships to them. Besides the glands themselves, also out of the «gland ledge» can develop mucous membrane pockets for the individual teeth (tooth sheath) or, instead of these, a continuous mucous membrane groove next to the teeth («tooth furrow»). The glands

thelial buds, independent of the tooth ledge and lying labially from it, which, later showing no distinguishable relationship to the teeth, open to the region of the lip. Accordingly we divide the Glandulae labiales of the reptiles into those associated with the teeth (Glandulae dentales) and those which are independent of the teeth (Glandulae labiales propiae). In the mammals the gums are free from glands; i. e. the Glandulae dentales are not present. Bolk has shown, however, that in the mammals, man included, in connection with the tooth ridge, a «gland ridge» exists, also supporting small aborted gland buds. Only in a few lower mammals (Trichosurus, Talpa), do actually functional Glandulae dentales develop. Thereby, the absence of the tooth glands in the mammals is due to their secondary involution. What we find in mammals as glands in the vestibulum oris are «Glandulae labiales propriae».

The quoted statement shows the probability that the glands on the upper jaw of *Haldanodon* are a relict of the Glandulae dentales, belonging to the reptilian saliva apparatus. As the actual mammalian saliva glands were probably not yet sufficiently developed, they supported mastication through their secretions.

An alternative to this theory is the possibility that the groove on the maxilla stood in conjunction with the secretory passage of the parotoid gland. Developed from the Glandulae labialis propriae, the parotis, located next to the ear, sends out a long secretory passage, crossing over the masticatory muscles and opening near the molars or further forward. Accessory glandular lobes, the Glandulae parotis accessoria, connect on the secretory passage (FAHRENHOLZ 1937). The secretory passage and accessory glands, however, do not lie in the gum, rather in the cheek tissue and are hardly suited to leave impressions in the upper jaw bone.

The canal opening above the groove on the lateral side of the maxillary probably served to innervate the saliva gland with a branch of the N. alveolaris sup. (N. V_2).

Seen from the side, the line of connection between the maxilla and the premaxilla, the Sut. premaxillaris, runs in the form of a lying parabola, with its vertex pointing in the frontal direction. Dorsally the suture begins above the fourth incisor. Its turning point lies above the border between the second and third incisive. The alveolar margin reaches the suture next to the last precanine tooth. It turns around in a hairpin-curve and runs forward again on the labial side of the tooth and then veers off in the medial direction onto the palate. Through the opening between the next to the last and the last precanine and on the retained portion of the palate, the suture is visible as a curving zigzag line. Consequentially, as the last precanine tooth sits fully intact in the maxilla, this results in conclusions of a nomenclatural, systematical and phylogenetic nature, that will be handled at the beginning of the following chapter on the teeth.

The Proc. zygomaticus of the maxilla begins between the M^2 and M^3. The portion of the nasal cavity belonging to the maxilla is provided with many grooves, projections and pocket-like depressions running in a rostro-caudal direction, enlarging the surface of the overlying nasal mucous membrane and serving as an insertion attachment for the maxilloturbinal and its lamina.

4.3.2 Premaxilla

Seen from the side the premaxilla has an almost acute triangle-like form. The two long sides of the triangle are formed on one side by the alveolar margin and on the other side by the edge of the nasal opening and adjoining sutures with the septomaxilla and the nasal bone. The short side is formed by the deeply indented Sut. premaxillaria.

On the end of the muzzle the two teeth-carrying halves of the premaxilla are bound by a small, curved bone strut whose dorsal part is rounded, whereas the basal part, belonging to the palate, forms a broad plate. This plate, filling the wide space between both I^1s, served as the antagonist for the front lower incisives. At the beginning of the joint between the two premaxilla halves, located on the outer surface of the bone, on both sides, is a large foramen. Because of the extreme deformation of the material, the palate is not preserved, however, it must have consisted primarily of large Foramina incisiva.

The posterior margin of the large undivided nasal opening was probably formed from two septomaxillae, which are not preserved. Their original presence can be derived from the hourglass form of the nasal opening, whose lateral margin at the half-way point bends in medially and dorsally. At the same time, above this narrowing of the lumen of the nares, the pattern of the up to now rounded margin changes to a sharp edge, showing that here a bone or cartilage adjoined. According to our knowledge of higher therapsides and Triassic mammals, this could only be the septomaxilla. This bone is generally widespread among the reptiles, however, in recent mammal groups, it is found only in the Monotremata. Both septomaxillae of *Haldanodon* must have had a somewhat half-moon form and also have adjoined caudally to the nasal bones.

In the caudal direction the premaxilla is over-lapped by the corpus of the maxilla. The over-lapping is so large that also the entire region of I^4's root lies in the premaxilla. The side of the viscerocranium is thus at this point double walled and formed from both the maxilla and the pre-maxilla. The overlapped area must have been of about the same extent as was proved by PAR-RINGTON (1971) for *Morganucodon*.

4.3.3 Nasal

The two nasal bones connect at about a right angle to the maxillae and the premaxillae, thus building the roof of the anterior skull. The nasal bones are two strong slightly curved bone plates, which are bordered to one another medially with a common suture. The lateral suture runs, in its anterior part, about parallel to the medial suture, swings out above the premolars in a ventro-lateral direction and adjoins finally above the molars alongside the anterior part of the jugal. As this is narrow and tongue-shaped, the nasal experiences, in its posterior portion, a substantial widening, which is about the width of the skull at this point. The caudal border of the nasals to the frontal bone is not known.

Above the nasal opening the nasal forms a straight edge, possessing medially an angular projection. At the beginning of this projection ends a groove, running along the ventral side of the bone. Close behind the anterior edge of the nasal is located a foramen merging into a cau-dally directed canal. As KIELAN-JAWOROWSKA (1971) reported, nasal foramina are very unusual in mammals and are known only in multituber-culates. However, they occur often in theriodonts. In recent lizards similar foramina carry branches of the lateral N. ethmoidalis ant., serving skin thickenings which are amply provided with nerves and vessels, that surround the cartilaginous nasal capsule (OELRICH 1956).

KIELAN-JAWOROWSKA supposed also that the foramina in the nasal of the multituberculates held parts of the N. ethnoidalis and not, as SIMPSON (1937) believed, bloodvessels. The opinion of KIELAN-JAWOROWSKA can also be applied to *Haldanodon*, where the foramina probably served the inervation of a short trunk-like muzzle.

4.3.4 Jugal

The jugal is certainly located on the anterior part of the left zygomatic arch (Fig. 11), where it was still covered ventro-laterally by the Proc. zygomaticus of the maxilla. A cross-fracture through the left zygomatic arch at the heighth of the posterior root of M^3 shows that the Proc. zygomaticus of the maxilla lies shell-like in a half circle around the jugal (Fig. 13). In this region the jugal had already taken over most of the mechanical function of the zygomatic arch.

4.3.5 Unidentified bones

In specimen V J 1009-155 several damaged bone-rests of the posterior left side of the skull are present that could not be further identified

2mm
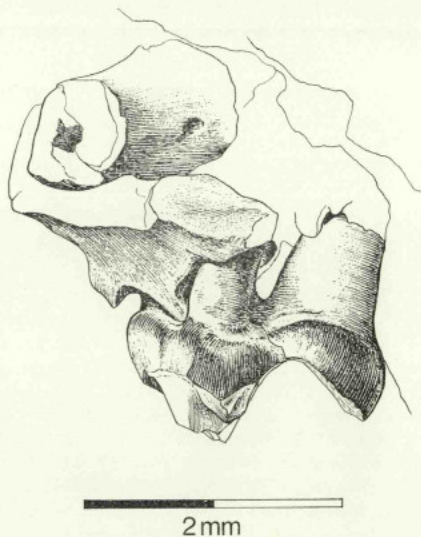
FIG. 13 — Anterior part of skull VJ 1009 - 155.
Fragment 4. Caudal view of the left jugal and the left maxilla with M^3.

as they do not have any recognizable sutures (Fig. 11). The most important of these bones is a plate that must have originally lain in the orbit or caudally from it in the Fossa temporalis. Noticeable are numerous impressions on the surface and two foramina on the upper part of the bone. The fragment in question was probably a part of the palatine (and) or the orbitosphenoid.

In the posterior portion of VJ 1009-155, fragment 2, located in situ is the anterior part of a thin bone cutting in tongue-like between the maxilla, which is situated in a ventral and frontal direction from it and a dorsally located bone rest (probably a piece of the posterior right nasal) (Fig. 12). On its suture to the maxilla lies the above mentioned foramen, out of wich the underlying saliva gland was innerved. PARRINGTON (1971) figured from his material of *Morganucodon* a skull fragment (p. 252; Fig. 6h), showing almost complete morphological conformity to the coinciding part of *Haldanodon*. A dorsally adjoining bone, because of the fragmentary character of the remains, cannot be verified here. PARRINGTON identified the bone in question as lacrimal on grounds of the following indications: He believed

1) to recognize the lower margin of the orbit in the dorso-caudal direction and

2) in the caudal direction, adjoining the foramen, the anterior end of the jugal, and finally

3) to be able to identify the foramen itself as «lacrimal foramen»; in other words as the opening of the Canalis naso-lacrimalis.

The first two claims cannot be argued, since from the schematic drawing it is not determined whether we are actually dealing with the orbital margin and the Sut. zygomatico-maxillaris or only fracture lines. The designation of the foramen, however, gives reason for doubt. As can be seen in the illustration, like in *Haldanodon*, the adjoining canal runs in a dorso-caudal direction, thus diagonally to the upper posterior. However, in order to serve its function, i. e. to divert fluids from the region of the orbit into the nasal cavity, a tear duct must run in a ventro-frontal direction, or diagonally to the lower anterior.

The problem remains, if 1) PARRINGTON's identification of the bone of *Morganucodon* as lacrimal is correct and if it 2) can be applied to *Haldanodon*?

The answer to these questions can be given only after the presentation of more complete material of *Morganucodon*, *Haldanodon* or other docodonts, so that, for the present, it must remain open. Still the possibility cannot be discarded, that the bone in question, at least in *Haldanodon*, is the anterior end of the jugal, and that the lacrimal and the orbit are located further in the dorso-caudal direction. The complete lack of evidence of the orbital opening, which should be seen in the area of the preserved bone in the artificial matrix backs up this view. A part of the palate (belonging either to the maxilla or to the palatine) is folded down behind the M³.

In summarizing it must be noted that, as it was the case with the lower jaw, also here the described part of the skull of *Haldanodon* is amazingly similar to the results that PARRINGTON (1971) published about *Morganucodon*. The form and location of the sutures are practically identical. The slight difference in proportions can be attributed to the differences in the dental formulas. Differing from *Haldanodon*, *Morganucodon* possesses two infraorbital foramina. The number of such foramina seems, however, to be variable and thus does not carry much weight. For example, a skull of *Didelphis*, in the Institute for Paleontology of the Berlin Free University, has on one side one and on the other side two infraorbital foramina. Because of the somewhat more complete *Haldanodon* material, the reconstruction by PARRINGTON should be slightly changed (Fig. 9). It is unlikely that the maxilla and nasal of *Morganucodon* have the steep dome that PARRINGTON suggests in his drawing. Also the position of the I¹ should be corrected, as it would be difficult in this position for the tooth to find a hold in the jaw.

From the described elements a mammalian skull joins together whose proportions still give a definite reptilian impression. Above all, this is due to the low maxillae and the broad nasal bones. The slight curve of these bones give also an angular, box-shaped cross-section to the anterior skull.

The form of the premaxilla and the anterior part of the nasales makes it seem probable that *Haldanodon* possessed a short trunk-like muzzle, similar to that of many recent insectivores. An indication of this is that the end of the snout was well supplied with nerves through the many foramina. Also the broad diastema between the two I^1s supports this assumption. Consequentially the primary sense organs of *Haldanodon* would have been the sense of smell and the tactile hairs at the end of the muzzle. A good sense of smell is also verified by the wide lumen of the nasal passage and the large surface of its inner walls. Unfortunately, because of a missing cranial skeleton, the expected large Bulbi olfactorii cannot be proven.

Reptile-like are also the probable occurence of septomaxillaria and of incisiviform teeth and Glandulae dentales in the maxillae. Up to now the only Mesozoic mammal in which the delicate and difficult to fossilize septomaxillaria could be proven is *Sinoconodon* (PATTERSON & OLSON 1961). PARRINGTON (1971) thought that for *Morganucodon* the presence of septomaxillaria was possible, however, could not prove it from his material.

4.4 Comparative anatomy of the dentition

In contrast to most of the reptiles, the majority of mammals have a heterodont dentition, whereby the teeth perform different functions to which they are adopted in form. The nomenclatural categorization of the teeth in incisors, canines, premolars and molars has been adopted from recent zoology and conforms to the tooth replacement and additionally the position in the upper jaw. Otherwise than the molars the incisors, canines, and premolars are replaced. The incisors of the upper jaw lie in the premaxilla, the other teeth in the maxilla. The development of these characteristics had already started in the forerunners of the mammals, the therapsides.

As is often the case with fossil and hence incomplete material, recent zoological nomenclature is also here only applicable to a degree. It is not possible to prove or with certainty to exclude the tooth replacement for all the existing teeth. In

addition there is a tooth present in the upper jaw showing the form and function of an incisive which, however, is situated completely in the maxilla. Theoretically this tooth should be termed the canine and the following actual canine a premolar. Also because of lacking evidence for tooth replacement, it would be correct after the accepted nomenclature to propose a categorization in incisivi- to molariform teeth. For practical reasons this alternative is dispensed with, and the teeth are termed solely as to their form and function as incisors, canines, premolars and molars. This method of nomenclature has already been intentionally used by various students of fossil mammals (e. g. MILLS 1971).

In identifying the orientation here, as has already been for a while generally accepted, are used the terms labial or respectively buccal for the outer side and lingual for the inner side of the tooth, as well as the terms mesial and distal. This terminology, derived from dental medicine, denotes the front and rear of the tooth in relation to its neighbour, i. e. the whole tooth row, as this does not run straight but instead describes a curve. The terms mesial and distal are, for this reason, not to be compared with the earlier used terms anterior and posterior, which orient with the longitudinal axis of the body. In contrast to PARRINGTON's (1971) view, the «new» terminology is not to be regarded as «gobbledegook» but allows an exact and correct orientation.

4.4.1 Incisors

Of the lower incisors only the two posterior ones in specimen VJ 1001-155 are preserved (Fig. 14). The form of the mandible shows, however, that originally at least two further incisors were present in each jaw half. Both teeth are single-rooted and possess a cusp surrounded by a half-circle-shaped cingulum in the mesial, lingual and distal directions. The cusp and the lingual adjoining low ridge show wear. The, in cross-section, oval roots taper slightly to their ends and show no vertical groove. The two I_x lie rather low and point to the outside. The missing anterior I_x must have lain lower and pointed more
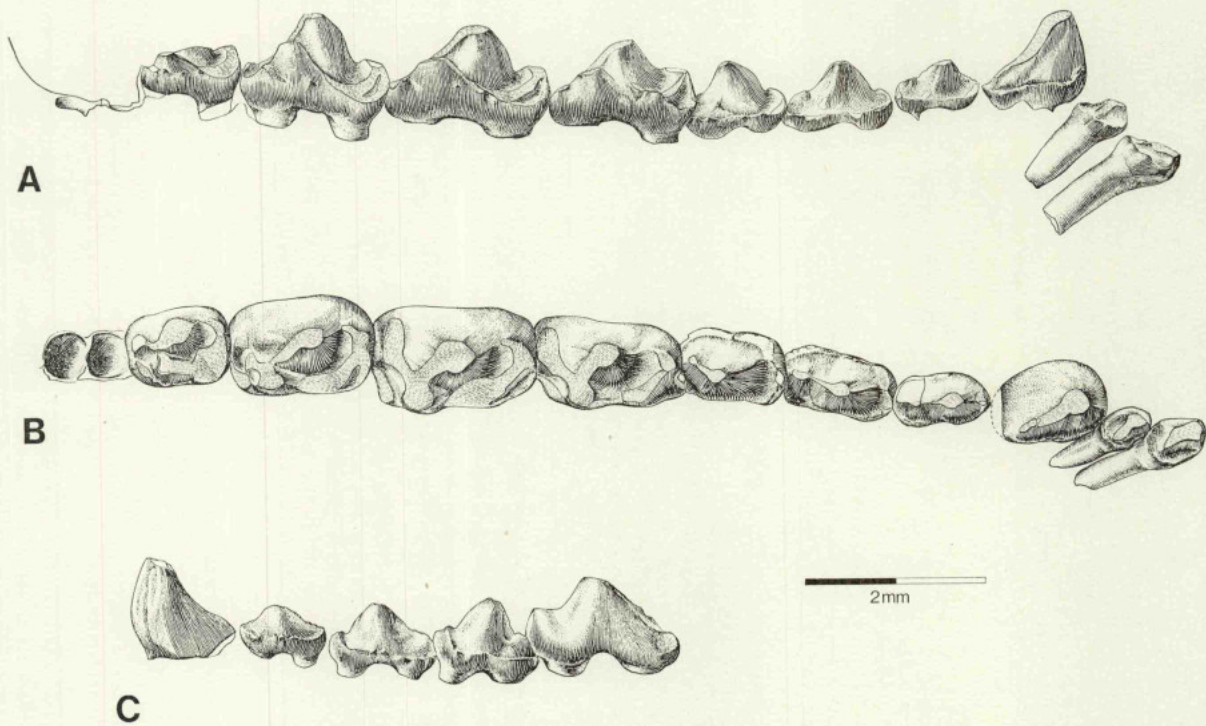
FIG. 14 — Dentition of the left lower jaw   VJ 1001 - 155 (holotype).
A: Lingual view.   B: Occlusal view.   C: Buccal view of C, P_1, P_2, P_3, and M_1.

to the rostral direction. The next to the last I_x is larger than the following one. Between the incisors and the canine are gaps, so that the teeth do not touch one another.

A complete row of upper incisors is present in the anterior skull VJ 1009-155 (Fig. 15). Here each jaw half has five precanines, of which the posterior four have the same basic form. (The I^1 is broken off below the root and thus does not allow a comparison). Their form differs somewhat from that of the lower incisors. The single-rooted teeth possess a main cusp, from which, both in the mesial and distal directions, goes out a slight crest. The posterior crest merges into a small accessory cusp. A further crest runs from the main cusp in the lingual direction. Between this

crest and the accessory cusp, an internal cingulum seems hinted. The sturdy roots have a swollen blunt apex. In the three middle incisors present, on both the labial and lingual sides, is a vertical groove on the root.

The teeth sit perpendicular in the jaw and do not touch one another. Particularly pronounced is the gap between the fourth and the fifth incisor. Between the first two incisors of each jaw half seems to be located a broad diastema. In order to anchor the tooth in the jaw, the short root of the I^1 is a its apex particularly thick.

The incisors of *Haldanodon* differ in their form from the spatula-shaped incisors of the same aged pantotheria, and are very similar to those that MILLS (1971) described for *Morganucodon*.
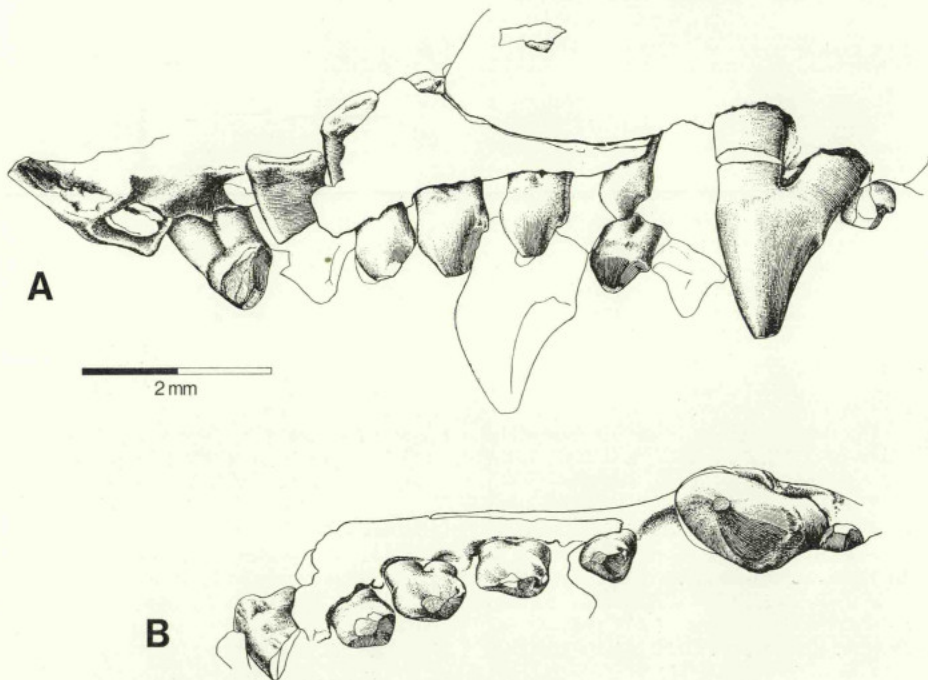
FIG. 15 — Front teeth of the anterior skull VJ 1009-155.
Fragment 1
A: Labial view of the left tooth row and lingual view of the right tooth row.
B: Occlusal view of the left tooth row.

In this form MILLS recognized also the alveola of a precanine tooth located on the maxilla, that he believed was functionally an incisor. PARRINGTON (1971) was able to show on the same spot a small tooth, however, because of the poor condition of his specimen, he could not identify the premaxillar suture. The form of the tooth was, unfortunately, not described. The two mammalian genera, although separated by a full stratigraphical system, have retained characteristics known in therapsids, such as *Phtinosuchus*, *Doliosaurus*, *Thrinaxodon* and *Cynognathus* (ROMER 1961). The retention of this reptilian characteristic for such a long period of time is a further indication of *Haldanodon's* slight evolutionary development above its Upper Triassic ancestors.

4.4.2 Canines

Canines preserved in situ are also known in the two incisivecarrying specimens. In VJ 1008-155, besides a last incisor, also a canine is present. Both teeth are, because of their bad condition, not mentioned in the description. The lower canine in *Haldanodon* is an enlarged replica of the posterior incisors. The cusp reaches approximately the height of the main cusp of the molars and changes linguo-distally into a blunt ridge. The cusp and ridge are especially worn down by the masticatory process. Linguo-distally the cingulum is only weakly present; it is, however, in the linguo-mesial direction strongly developed. The canine has two roots lying close together.

Also the upper canine follows the form of the incisors (Fig. 16). On a whole, it is more slender and taller than its antagonist. Two ridges go out from the cusp distally and lingually, between which runs a cingulum. Distally is formed a small shelf-like accessory cusp. The two long sturdy roots diverge at an angle of 30°.

In the form of the crown, the canines of *Haldanodon* are similar to those of *Morganucodon* and *Docodon*. However, the canines of *Morganucodon* are each equipped with only one very long root (MILLS 1971), in this way differing from the double-rooted dog teeth of the two Upper Jurassic forms.

4.4.3 Premolars

Haldanodon possesses three premolars on each jaw half. The size of the teeth, in the upper as well as the lower jaw, increases successively from front to back. In the same manner, the premolars

2mm
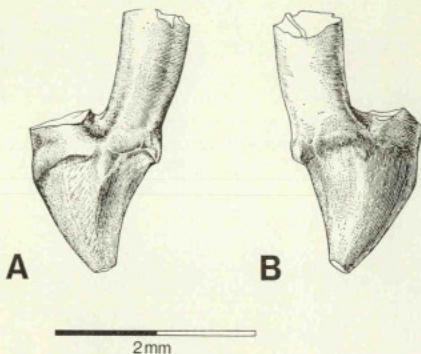
FIG. 16 — The right canine of the anterior skull VJ 1009-155.
A: Lingual view.
B: Labial view.

are increasingly molar-shaped. A complete row of premolars in situ is found in specimens VJ 1001-155 and VJ 1002-155. The premolars in both examples differ mainly in that the second form does not have an external cingulum. However, in spite of the differing sizes and proportions, in the rest of their form the lower premolars have the same basic construction.

Seen from the occusal view, the basic form of the tooth crown is that of a more or less extended oval, whose lingual and labial sides run parallel or are even concavely pulled in. The teeth possess a main cusp which is flattened to the sides and curves in the distal direction. In the mesial and distal directions, the main cusp developes into a sharp ridge. The distal ridge ends in a secondary cusp. Lingually another very weak ridge runs out from the main cusp on whose base in VJ 1001-155 a very small bud is developed. The tooth crown is surrounded by a cingulum which is particularly broad on the mesial and distal sides, forming there two small rises that are in line with both

cusps. The mesial part of these rises can in the premolars of the first form be so strongly developed that it exceeds the distal accessory cusp in size. In the second form (= A-form?, VJ 1002-155) the cingulum is, on a whole, more weakly developed and is missing completely on the outside of the main cusp. This form corresponds with the lower premolars of *Morganucodon, Borealestes* and *Docodon*, which are also lacking an external cingulum. On a whole, the premolars of the second form seem to be in proportion to their length higher and steeper.

The two roots of the lower premolars in *Haldanodon* sit quite close to one another and have a practically round cross-section. The teeth imbricate strongly, so that on the mesial and distal surfaces are signs of wear caused by pressure.

The tendency to increasing molarisation is even more extreme in the upper premolars. The first premolar, sitting close to the canine, has two roots of the same size and only one cusp, from which in the mesial and distal directions run two distinct crests and in the lingual direction a weak one. On the mesial, distal and lingual sides, the tooth crown is enveloped by a cingulum, which forms distally a shelf-like rise. The second premolar has on its distal crest an accessory cusp. It is surrounded by a cingulum having a rise on both the mesial and distal sides. In the distal portion of the lingual side the cingulum becomes broader. The anterior root is round in its cross-section, whereas the posterior root has an oval cross-section which diverges with the longitudinal axis. In this manner also the broader part of the lingual cingulum is supported. Finally, the third premolar likewise possesses a main and an accessory cusp and is enveloped by a cingulum with mesial and distal rises. In addition, the distal part of the lingual side of the tooth is strongly protruding. The protrusion has developed out of the cingulum and has a accessory cusp in anticipation of the cusp «X» of the upper molars. The posterior root is often divided so that three roots can be present, of which the anterior one is the largest. The third of the roots, which have a round cross-section, supports the lingual protrusion.

In comparison with related forms, a great similarity of the lower premolars with the three

preserved in *Borealestes* is noticeable (WALDMAN & SAVAGE 1972). The four lower premolars in *Docodon* are all double-rooted. In addition, P_3 and P_4 possess here an anterior accessory cusp. Noticeable is the condition of the P_2, which is much smaller and more primitive than in its predecessor (SIMPSON 1929). The upper premolars of *Docodon* became also increasingly molariform. SIMPSON (1929) writes:

«This genus is the only one known from the Jurassic in which there is really any close comparison between the last upper premolar and the first molar. P^3 has all the elements of M^1 and they are arranged in the same way. Nevertheless there is a definite break between the two series. P^3 is much smaller than M^1, its external cusps are whithout furrows, its internal cusps relatively smaller, the anterior basin less developed, etc. It is, however, unique among Jurassic mammals in that it is patently becoming molariform and that its parts are severally homologous with those of the molars».

The P_1 of *Haldanodon* differs with that of *Docodon* in that it is single-rooted, however, it already possesses a lingual protrusion with a small cusp. By the double-rooted P^2 and P^3 a posterior accessory cusp is developed, by P^3 also two cusps on the lingual protrusion. None of the upper premolars of *Docodon* possess an external cingulum.

The premolars of *Morganucodon* differ above all in their form, and accordingly in their function, from those of the Jurassic docodonts. With exception of the last, the four to five lower premolars have approximately the same form and increase in size only from front to back. They possess a strongly backward curved main cusp with a distal crest as well as a lingual cingulum that builds distally a shelf. In the mesial direction the round swollen anterior part reaches far over the front one of the usually two roots. The last premolar is relatively larger that its predecessor. Its main cusp reaches or perhaps even exceeds the height of the canine. Mesial and distal crests,
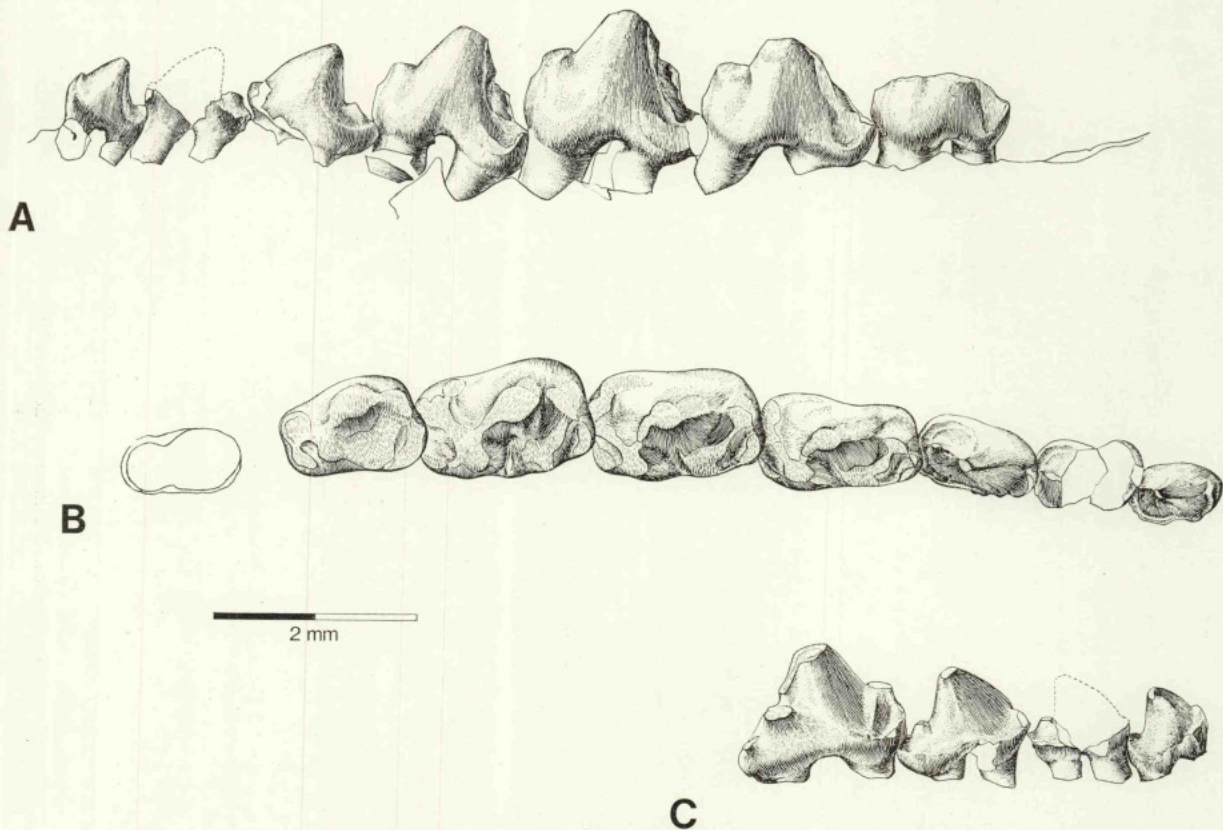
FIG. 17 — Dentition of the left lower jaw VJ 1002 - 155.
A: Buccal view.   B: Occlusal view.   C: Lingual view of P_1, P_2, P_3 and M_1.

running out from the main cusp, end in small cusps. The lingual cingulum is well developed and carries several buds which correspond with those of the lower molars. The double-rooted upper premolars possess a blunt main cusp merging mesially and distally into crests on whose ends small cusps are formed. The mesial cusp may be absent in the most anterior of the up to five upper premolars. A very weak lingual cingulum is more marked in the posterior teeth. The posterior premolar is very large; it is a long as the largest molar and higher.

The anterior premolars of *Morganucodon* show no wear and do not seem to have come into occlusion. Both of the last large premolars of each jaw half form according to PARRINGTON (1971) a «carnassial». It is interesting that the premolars and molars were in the course of the ontogenesis partially discarded without replacement, whereby their alveoles were filled with bony substance. (The data on the premolars of *Morganucodon* were taken from the works of MILLS 1971 and PARRINGTON 1971).

4.4.4 Lower molars

SIMPSON (1929) wrote about the molars of *Docodon:*

«Their molars are much the most complicated dental structures known from the Jurassic or, indeed, with the possible exception of some of the Cretaceous multituberculates, from the entire Mesocoic».

Somewhat softened, this statement is true also for *Haldanodon* and the rest of the Jurassic docodonts. The construction of the molars in all these specimens is about the same, whereby the genus *Docodon*, being the youngest known form, shows a somewhat more complicated arrangement through additional enamel crenelations and buds. Other differences are found only in the differing proportions and dissimilar arrangement of the crests joining the cusps. The derivation of the Upper Jurassic docodont molars from ones such as are found in the Upper Triassic morganucodonts, which following the encouragement of P. M. Butler, KÜHNE (1950) and PATTERSON (1956) already had postulated, can be considered through the work of CROMPTON & JENKINS (1968), JENKINS (1969) and HOPSON & CROMPTON (1969), as being definitively proven. Thus the terminology introduced by CROMPTON & JENKINS (1968) in refering to the cusps and wear surfaces is used here (s. Fig. 18).

From the occlusal view the five lower molars of *Haldanodon* have the form of a rounded rectangle that, particularly by the anterior M_x, can be broader distally than mesially. The teeth are equipped whith two rows of cusps running in a mesio-distal direction, between which lies a longitudinal valley crossed by several crests. The buccal row is dominated by the main cusp «a», taking in the middle third of the tooth's outer side. The cusp is rounded buccally and is provided on the inner side with up to five crests. In the mesial direction from this is a strong accessory cusp «b» having a similar form as the main cusp, being howe-
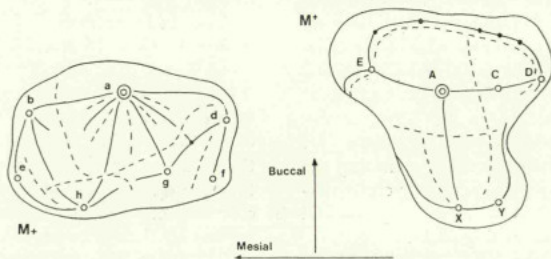
FIG. 18 — Nomenclature of the cusps of the lower and upper molars of *Haldanodon*.

ver, only a third of its size. The two cusps are joined by an indented crest. Two further small accessory cusps of the inner row can be infered from the internal cingulum of the morganucodonts. The largest of these cusps, «g», lies about lingual to the main cusp «a», and is connected with it by a grooved crest. The size of cusp «g» is about the same as the anterior accessory cusp «b». It is often situated further in to the tooth middle as the neighbouring cingulum cusps. Anglo-American authors sometimes refer to the cusp as the «kuehnecone» as it can be traced to a prominent hump on the cingulum of *Morganucodon*, which was first described by KÜHNE(1950). Two further small cusps are connected with the cusp «g» by grooved crests. These are the cusp «f», lying linguo-distally from the cusp «g», and the cusp «d», at the distal end of the molar. Cusps «f» and «d» are connected together by a crest continuing beyond cusp «d», thus forming a broad cingulum running around the distal part of the tooth. Often a crest runs down out of the distal flank of the main cusp «a», joining the crest between the cusps «g» and «d» at the start of its lower third. At the junction emerges a sharp bud. Another bud is often found where the mesial cingulum joins the buccal flank of the main cusp «a». In the mesial part of the lower molars are also found two small cusps, joined to one another and to the accessory cusp «b» by a grooved crest. Thus they form a small cingulum, similar to the one between the cusps «f» and «d». The mesial cusp «e» is often only very slightly developed. The cusp «h», lying further lingually, can in fact be quite larger, however, is often only present in the form of several small buds lying together. Additional buds can also be built on the lingual base of cusp «g» (i. e. in VJ 1001-155) and on the edge of the distal cingulum. Between the cusps «h» and «g» a joining crest is not present. Here a broad depression opens in which the valleys between the cusps «a», «b», «h» and «g» join facing outward on the lingual side. Other than the mentioned crests connecting the cusps, there are also several accessory crests running down the lingual flanks of the cusps «a» and «b» forming additional cutting edges.

Seen as a whole, the front two thirds of the lower molars of *Haldanodon*, with the cusps «a», «b» and «g», are faintly similar to the trigonid of the pantotheria, whereas the posterior third takes the role somewhat of the talonid.

All of the lower molars are double-rooted. The roots, sitting one behind the other, have an angular oval cross-section (with the long axis of the oval perpendicular to the long axis of the molar) and tapering slightly in the direction of their apex. On the sides of the roots facing one another, runs vertically a groove. Close underneath the crown the roots are completely encircled by a furrow. The thus caused weakening probably is also the reason why isolated molars generally do not have roots.

Within the tooth row of a single individual of *Haldanodon* variations are present effecting the size and form of the individual molars. The largest of the lower molars is generally the M_2, followed closely by M_3 and M_1. M_4 and M_5 are considerably smaller, whereby the latter can only be estimated from the size of its alveola. Of the isolated teeth two M_x are present, which, assuming their size and form, are probably ultimi, i. e. M_5. The crowns of these molars are short and squat and very rounded. The curved roots are joined together, yet have separate root channels.

The anterior molars are in relation to their length relatively narrow and give a more elongated appearance than the posterior ones which are more compact. The form of the anterior M_x is anticipated by the milk molars, which are, however, in relation to their length somewhat more narrow. The degree of imbrication between the individual molars is very high, so that at the mesial and distal points of contact there is wear caused by pressure.

The six lower molars of Borealestes are very similar to those of *Haldanodon*. Thus the very broad genus diagnosis of WALDMAN & SAVAGE (1972) is also true for *Haldanodon*, even though we are definitely dealing with two different genera. Other than the fact that *Borealestes* has an additional molar, the most obvious difference is that the cusp «g» is in this form much larger than the cusp «b». On a whole the lower molars of *Borealestes* are smaller than those of *Haldanodon*.

The molars of *Docodon* could be compared with the help of excellent models which W. G. Kühne
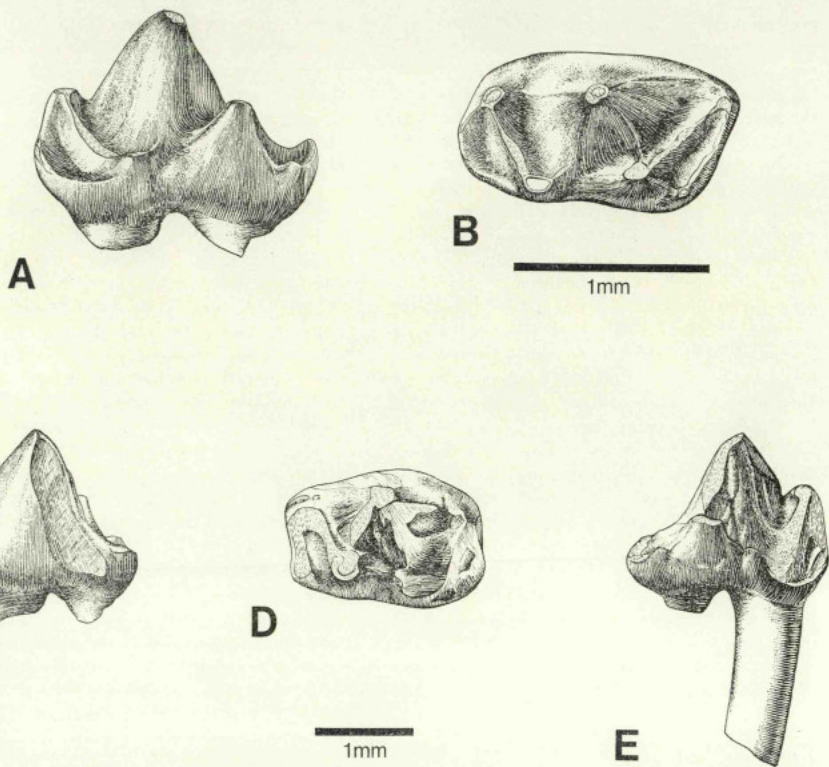
FIG. 19 — M$_1$ of the right lower jaw VJ 1005 - 155.
    A: Lingual view.
    B: Occlusal view.

— M$_{3?}$ of the left lower jaw 1003 - 155.
    C: Buccal view.
    D: Occlusal view
    E: Lingual view.

recieved from F. A. Jenkins and kindly made available. *Docodon* possesses as many as eight lower molars, which occlusally seen have the basic form a rectangle with rounded edges and almost parallel sides. It is noticeable at first that the posterior part of the tooth distally from the main cusp «a» takes in about half of the entire length, whereas in *Haldanodon* it takes in only a third of the length. Along with this enlargement of the posterior section of the tooth, a basin is developed within it, opening in the distal direction.

This is formed mesially by the main cusp «a», lingually by cusp «d» and «f» as well as buccally by cusp «d» and the crests joining them. A connection of crests from cusp «g» and cusp «f» to cusp «d» is no longer present, or is only very weakly suggested. Contrastingly, ridges between the cups «g» and «f» and the cusps «a» and «d», which

are only very weakly present in *Haldanodon*, are well defined in *Docodon*. The linguo-distal cingulum is practically no longer present in *Docodon*.

Small differences exist in the mesial part of the lower molars. The accessory cusp «b» has here increased in size relative to the main cusp «a» and reaches about half of its height. Due to the fact that the cusps «b» and «g» have also increased in size relative to cusp «h», here also a basin is formed opening in the linguo-mesial direction. The distal basin of a lower molar, opening distally, joins with the anterior basin of the following tooth, which opens linguo-mesially, forming a large trough for receiving the lingual half of an upper molar. The linguo-mesial cingulum is likewise reduced in size and consists only of a small shelf without cusp «e». Instead of this, another small cusp has been formed from the crest between the cusps «b» and «h». In addition numerous sharp accessory ridges have developed, particularly on the inner flanks of the main cusp «a», which substantially increase the number of effective cutting edges (JENKINS 1969).

Today, BUTLER's (1939) opinion is generally accepted that at least the anterior of the five molars of *Peraiocynodon* described by SIMPSON (1929) were the milk molars of the juvenile form of a *Docodon*-like mammal. Thus the teeth will be discussed in the chapter on the tooth replacement of *Haldanodon*.

4.4.5 Upper Molars

The evolution of the upper molars in Jurassic docodonts is principally the same as that of their antagonists, yet their morphology is quite different from them. Here also a buccal and a lingual row of cusps are present. The buccal row is made up of a main cusp «A», a distal accessory cusp «C» and one mesial and one distal cingulum cusp «E» and «D». The main cusp «A», occupying about half of the buccal cusp row, has the form of a blunt cone, that is stretched in the mesial and distal direction and provided with cutting crests. In relation to the diameter of their base, the main cusps of the upper molars are not as high as those of the lower molars. In the buccal direction the main cusp «A» is rounded; in the lingual direction

a ridge runs out from it to the lingual cusp row, at about right angles to the long axis of the tooth. The accessory cusp «C», which is connected with the main cusp «A» by the grooved, distal crest, has a similar form as this, but however, only half the size. Starting from it, the lingual ridge runs along its flank. Running around both cusps «A» and «C» is a broad external cingulum, which continues also on the mesial and distal side. On both ends of the teeth on the cingulum are formed cusp-like mounds. The mesial cusp «E» is quite sturdy and is connected to the main cusp «A» by the grooved, mesial crest. Often, especially in the posterior molars, the cusp «E» is located further in the distal direction so that mesially a broad shelf is formed. The cingulum cusp «D» is substantially weaker, usually only a small bud. It is also connected by a grooved crest to a cusp, the accessory cusp «C». Other bud-like formations can also appear on the buccal part of the cingulum (for example see Fig. 20 E). On a whole, the elongated buccal cusp row has the appearance of a triconodont tooth.

In comparison, the lingual cusp row of the upper molars is, in its size and number of cusps, substantially reduced. It is a drawn out, often distally curved protrusion of the middle lingual side of the buccal cusp row, giving the molars somewhat the form of a figure eight lying perpendicular to the longitudinal axis of the jaw. The lingual row is equipped with two cusps. The by far largest cusp «X», which is connected with the main cusp «A» by a crest, is located at the mesial beginning of the second third of the lingual cusp row. The second cusp «Y» joins distally. Both cusps are connected by a crest which, running out beyond them in a half circle, builds up the mesial, lingual and distal margin of the lingual part the tooth. On both sides of the buccolingual crest which connects the cusps «A» and «X» are located elongated depressions, bordered mesially and distally by the surrounding marginal crest.

Among the isolated lingual halves of upper molars were also found examples where the two cusps «X» and «Y» are about equally developed and where the connecting crest is missing. On the other hand, the two crests running from the cusps to the buccal tooth half are very sharp and
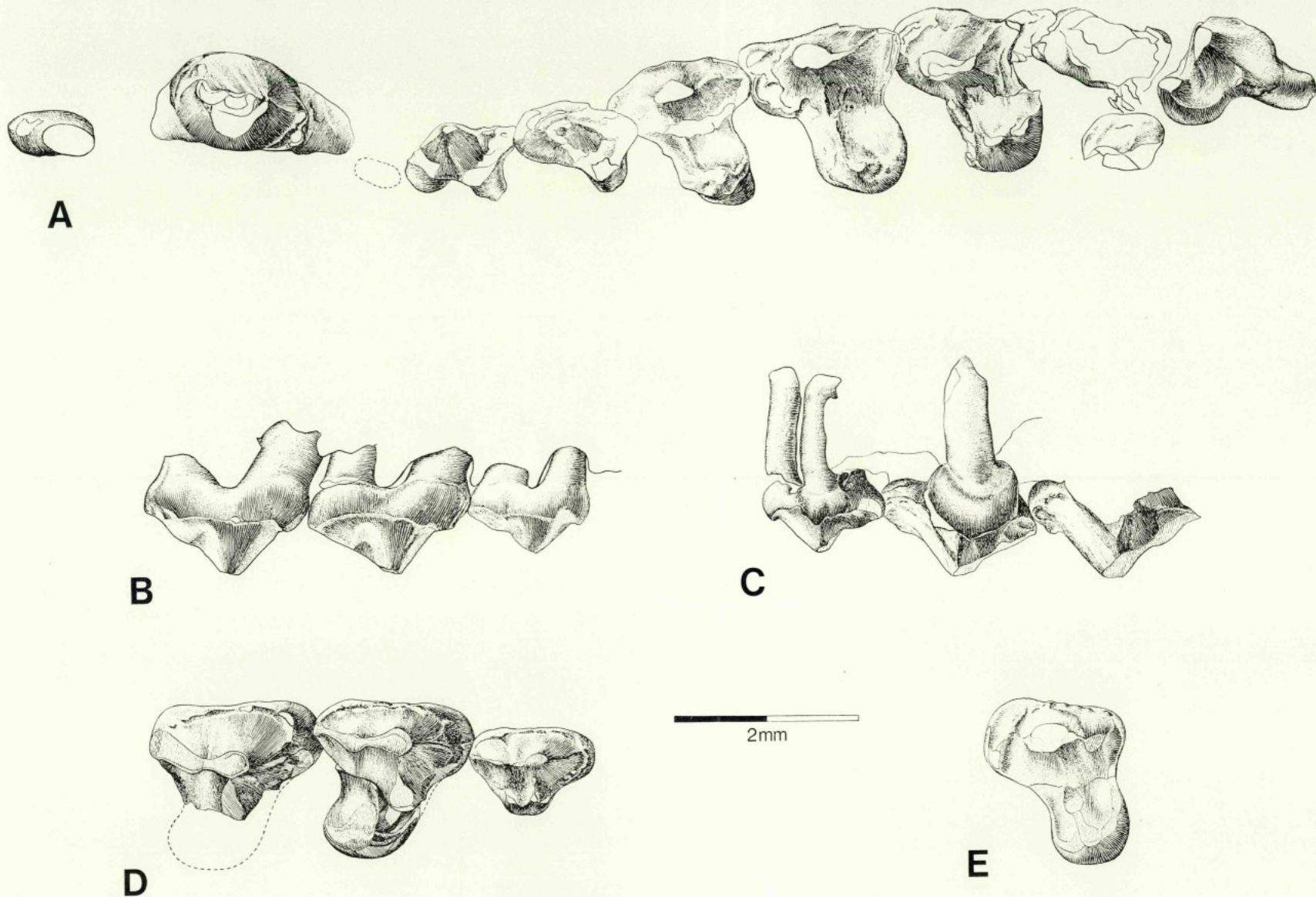
FIG. 20 — Dentition of the left upper jaw VJ 1008 - 155.
A. Occlusal view.

— Dentition of the anterior skull VJ 1009 - 155. Fragment 2 (P^3, M^1 and M^2).
B: Buccal view.
C: Lingual view.
D: Occlusal view.

— Dentition of the anterior skull VJ 1009 - 155. Fragment 4 (M^3).
E: Occlusal view.

high. These upper molars have then, as a special feature, on their lingual halves two parallel running cutting edges perpendicular to the longitudinal axis of the tooth. The roots, which support the lingual halves, have a flat oval cross-section. The unusual size that these lingual halves can reach, suggests that they belong to the upper molars of the A-form of *Haldanodon*. Complete teeth of this type as well as the corresponding buccal halves could not be found.

The lingual part of the upper molars with the cusp «X» corresponds mophologically somewhat to the paracone of the pantotherians. The fact that the connection between it and the buccal main part is drawn in strongly concave in the mesial and distal as well as occlusal and radical directions caused here a weak zone that encourages breakage. Thus among the isolated teeth practically no complete M_x were found, the majority being only separated buccal or lingual parts.

The upper molars of *Haldanodon* are all provided with three roots which in general have a round cross-section. Two of the roots sit, one behind the other, above the buccal part of the molar, while the third supports the lingual part. The roots seem to be of about the same length and taper slightly towards their apex.

Also the molars of the upper tooth row vary among themselves. Their size relationship follows the norm of their antagonists, i. e. the largest tooth is the M^2, followed by M^3, M^4 and M^1, as well as with some disparity M^5. At M^3, which sits on the beginning of the zygomatic arch, it is apparent that the lingual part joins far distally and is slightly curved in the mesial direction (Fig. 20 E). The M^5 is not only substantially smaller than the other molars but also more primitive, as it possesses only cusps «A» and «X». The buccal part of the tooth otherwise dominating in size appears here, in relation to the lingual part, small and compact.

In comparing the upper molars of *Docodon* with those of *Haldanodon* it is readily noticeable that the lingual part of the teeth has vastly enlarged, almost reaching the extent of the buccal part. The area of transition between the lingual and buccal parts of the teeth have not been effected by the enlargement, so that at this point a

constriction appears, giving the molars in occlusal view an hour-glass shape. Another noticeable enlargement is that of the cusps «A» and «Y». On the other hand, the cusps «E» and «D» are vastly reduced. Running down the lingual surface of the main cusp, are several sharp-edged «accessory crests».

4.4.6 Molar development Morganucodon — Docodon

The molars of *Morganucodon* were described in particular detail by KÜHNE (1949, 1959), KERMACK (1965), CROMPTON & JENKINS (1968), PARRINGTON (1967, 1971) and MILLS (1971). Their form is quite similar to the molars of Jurassic Triconodontinae. Like these they possess a main cusp, as well as a mesial and a distal accessory cusp. Besides the three cusps «A», «B» and «C», the upper molars also have a buccal and a lingual cingulum, on which two small cusps «E» and «D» as well as many buds are developed mesially and distally. The lower molars are equipped with the three cusps «a», «b» and «c» and a lingual cingulum which is also studded with many buds and the small cusps «e», «d» and «g» («kuehnecone»). Also the development of the «wear facets» is comparable to that on the teeth of Triconodontinae. On the other hand, the position of the teeth in the lower jaw is different from these. In the Triconodontinae the tooth row ends in front of the Proc. coronoideus, whereas in *Morganucodon* it runs medially somewhat further (MILLS 1971). The question if the comparable tooth construction of *Morganucodon* and the related forms in the Triconodonta allow a classification, will be discussed later.

The molar development from *Morganucodon* to *Docodon* took place in such a manner, according to the convincing theory of CROMPTON & JENKINS (1968), that the teeth gradually enlarged their lingual cingulum, and each lost a cusp (M^x=cusp «B», M_x=cusp «c»). In the lower molars, the margin between the cusps «a» and «b» and the cingulum enlarged, and their small cusps increased in circumference and height. The upper molars developed a protrusion out of the relatively weak lingual cingulum, that gradually enlarged, creating the two new cusps «X» and «Y». The development

process is schematically represented in Fig. 21 (redrawn after Jenkins 1969).

At this point a curious parallel development to the docodont molars should be mentioned, which W.G. Kühne called my attention to. In a paper, Szalay (1969) describes the teeth and jaw fragments of different species of the condylarthtragenus *Hapalodectes* from the Eocene of North America and Asia. These animals possessed, like the docodonts, a narrow jaw with an «internal groove» and had a similar molar form. The extended molars of the lower jaw have a tricodont arrangement of a central main cusp, two accessory cusps in line with it and a small lingual cusp. On the other hand, the upper molars imitate the form and cusp arrangement of the corresponding teeth in *Haldanodon* and *Docodon* (Fig. 22). Only the buccal cingulum and the crest running buccal-lingually between the two large cusps seem to be more weakly developed. In a orientation after the dental characteristics alone, neither this small difference in the dental anatomy of M^x, nor the similarity of M_x to those of *Morganucodon* and the triconodonts, nor their relatively imposing size would contradict a categorization as a somewhat aberrant docodont.
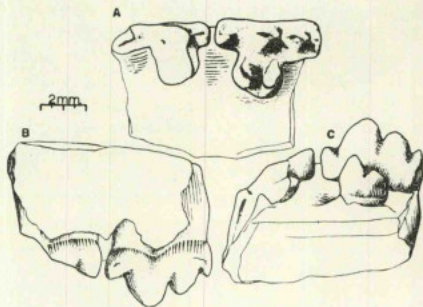
FIG. 22 — *Hapalodectes serus* Matthew & Granger 1925 (from Szalay 1969). Fragment of left maxilla with M^1 and a broken P^4.
A: Occlusal view.
B: Buccal view.
C: Lingual view.

FIG. 21 — Schematic representation of the molar development and cusp homology of the docodonts, no scale (changed after Jenkins 1969).
A: *Morganucodon*, Rhaet.
B: Hypothetical intermediate form of the Lower Jurassic.
C: Kimmeridgian form, similar to *Haldanodon*.
D: *Docodon*, Morrison Formation of the Upper Jurassic.

4.5 Tooth replacement and milk molars

The nature of the transition from a polyphyodont tooth replacement, also that of highly developed reptiles (Crompton 1963 a, Hopson 1971), to the diphydont tooth replacement of the mammals is an interesting problem, that can be solved only through the study of Mesozoic mammals. Unfortunately, the jaw rests that are known to us came almost only from individuals that at the time of their death did not undergo tooth replacement. Thus reference to this subject appears only rarely in publications. Recently, however,

MILLS (1971) and PARRINGTON (1971) have given a detailed description of the tooth replacement and milk teeth of *Morganucodon*.

Between several hundred jaw rests of this genus, MILLS found two mandibles with tooth replacement. In both cases signs of a replacement of the last premolar were present. From negative evidence pointing against the discarding of the teeth lying further forward and from the particular functional position of the last premolars, MILLS assumed that only these teeth were replaceable. (Replacement of only the last premolars is characteristic of several non-related mammalian groups, particularly the marsupials).

PARRINGTON, in studying similar yet more abundant material, came to different conclusions than MILLS. He was able to prove that *Morganucodon* replaced in the lower and upper jaw all the premolars and canines as well as probably the incisors. The tooth replacement took place at a relatively early age and was complete before the last molar had erupted. The proof of a diphyodont tooth replacement in *Morganucodon* by PARRINGTON coincides with observations of *Erythrotherium* and *Triconodon*. The holotype of *Erythrotherium* is the small undeveloped dentary of a youth form with an incisor in replacement, an incompletely erupted premolariform tooth and a molar with a not yet developed crown (CROMPTON 1964). A dentary from *Triconodon mordax* shows the replacement of the canine and the replacement of a molariform tooth by a premolariform one (SIMPSON 1928 a).

The observations on *Haldanodon* are also in agreement with PARRINGTON's findings. Here, through a stroke of luck, from seven mandible fragments two are found which were in the process of tooth replacement and two where the already completed replacement remains provable. Further, about a fifth of the isolated teeth are discarded milk molars. In specimen 1005-155, already identifiable as being part of a young animal from the jaw bone constitution, are found five postcanine teeth in a row. The most anterior as well as the most posterior tooth are in eruption and sit almost completely within the jaw bone. The second, relatively small tooth, is completely worn down. Of the two following teeth, the first is smaller and

by far more chewed down than the second one. These two teeth have the same basic form, however, differ from one another in that the third, smaller tooth in relation to its length seems to be very narrow, is mesially much less broad than distally and is lacking the mesio-lingual accessory cusp «h». The fourth, larger tooth, shows the typical form and size of the M_1 of the other mandible fragments of *Haldanodon*. Thus there is reason to believe that this is the M_1 and that the following erupting tooth is the M_2. The foremost tooth can be interpreted as the erupting P_1. The second tooth would thus be a used up Pd_2 shortly before being discarded and the third tooth a still usable Pd_3 (Fig. 23).

Specimen VJ 1004-155 belonged to an individual that was already somewhat more advanced in its ontogenetical development. Here, following three molariform teeth, are a large empty alveola and an open crypt containing a tooth bud. In front of the first of the molariform teeth the cusp of an erupting tooth is visible and in front of this the rest of a root of a further postcanine. The second and the third molariform tooth is similar to the Pd_3 of specimen VJ 1005-155. The following can be concluded: Present are already the M_1, M_2 and M_3. M_4 is still in development and M_5 is still so small that it has left no marks on the jaw bone. In the area of the premolars the P_2 is just erupting. The P_1 has already been replaced, whereas the Pd_3 is still fully in function (Fig. 24).

It can thus be proved that all three lower premolars had a predecessor probably in all cases molar-formed. Replacement of the incisors and canines can thus also be assumed. The replacement between Pd_x and P_x and the eruption of the permanent molars occured in the order from front to back. The M_1 erupted before the appearance of the P_1. The P_2 replaced the Pd_2 only after the M_3 was already functional.

As to the time of replacement from Pd_3 to P_3 no data are directly available, because the jaw fragments of adult animals, VJ 1001-155 and VJ 1002-155, show a complete postcanine tooth row of permanent premolars and molars. The premolars are, in contrast to the molars, almost not at all worn down.
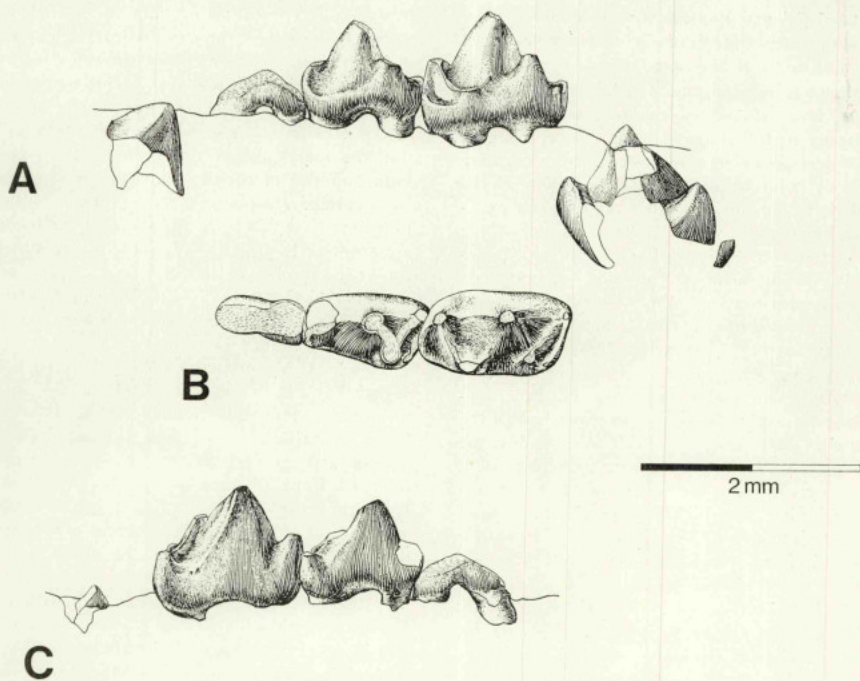
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FIG. 23 — Dentition of the rigth lower jaw VJ 1005 - 155.
A: Lingual view of P_1, Pd_2, Pd_3, M_1 and M_2.
B: Occlusal view of Pd_2, Pd_3, and M_1.
C: Buccal view of Pd_2, Pd_3, M_1 and M_2.

On the mandible remains of an old individual (VJ 1007-155), in front of molars almost worn to the roots is preserved a fully unworn $P_{3?}$, which had obviously not yet completed its eruption phase. A further mandible fragment, VJ 1006-155, shows likewise a new premolar in front of a totally worn-out molar. From this evidence two possibilities can be drawn. Either the last premolar (or also all the premolars) were once again replaced at an advanced age by a premolariform tooth, or the replacement between the Pd_3 and the P_3 could take place in different individuals at different times in their ontogenetical development. The second possibi-

lity is the much more likely one and is additionally supported by observations of isolated milk molars, that are equivalent in size and form to the Pd_3 of specimen VJ 1004-155 and VJ 1005-155. The resorbed roots of these teeth show that they were shed. The fact, however, that the milk molars are worn to very differing degrees leads to the postulation that the time of their disposal and thus their replacement by permanent P_3 was individually different.

The isolated teeth, that could be indentified as shed milk molars, have as a common characteristic completely resorbed roots. The pulp chamber is wide open having sharp irregular
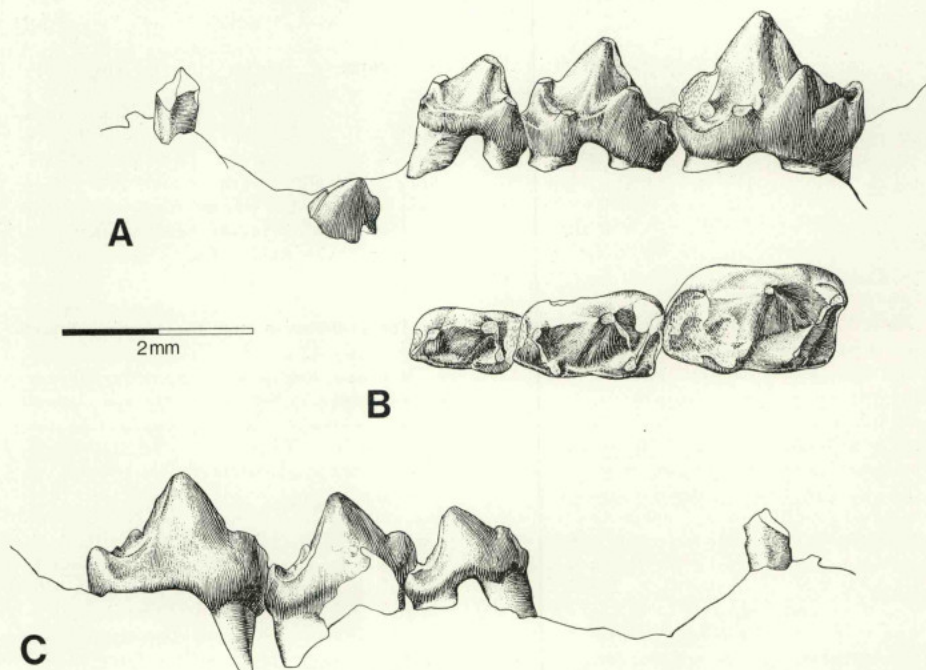
FIG. 24 — Dentition of the right lower jaw VJ 1004 - 155.
    A: Lingual view of P_1 (root), P_2, Pd_3, M_1 and M_2.
    B: Occlusal view of Pd_3, M_1 and M_2.
    C: Lingual view of P_1 (root), Pd_3, M_1 and M_2.

edges. Its inner surface is dissolved by osteo-clasts in numerous small shallow grooves (see Plate VIII, I and K). The newly formed permanent premolars and molars that were found isolated also do not possess roots, as these developed only after the tooth crown during the eruption process. The wide open pulp chamber, however, possesses here a smooth surface and even, rounded edges (see Plate IX, A and B). Besides their resorbed roots, the discarded milk molars differ also from the molars found isolated in their smaller size, which is about that of the permanent premolars. The remaining characteristics of the Pd_x have already been described. The buccal half of the Pd^x seems, in contrast to the M^x, slimmer and more elongated. The tooth which KÜHNE (1968) illustra-ted on p. 116 and considered a lower milk molar of *Haldanodon*, is a permanent anterior molar.

Nearly the complete material of premolars from *Haldanodon* found isolated consists of new and unused teeth. This is probably due to the fact that the roots of the newly erupting premo-lars were not yet completely developed. Thus the teeth were not solidly anchored in the alveolas, which facilitated post mortem dislodgement from the jaw. In isolated molars, this stage in growth is also often encountered. Along with these, however, many teeth are found which are very worn, originating from old individuals. Here dislodgement of the molars occured probably

because of senile changes in the jaw bone and a beginning resorption of the roots.

A particularity in *Haldanodon* is that in the adult stage of the lower jaw the last molar is shed including the root, and the empty alveola then fills in with bony material. The only complete maxilla dentition present here (VJ 1008-155) has the M^5 in situ. This means that the last molar of the upper jaw was either shed later than its antagonist in the lower jaw or not at all.

In closing this chapter the docodont genus *Peraiocynodon* from the Purbeckian of England will be discussed. The holotype and only preserved remainder of this mammal is the posterior portion of a small, not yet developed mandibula, with four postcanine teeth in a row (Fig. 1C). Located between the most posterior tooth and the Ramus mand. is a tooth bud. SIMPSON (1929) interpreted the teeth as the M_1 to M_5. On the other hand, BUTLER (1939) came to the conclusion that the jaw remains of *Peraiocynodon* had a dentition consisting only of milk molars (Fig. 25). Observations of the milk molars of the somewhat older but closely related genus *Haldanodon* allow a partial revision of this view. The form and size of the first postcanine tooth corresponds to that of the P_1 in *Haldanodon*, whereas the following two teeth are molariform and, to a great degree, resemble the milk molars of the older form. On the other hand, the fourth tooth, also molariform, compares closest to the M_1 of *Haldanodon*. This justifies the assumption that the holotype of *Peraiocynodon* possessed an already replaced premolar and two milk molars (probably P_1, Pd_2 and Pd_3). Also the M_1 was already present, whereas the M_2 had not yet completely erupted. The posterior molars were not yet established. Thus *Peraiocynodon* corresponds in its development stage somewhat to the *Haldanodon* paratype VJ 1005-155. The similarity between the teeth of both genera is so great that the discovery of further and better material of *Peraiocynodon* could possibly prove a synonym with *Haldanodon*.

4.6 Tooth Occlusion and the Chewing Process

Mammals meet the large energy demand needed to sustain their homoiothermal organism by a particularly intensive utilization of their food. This process is started before actual digestion through preparation in the mouth; the chewing phase. The feeding process of the reptiles, who, with their usually simple conical shaped teeth, only grab their food or at the best dismember it in crude chunks, is repeated only by a few mammals (for example the recent odontocetes). The analysis of the chewing process of fossil mammals gives important clues to their stage of development and to the nature of their food, which would otherwise not be obtainable. The chewing motion of fossil mammals is reconstructable by studying the manner in which the teeth (especially the molars) were worn. Such special studies on tooth wear had been first
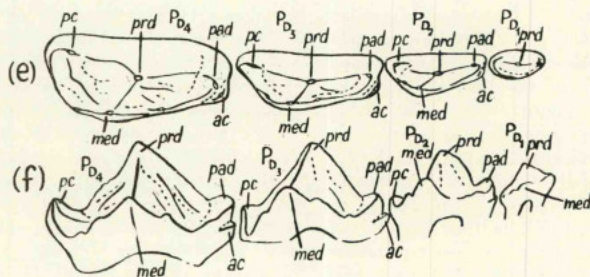
FIG. 25 — Dentition of *Peraiocynodon* (from BUTLER 1939).
(e): Occlusal view of P_1, Pd_2, Pd_3 and M_1.
(f): Lingual view of the same teeth.

published in relatively recent times. Here, especially to be noted, are BUTLER (1961, 1972) and MILLS (1964, 1966, 1971). Other important contributions came from CROMPTON (1971), JENKINS (1969) and CROMPTON & JENKINS (1968). EVERY (1970), (EVERY & KÜHNE 1969, 1971) introduced the term thegosis. By this term he understands a means of sharpening the cutting edge of the teeth by grinding it on its antagonist. Until now this process, working against the natural dulling effect of chewing, has been tried to be proven for the Pantotheria (KREBS 1971) and many of their descendants. EVERY's studies of recent mammals show that thegosis is an unconscious act and occurs especially when an animal readies for attack or defence («gnashing» the teeth).

Wear on the teeth is, according to BUTLER (1972) caused by two different forms of utilization, called «abrasion» and «attrition». These terms, taken from dental medicine, are applied here. Under abrasion is understood tooth wear resulting from contact with the food, especially causing the cusps to be dulled. In contrast attrition results from the movement of the occluding teeth against one another. Thereby wear facets are formed at those points where the teeth are in closest contact with one another. The wear facets are ground flat and smooth, having fine parallel running striae. From the direction of the striae, the movement of the teeth which caused them can be determined. However, only that movement can be recognized which forms the second half of the chewing process; namely, when the jaw is closed to the extent that the teeth come into contact with one another. CROMPTON & HIIMÄE (1970) have studied the chewing movement of the living Didelphis. Here it was shown that abrasion occurs in the first stage of mastication, first when the cusps penetrate the food mass, and next when this is crushed between the tooth crowns. Only in the second stage, when the teeth in a cutting movement slide past one another, are the attrition marks produced. Thus they are comparable to the striations occuring on tectonic sliding planes and can be interpreted in a similar manner.

BUTLER (1972) understands as thegosis merely a special form of attrition, whereby the chewing movement is carried out without food being between the teeth. This explains also the problem in deciding from fossil material whether the animal in question was capable of practising thegosis. Proof for thegosis can be found only there where, through the working of one tooth on another, a sharp cutting edge is kept on a surface which undergoes constant dulling by abrasion. This is not the case in Haldanodon.

Abrasion marks in Haldanodon are found already on not yet fully erupted molars that didn't come in contact with an antagonist. Wear surfaces arising from attrition are first formed slowly on the flanks, especially of the main cusps. They are more difficult to evaluate, as one movement can produce several planes facing in different directions. However, an interpretation is possible because all the striae that were formed at the same time lie parallel (BUTLER 1972). Besides the direction of the chewing motion, from the form and position of the attrition facets also the occlusion of the teeth by closed jaws can be identified. In this manner, the relationships between separately found upper and lower dentitions can be analyzed. From the wear on a molar it is even possible to identify, with a good degree of certainty, the form of the yet unknown antagonist belonging to it (KERMACK & LEES & MUSSETT 1965).

Here the wear facets of several tooth types of Haldanodon will be described. In concluding, the compiled data will be used in an attempt to determine the relationships between the lower and upper jaw and the feeding habits of Haldanodon.

Incisors and Canines

From their form and position the incisors of Haldanodon were designated to grab food particles in a pincer-like manner. For this purpose they are assisted by the long dagger-formed canines, which by their form are particularly suited to hold a smooth surfaced food chunk or to kill a struggling prey.

The cusps and the mesio-distal crest of incisors and canines, after long use, develop an abrasion wear, whose surface is slightly rounded and

lies parallel to the plane of occlusion. Contrastingly, on the labial flanks of the lower incisors and canines and on the lingual flanks of the upper incisors and canines striated facets emerge, which can be attributed to attrition. Whereas the postcanine teeth take an active part in the chewing process, the front teeth move past one another. With closed jaws the lower of these teeth sit finally mesiobuccally from their antagonists. Because of their rounded flanks the front teeth are not capable of cutting in a shearing fashion. Thus, they obtain their side wear facets in the same manner as reptile teeth, which with the opening and closing of the jaws grind on one another (Fig. 26).

On the lower front teeth the striae of the attrition facets point from distally above to mesially below. Correspondingly, on the upper teeth the striae run from mesially below to distally above.
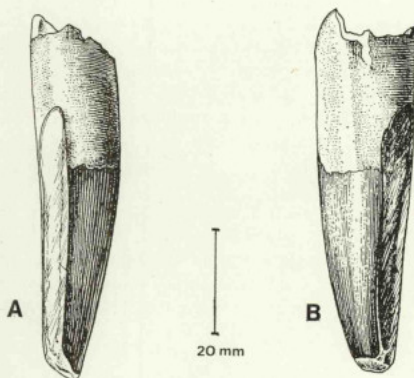
FIG. 26 — Upper right tooth of a (?) crocodilian out of the Infra-Cenomanian of Taouz (Southern Morocco) with abrasion wear (cusp) and striated attrition plane (linguo-distal tooth flank).
A: Distal view.
B: Lingual view.

Premolars

The three lower and the three upper premolars of *Haldanodon* are from front to back increasingly more molariform. They take over, thereby, in the same degree the occlusion form of the molars.

While the anterior premolars slide past one another by jaw closure, the posterior ones come into direct opposition. It is worth noting that the premolars are not particularly worn by either abrasion or attrition but retain their original form even with very badly worn molars present.

Molariform Teeth

BUTLER (1972) separates three consecutive degrees of function in the evolution of the mammalian molars: the «shearing», the «crushing» and the «grinding» stage. The molars of the Upper Jurassic docodonts differ functionally from those of the same aged pantotheria in that they do not only glide by one another in a shearing process but, in terminating the chewing movement, stand in direct opposition to one another and also crush and squash their food. This chewing modus, which also opens the way to plantal and harder food stuffs, was attained by the Pantotheria first in the Lower Cretaceous with the development of the tribosphenic molar. On the other hand, the multituberculates and their probable forerunners, the haramyids had already developed molars corresponding functionally to the third degree and capable of a grinding mastication.

CROMPTON & JENKINS (1968) and JENKINS (1969) stress the importance of the shearing mastication in the docodonts and see in the line of evolution *Morganucodon—Docodon* a transition from a simple longitudinal shearing movement to a complex longitudinal and transversal motion. The latter was made possible by the acquisition of further cutting edges and shearing surfaces.

Here it shall be shown that both shearing as well as crushing components took part in the chewing modus of *Haldanodon*.

CROMPTON & JENKINS (1968) gave a representation of the occlusion-conditions by the molars of a hypothetical form similar to *Haldanodon* (Fig. 27). This representation was later adapted by HOPSON & CROMPTON (1969) and directly applied to *Haldanodon* (Fig. 28).

There is little to add to the information given by the two author teams. However, they disre-
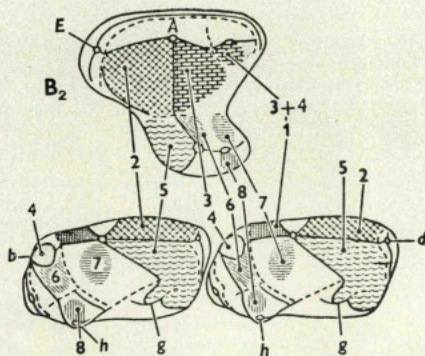
FIG. 27 — Schematic illustration of the wear facets caused by attrition on the molars of a hypothetical stage between *Morganucodon* and *Docodon*; partially based on *Haldanodon* (from CROMPTON & JENKINS 1968).

garded to make a difference between wear resulting from attrition and that resulting from abrasion. The abrasion wear influences very strongly the wearing down of the molars and, by its constant increase in size overlaps, to a degree, also the attrition surfaces.

Smaller discrepancies between the above mentioned illustrations and my own observations will be discussed later.

The abrasion on the lower molars encompasses, first of all, the buccal cusps and the crest between the main cusp «a» and the lingual cusp «g». Later, the other lingual cusps, and the mesial crests, to a lesser degree, are also worn by abrasion. In the upper molars also the buccal cusps and their connecting crest are favored by abrasive wear. Thus, in the mesial portion or the tooth, a sloping occurs, which runs from the partially worn down main cusp «A» over the completely worn away accessory cusp «C» to the mesial margin. The abrasion surfaces follow the inclination of the crests but lie otherwise perpendicular to the plain of occlusion. With increased enlargement of the worn surfaces the dentin here wears more rapidly than the bordering enamel, so that slightly concave depressions can occur.

The origin of the attrition facets can be explained by the nature of occlusion of the molars in *Haldanodon* (Fig. 29).

With closed jaws, an upper molar comes to rest here just about interpositional between two lower molars. Thereby, the buccal half of the upper molar lies buccally besides the antagonist. Contrastingly the lingual half sits in direct opposition on the lower teeth. Between these lies the crest connecting cusp «A» with cusp «X». Thereby, the mesial portion of the respectively posterior M_x is more overlapped than the distal portion of its predecessor. The facets can be

FIG. 28 — Schematic illustration of the wear facets caused by attrition on the molars of *Haldanodon* (from HOPSON & CROMPTON 1969).
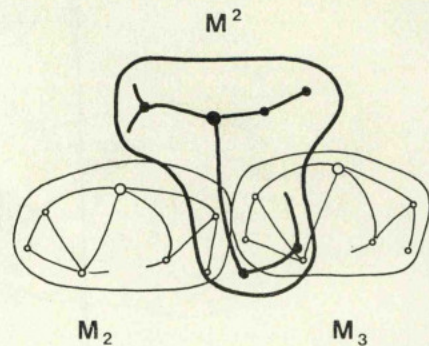
FIG. 29 — Occlusion model of the lower and upper molars of *Haldanodon*, reconstructed from VJ 1001 - 155 and VJ 1009 - 155.

divided into those, respective of their place of origin, resulting from action on the buccal half of the M^x and those resulting from action on the lingual half of the M^x. The facets of the first group are found in the lower molars on the buccal flanks of the main cusp «a» and on the mesial accessory cusp «b». On the upper molars, they lie lingually from the longitudinal crest that leads from the mesial accessory cusp «E» across the main cusp «A» and the accessory cusp «C». They arise in that the bucco-distal flank of the main cusp «a» of M_x slides up along the linguo-mesial flank of the main cusp «A» of the M^x. At the same time, the bucco-mesial flanks of the main cusp «a» and the buccal flanks of the mesial accessory cusp «b» of M_x move against the linguo-distal flanks of the main cusp «A» and the distal accessory cusp «C» of M^x. The facets are at first long and narrow, and on the M_x they appear

first on the lower swollen margin of the crown. Later they take over the major portion of the above mentioned tooth flanks.

The result of the movement produced by the first group of facets is a shearing cut, running in a zigzag fashion. The zigzag cut resulting from the angular position of the individual cutting planes produces an extension of the cutting edges and guides the lower molars exactly past the upper ones.

The position and form of the facets point further to the fact that — while closing the mouth — the mandible was moved substantially also in the lingual direction. (The studies of CROMPTON & HIIEMÄE 1969 and 1970 have confirmed that the mammals use alternatively only one tooth row for mastication). The striae on the facets allow identification of an additional, slighter, anterior-posterior movement component.
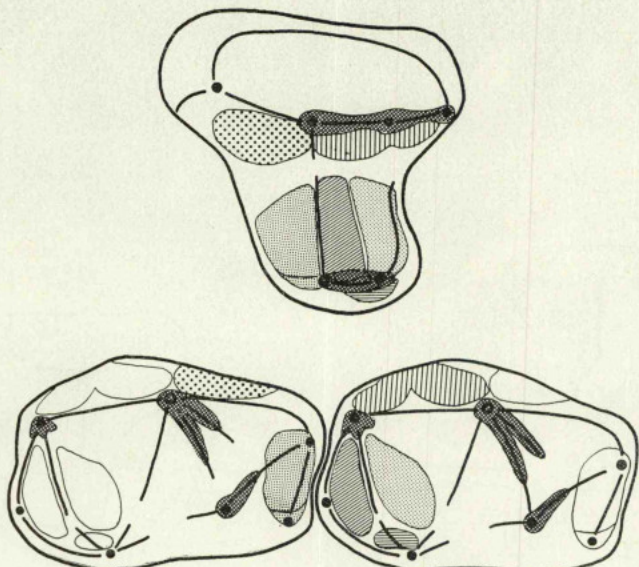
FIG. 30 — Schematic representation of slightly worn right molars of *Haldanodon*. An exact fitting of the wear surfaces, illustrated here on the lower and upper molars from different individuals, was purposely dispenced with in the drawing. Abrasion wear is represented by the dark shade. The attrition surfaces with identical grid patterns came in direct contact during chewing.

The wear facets of the second group are not to be defined as being merely the results of a cutting movement. Here the food particles, sheared off by the buccal tooth half and pushed inward by the jaw movement, are further processed between the linguo-distal and the lingual-mesial areas of the M_x and the lingual halves of the M^x. In this manner, the crests and accessory crests work like the edges of a grater. At the end of the jaw closing mastication process, the accessory cusps «b» and «e» of M_x and the accessory cusp «Y» of M^x pound in depressions of the respective antagonists and perform the same task as the pestle in a mortar. The wear facets attributed to such an attrition process are located at the lower molars especially in the linguo-mesial portion of the respective posterior tooth. To a lesser degree also the linguo-distal portion of the respective anterior M_x is affected. The facets on the lingual half of the upper molars are correspondingly developed.

A schematic illustration of wear surfaces due to abrasion and attrition on only slightly worn molars of *Haldanodon* is given in Fig. 30. In a similar form it is also applicable to the milk molars. In comparing this with the statements that CROMPTON & JENKINS (1968) or respectively HOPSON & CROMPTON (1969) had made about the wear facets of the molars of *Haldanodon*, several differences are apparent. Next to differences as to the spatial position of individual facets, which could be due to individual variations in the observed teeth, the opinions about the wear of cusp «b» of M_x are especially conflicting. According to CROMPTON & JENKINS (1968), this wear was due to action on the linguo-distal flank of cusp «C» of M^x (Fig. 27). Contrarily HOPSON & CROMPTON (1969) believe that the wear facets were caused by contact with the linguo-mesial flank of the main cusp «A» of M^x (Fig. 28). Observations of various M_x have shown that the facet of cusp «b» did not occur through contact with the occluding M^x but is in fact a typical lingually tilted, abrasion facet.

Through the action particularly of abrasion, first of all the tooth cusps and crests are dulled. On the linguo-mesial portion of the M_x a depression is formed, whereas the part of the lingual

half of the M^x fitting into this is rounded off. Finally, however, the wear leads to the leveling off of the entire occlusion surface of the molars. It is to be observed that the lower molars of older individuals form a rounded off surface that is slightly tilted in the linguo-mesial direction and shows no cusps, cutting edges or the like (Fig. 31). Although a shearing bite is certainly no longer possible with such teeth, animals thus equipped are obviously still viable. It is probable that, in this situation, the until now little used premolars prepare the food for the molars by shearing it. It is also worth noting that the degree of wear on the molars increases from front to back; so that the last erupting molar shows the strongest degree of wear. From this it can be concluded that the strength of the bite in *Haldanodon* is concentrated on the posterior molars.

PARRINGTON (1967) describes also cases of very hard wear on the molars of *Morganucodon*. However, here the teeth are first reformed into a triangular wedge and finally into a stump with a kind of a spike in the middle. It can be assumed that a, certainly not very effective, shearing bite was still just possible in this condition. As an explanation PARRINGTON (1971) stated that the life cycle of a small mammal, like *Morganucodon*, was probably so short that two generations of molariform teeth were sufficient. Also the hard prismatic enamel of the later mammals was not yet present in these early forms.

Recognizing these arguments allows us to postulate that *Haldanodon* processed a hard, tough and abrasive food. Nevertheless, a self induced sharpening of the teeth through thegosis could not be proven. The food was either of such a nature that even with fully worn down molars it could still be handled, or the animal changed over to another regimen in advanced age. The chewing process of the not yet heavily worn molars can be so classified:

1) Firmly holding and tearing the food particles with the penetrating cusps.
2) Cutting with the shearing crests and edges, and further transport to the inside through the lateral movement of the lower jaw.
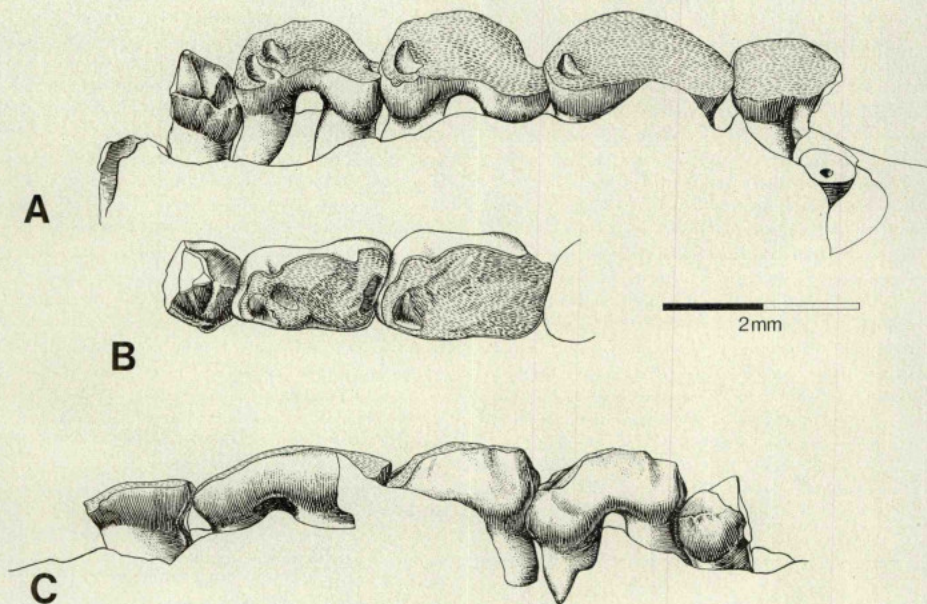
FIG. 31 — Dentition of the right lower jaw VJ 1007 - 155.
A: Lingual view of P_3 and M_1 - M_4.
B: Occlusal view of P_3, M_1 and M_2.
C: Buccal view of P_3, M_1 and M_2.

3) Further mincing by crushing and grinding between the lingual tooth portions, and dissolving it into a mash by mixing with saliva.

From the given data on the anatomy of the jaw, the masticatory musculature and the dentition, an attempt will be made to reconstruct the feeding habits of *Haldanodon*. It could be shown that *Haldanodon* dit not possess a simple orthal jaw movement, but rather its lower jaw underwent a complicated process of movement, that was also directed lateral-medial and rostral-caudal. Contrary to that of *Morganucodon*, the condylus lies by *Haldanodon* far above the level of the cusps. The mastication musculature is controlled by the muscles of the temporalis and masseter groups. There is only one, however for this reason very sturdily developed, pterygoid muscle present. A Proc. pseudangularis provided for a strong bite by almost closed jaws. The molars were not only suited for a shearing mastication but were also capable of grinding and could process an abrasive food.

All this evidence leads to the conclusion that *Haldanodon* was omnivorous, feeding to a great extent on vegetable material (CROMPTON & HIIE-MÄE 1969). The same applies to the other similarly characterized Upper Jurassic docodonts. Thus, next to the carnivorous or piscivorous triconodonts, the herbivorous multituberculates and the more of less insectivorous pantotherians and symmetrodonts, they occupy a special ecological position. This is best described by comparison with recent small mammals that also prefer such food habits. A rodent may serve as such an example. The insect feeding forest mouse

(*Deomys ferrugineus*) has a body length of 12-16 cm, weighs between 50-70 g, has a pointed head and possesses molars with pointed cusps. It lives in the african rain forest coming out at night on the forest floor or wading in shallow water. Its food consists of the small animals that it can capture (termites, ants, water insects, beetle larva, worms, snails, frogs, etc.) and tree fruits and seeds (DIETERLEN 1969; SANDERSON 1956). Such a food supply and such an environment were also available for *Haldanodon*.

4.7 Ecology

Haldanodon's environment can be characterized, by means of the hypodigma of animal and plant fossils, as being a tropical forest near the coast and on the edge of a brackish lagoon. From an ecological standpoint, the fauna composition fits very well that of a recent biotope of this type. The role of the large mammals is represented here by various dinosaurs. The three mammal groups found in the Guimarota coal must have likened recent insectivores and rodents in their living and feeding habits. *Haldanodon* was equipped with a good sence of smell and touch. This suggests that it preferred night activity. By day the Mesozoic mammals were potential prey for potent enemies in form of the smaller carnosaurs and crocodiles, whereby nocturnal beasts of prey which specialize on warm blooded animals, such as snakes and owls, had not yet developed. For this reason it can be assumed that they prefered concealed living habits. The predatory triconodonts, which possibly preyed on other mammals, are not yet evident in the Guimarota sediments. In food competetion were above all the, at that time flourishing, lacertilian reptile group and to a degree other mammalian groups, who's development, like that of the docodonts, was dependent on the evolution of higher plants and insects (CLEMENS 1970).

On a whole, the paleocological conditions of the Kimmeridgian coal from the Guimarota mine are very similar to those of the English Purbeckian, described so vividly by SIMPSON (1933). The equivalent of the following clastic fluvial deposits of the Wealdian can be found in the other Portuguese finding place of Mesozoic mammals of Porto Pinheiro (Upper Kimmeridgian). Here the very fragmentary faune consists of, next to many multituberculate and pantotherian teeth, also a few molars of triconodonts and symmetrodonts (KRUSAT 1969), however, no remains of docodonts have been found.

5. PHYLOGENY AND TAXONOMY OF THE DOCODONTS

The distinctions used for mammals in recent zoology (for example possession of hair, milk glands and a four chambered heart with the aortic arch on the left side) are, as is well known, of no use to paleontology, because the morphological-physiological characteristics are practically never preserved as fossil evidence. For this reason in paleontology certain characteristics of the skeleton and tooth construction are used, whereby the most important one is the possession of a secondary jaw joint. For many Mesozoic mammals this possibility of differentiation from reptilian forerunners is also inadequate, because the complicated mosaic development of mammalian characteristics does not allow a clear separation between primitive mammals and highly developed therapsids. Particularly responsible for the emergence of this dilemma is the progress in modern vertebrate paleontology, which has considerably broadened our knowledge about the evolutionary process, especially in the lower Mesozoic. Accordingly, it is no longer possible to give a valid definition of the Class Mammalia in simple morphological terms, the so-called Mesozoic mammals included (SIMPSON 1971), and also for the interpretation of the phylogeny not necessary. According to a silent agreement among researchers in this field, those tetrapods have reached the status of mammals, which can be categorized in one of the well defined groups, that is:

— Monotremata
— Multituberculata
— Triconodonta — Docodonta
— Theria sensu lato

(SIMPSON 1971).

In this sense also *Haldanodon*, characterised as a member of the order Docodonta, is to be considered a mammal even though, from the state of its development, it is not so different from the «reptiles» of the Middle and Upper Triassic.

Wereas it is relatively insignificant whether a group of transitional forms is assigned to the reptiles or to the mammals, the taxonomic classification within the orders and the lower systematic units is thus important, because thereby the successive historical line of development and the degree of affinity between the individual forms should be documented. The relationships between the families Morganucodontidae and Docodontidae were repeatedly refered to in the present work. The here established correspondence in the construction of the visceral skeleton and of the lower jaw of *Morganucodon* and *Haldanodon* supplements the already established inference of the molars and allows the, up to now only supposed, derivation of the Docodontidae from members of the family Morganucodontidae to be regarded as proven.

The, to a degree, baffling homologies between *Morganucodon* and *Haldanodon* make it necessary to discuss once again the systematic position of the Morganucodontidae family. CROMPTON & JENKINS (1968) had indeed determined that the molars of *Docodon* evolved from those of *Morganucodon*, however, following PARRINGTON's (1967) view, they placed the Morganucodontidae in the Tricodonta. This view is based solely on the form of the molars of *Morganucodon*, which comes close to that of certain Upper Jurassic Triconodontidae, and the resulting similarity in tooth wear. Certain correlations are also present in the structure of the cranial skeleton (KERMACK 1963). Decisive proof, however, cannot be accepted for either of these characteristics. Parallel develop-

ment of the tooth construction is known for many not closely related mammal groups that feed on a similar food. The posterior skull of a member of the docodontidae is not yet known. It can, however, be assumed that it has principally the same construction as the cranial skeleton of *Morganucodon*. The morphological conformities and deviations between *Morganucodon* and the triconodonts, on the one hand, and between *Morganucodon* and the docodonts on the other are compared in the following table.

	Triconodontidae	*Docodontidae*
Incisors	no evidence	the last upper precanine situated in the maxilla
Molars	similar, derivable from one another	not similar, derivable from one another
Cranial skeleton	partial conformity	no evidence
Visceral skeleton	no apparent conformity	strong conformity in the morphology of the bones and the bone sutures
Lower jaw	strong deviations in the construction of the lower jaw and masticatory muscles	strong conformity in the construction of the lower jaw (sulcus with accessory bones, Proc. pseudoangularis) and the masticatory muscles

This shows clearly that the origin of the Docodontidae must be traced back to the Morganucontidae group. Compared to *Morganucodon*, the Upper Jurassic forms merely further degenerated the primary jaw joint and adapted the molars to another food supply. Thus PATTERSON's (1956) and KERMACK & MUSSET's (1958) classification of the family Morganucodontidae in the order Docodonta must be accredited, as those nearest related to the Morganucodontidae are the Docodontidae. This does not deny, however, that the two orders Docodonta and Triconodonta have closer relationships to one another than to other groups, and are thus correctly combined by HOPSON (1970) in the infraclass Eotheria. A simplified phylogenetic tree of Mesozoic mammals is attempted at in Fig. 32.

It seems that the docodonts had, already on the boundary between the Jurassic-Cretaceous, become the first mammal order to be extinct.

The reason for this circumstance is not yet known. Compared with mammals of the same age, the Upper Jurassic docodonts cannot at all be regarded as being phylogenetically retarded, let alone «living fossils». Also the pantotheres, symmetrodonts, triconodonts and multituberculates, that survived into later times, still possessed in the Upper Jurassic many reptilian characteristics. Only in one respect did the Docodontidae not follow the general mammalian development; namely that by them the bones of the primary jaw joint were not or were only incompletely incorporated into the middle ear. The retention of the reptilian hearing apparatus could not, however, have been sufficient to make the Docodontidae less competitive than other mammal groups, in as much as their dental development was very advanced.
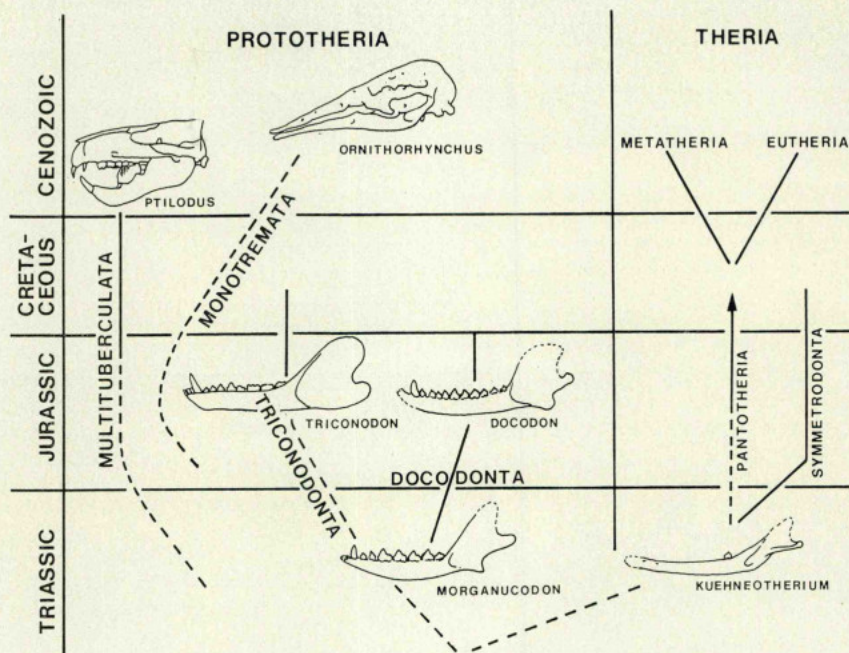
FIG. 32 — Attempted phylogenetic tree for the Mammalia (changed after HOPSON 1969).

6. SUMMARY

Haldanodon exspectatus Kühne & Krusat 1972 from the Kimmeridgian of Portugal belongs to the family Docodontidae (O. Docodonta, C. Mammalia), whereby three further genera are known. The Docodontidae evolved out of the family Morganucodontidae. The inclusion of the Morganucodontidae in the Docodonta is based on the morphological homologies between *Morganucodon* and *Haldanodon*.

In respect to its Upper Triassic ancestors, *Haldanodon* had merely further reduced the primary jaw joint and developed a new molar type. The accessory bones of the reptilian lower jaw are rudimentarily located on the medial side of the dentary and no longer serve articulation. The mammalian middle ear is not present in *Haldanodon*. The Meckelian cartilage persists also in adult individuals of *Haldanodon* and is led together with Arteria and Nervus mylohyoideus in a Sulcus primordialis et mylohoideus, which reaches as far as the symphysis of the lower jaw. *Haldanodon* has retained many further reptilian characteristics; among others the carrying of the last upper precanine in the maxilla, probable possession of septomaxillae and a reduced reptilian saliva apparatus. On the other hand, *Haldanodon* had a sturdily developed secondary jaw joint and a heterodont dentition. Diphyodont tooth replacement could be proved in much detail for *Haldanodon*.

It is very likely that the dentary of *Haldanodon* was equipped with a Processus pseudangularis, on which caudally, homologous to the monotremates, a Muscuslus detrahens mandibulae inserted, as well as laterally a Musculus massetericus and medially a portion of the Musculus temporalis. The Musculus pterygoideus ext. inserted on the Crista pterygoidea, which was enlarged by a depression in the jaw bone. The Musculus pterygoideus int. was not present.

The dental formula of *Haldanodon* is · $\dfrac{5\,\mathrm{I}:\mathrm{C}:3\,\mathrm{P}:5\,\mathrm{M}}{+\,2\,\mathrm{I}:\mathrm{C}:3\,\mathrm{P}:5\,\mathrm{M}}$

Differences in the construction of the lower jaw and the dentition of adult individuals reveal a, probably sexually based, dimorphism. *Haldanodon* possessed, considering its low stage of development, a very advanced degree of occlusion of the molars, making a shearing and grinding mastication possible. Considering the jaw musculature, the form of the Condylus madibularis and the occlusion relationship in the dentition, omnivorous feeding habits would be most expected. The living habits of *Haldanodon* can, with some discretion, be identified as that of a nocturnal omnivore, in a tropic-humid, heavily grown biotope, in which reptiles (dinosaurs, crocodiles, turtles, lacertilians) were dominant.

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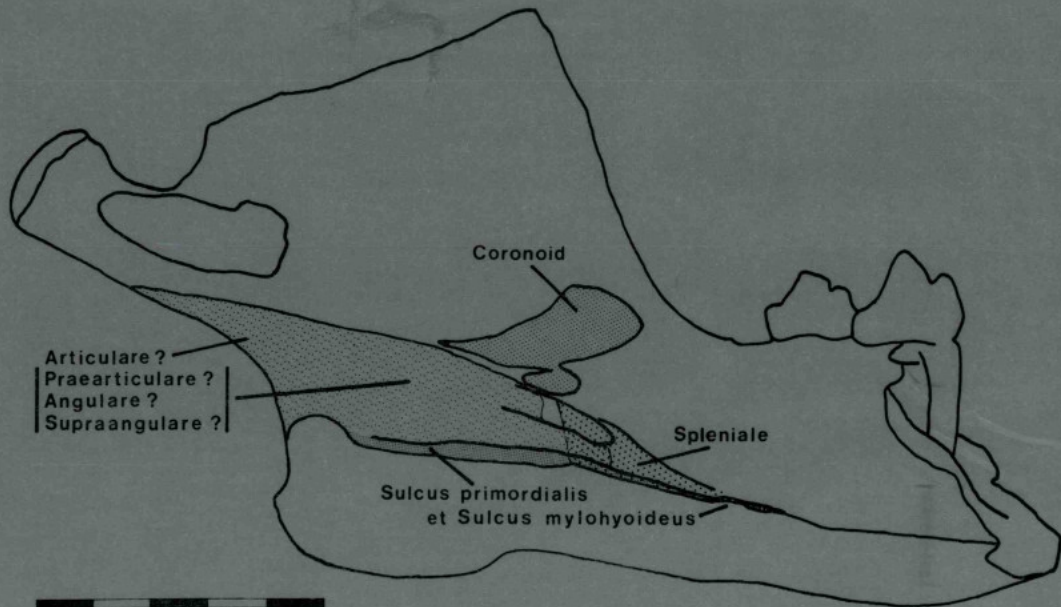
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8. PLATES AND EXPLANATIONS

Plate I

Location of accessory bones on the medial side of the dentary of *Haldanodon* (specimen VJ 1003-155).

Coronoid

Articulare ?
Praearticulare ?
Angulare ?
Supraangulare ?

Spleniale

Sulcus primordialis
et Sulcus mylohyoideus

5 mm

Coronoid

Articulare ?
Praearticulare ?
Angulare ?
Supraangulare ?

Spleniale

Sulcus primordialis
et Sulcus mylohyoideus

5 mm
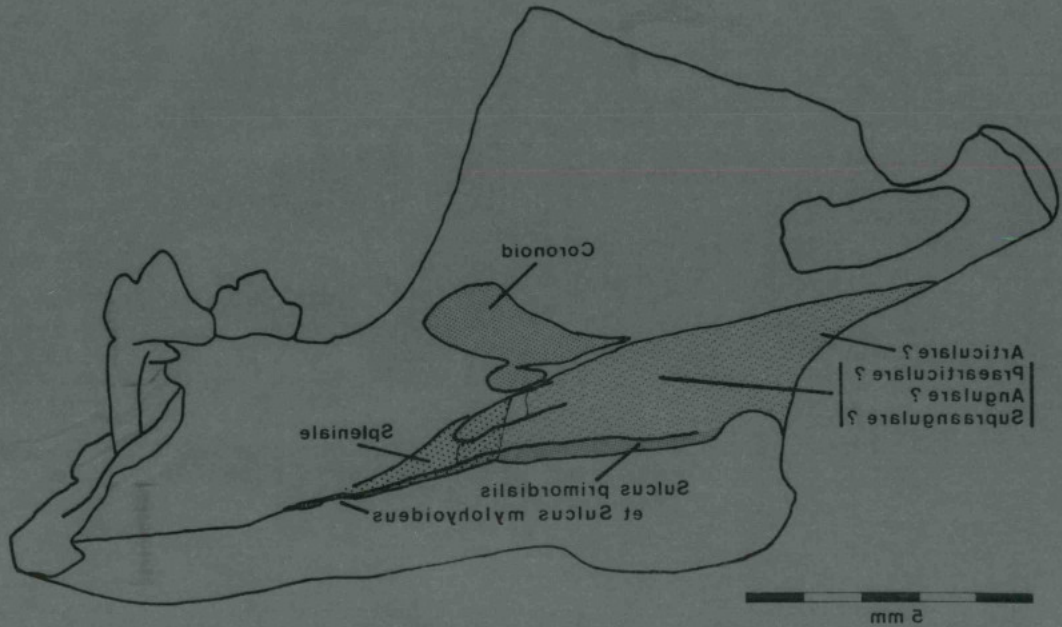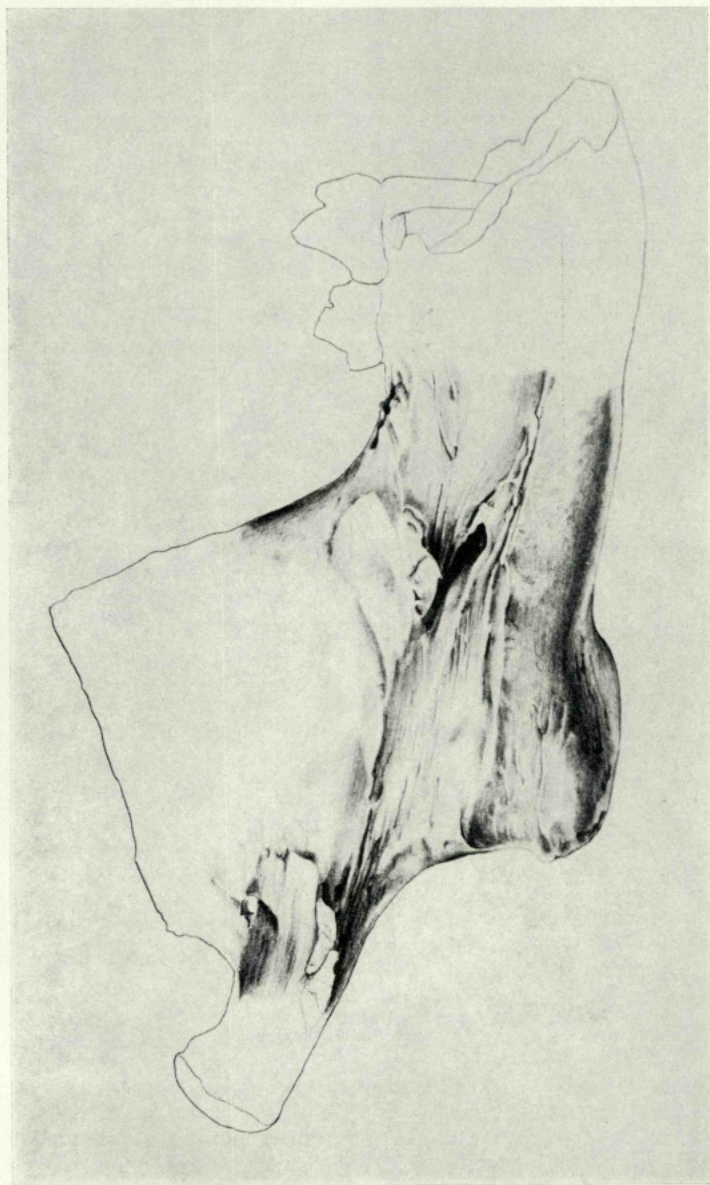
Plates II - V: Stereo photo pairs of jaw fragments of *Haldanodon*.
The line of scale is in each case 5 mm.

Plate II

A: Lateral view of the left lower jaw VJ 1001 - 155, fragment 2, (holotype of *Haldanodon exspectatus* KÜHNE & KRUSAT 1972).
B: Medial view of the same specimen.
C: Dorsal view of the same specimen.
D: Lateral view of the left lower jaw VJ 1002 - 155, fragment 2.
E: Medial view of the same specimen.
F: Dorsal view of the same specimen.
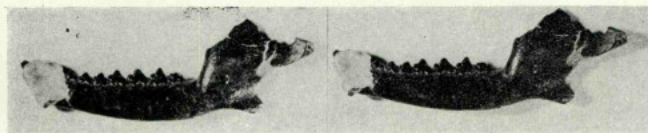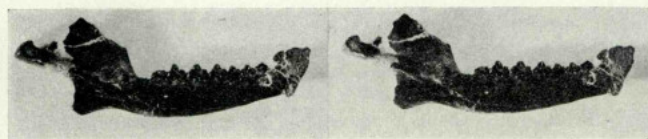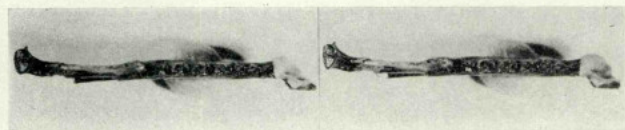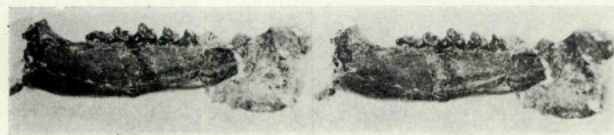
Plate III

A: Lateral view of the left lower jaw VJ 1003 - 155.
B: Medial view of the same specimen.
C: Lateral view of the right lower jaw VJ 1004 - 155, fragment 1.
D: Medial view of the same specimen.
E: Lateral view of the right lower jaw VJ 1004 - 155, fragment 2.
F: Medial view of the same specimen.
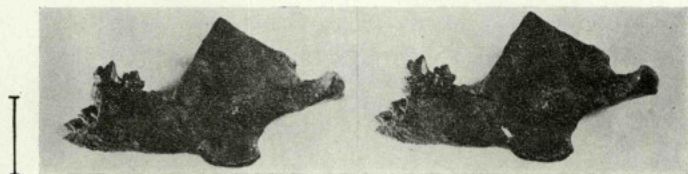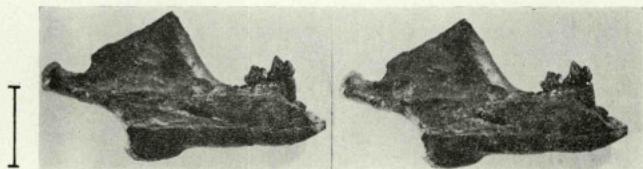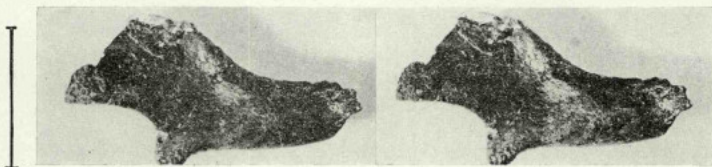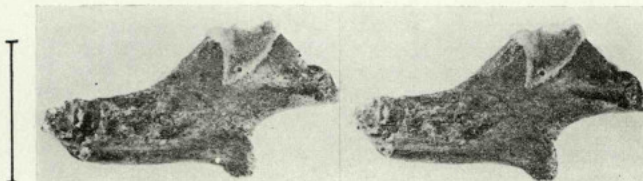
Plate IV

A: Lateral view of the right lower jaw VJ 1005 - 155, fragment 2.
B: Medial view of the same specimen.
C: Medial view of the right lower jaw VJ 1005 - 155, fragment 1.
D: Lateral view of the right lower jaw VJ 1007 - 155, fragment 1.
E: Medial view of the same specimen.
F: Lateral view of the right lower jaw VJ 1007 - 155, fragment 2.
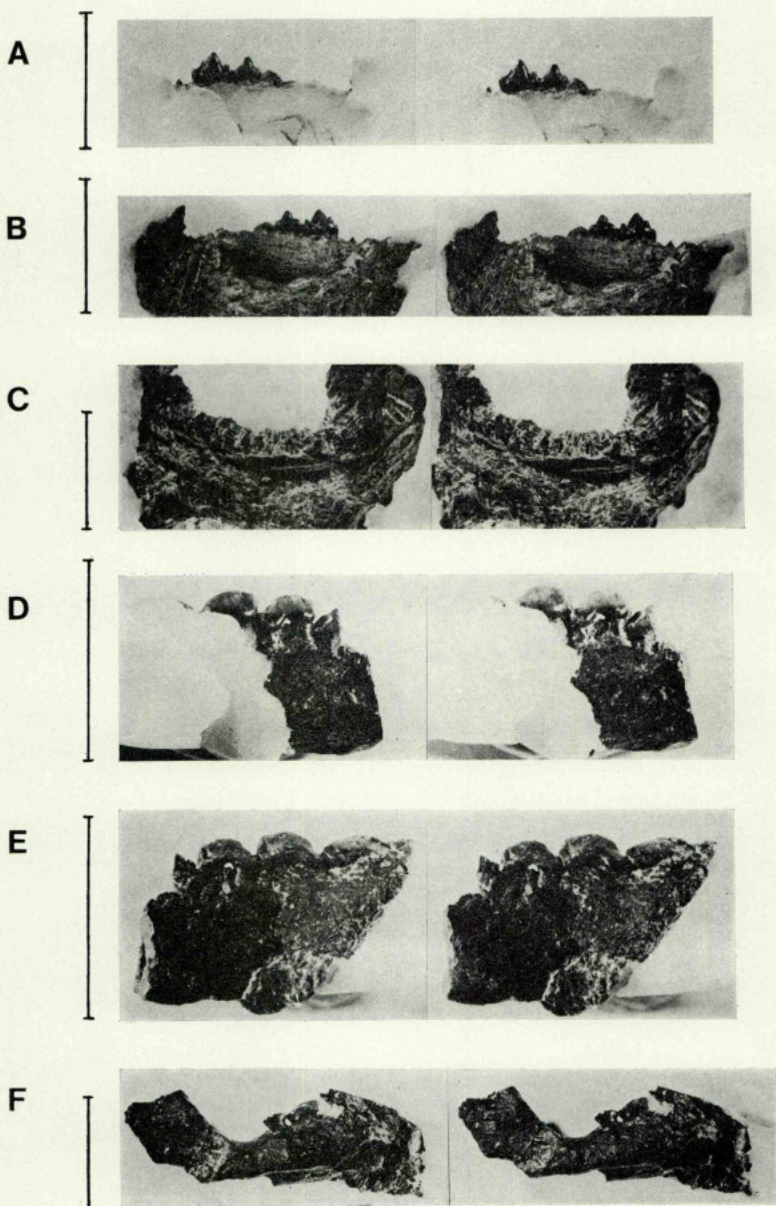
Plate V

A: Medial view of the right lower jaw VJ 1007 - 155, fragment 2.
B: Lateral view of the left anterior skull VJ 1009 - 155, fragment 1.
C: Ventral view of the same specimen.
D: Lateral view of the right anterior skull 1009 - 155, fragment 2.
E: Lingual view of P^3, M^1 and M^2 on the same specimen.
F: Occlusal view of P^3, M^1 and M^2 on the same specimen.
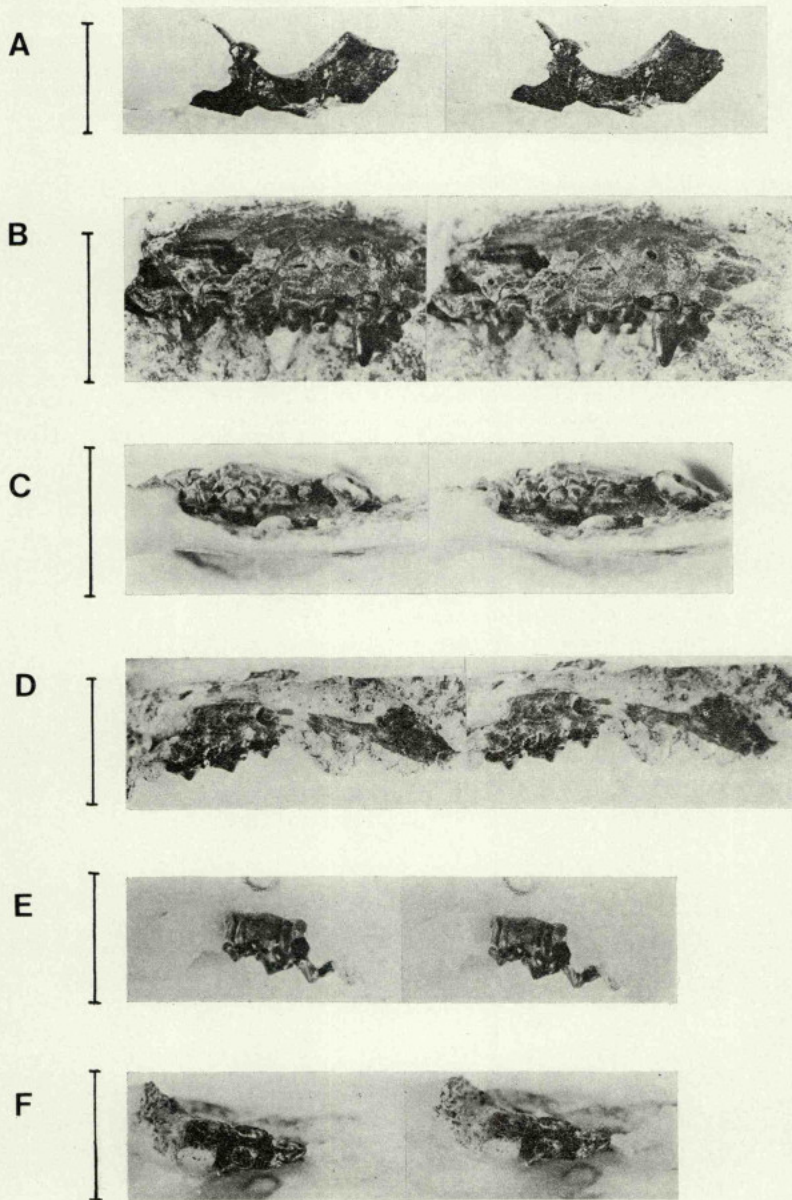
Plates VI - XII: Depiction of isolated teeth of *Haldanodon* made with the help of the scanning electron microscope.

The photos were taken with the Stereoscan Mk. II produced by Cambridge Scientific Instruments. By means of an elastic glue («Pattex») and a conductive silver paste, the objects were fastened to a flat headed brass rivet, who's shaft fits into the specimen holder of the apparatus (3 mm in diameter). They were finally rendered electrically conducting by metal evaporation of gold palladium. The exposure data are as follows:

— secondary electron image.
— record time (line speed) = 0,1 sec.
— scanning speed = 200 sec.
— negative size = 55 × 55 mm.
— Steinheil oscillograph camera with a Cinerollex cassette.

On the teeth can be observed fractures that were probably partially due to the high evacuation of the specimen chamber. For optical reasons the teeth had to be arranged in the same position in the plates that was prearranged because of the limited «lighting» possibilities at the time of exposure. Therefore, for example, most of the upper jaw teeth were mounted with the cusps pointing upward. On the occlusal views the lingual side is pointed downward.

Plate VI

A: Left P_1 VJ 1039 - 155. Occlusal view. 89 × enlarged.
B: As above. Lingual view. 89 × enlarged.
C: Left P_2 or P_3 VJ 1035 - 155. Buccal view. 60 × enlarged.
D: As above. Occlusal view. 60 × enlarged.
E: As above. Lingual view. 63 × enlarged.
F: Left P_2 or P_3 VJ 1038 - 155. Buccal view. 75 × enlarged.
G: As above. Occlusal view (the lingual side faces here upward). 75 × enlarged.
H: As above. Lingual view. 75 × enlarged.
H: As above. Lingual view. 75 × enlarged.
I: Left P^2 VJ 1013 - 155. Occlusal view. 75 × enlarged.
K: As above. Lingual view. 75 × enlarged.
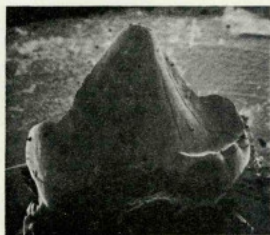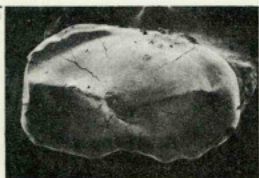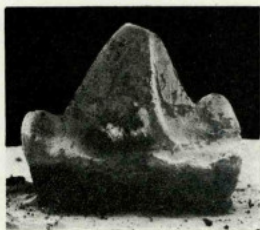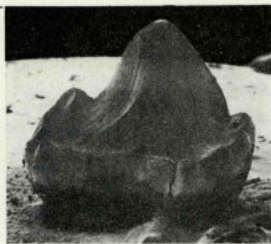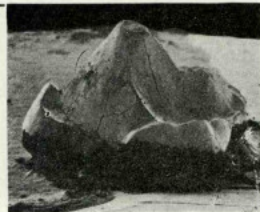
Plate VII
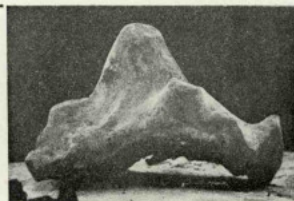
A: Right P^3 VJ 1012 - 155. Buccal view. 55 $\times$ enlarged.

B: As above. Occlusal view. 53 $\times$ enlarged.

C: As above. Lingual view. 55 $\times$ enlarged.

D: As above. Mesial view. 55 $\times$ enlarged.

E: As above. Distal view. 55 $\times$ enlarged.

F: Left P^3 VJ 1032 - 155. Linguo-occlusal oblique view. 64 $\times$ enlarged.

G: As above. Distal view. 64 $\times$ enlarged.

H: Right Pd_+ VJ 1043 - 155. Occlusal view. 53 $\times$ enlarged.

I: As above. Lingual view. 80 $\times$ enlarged.
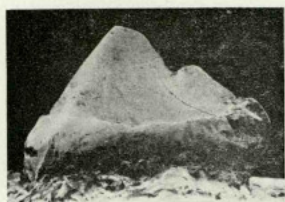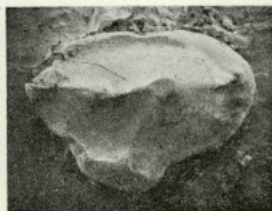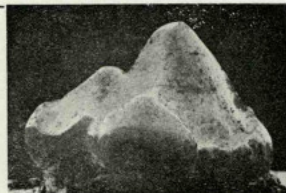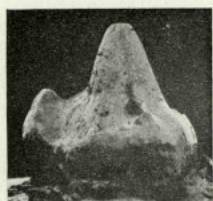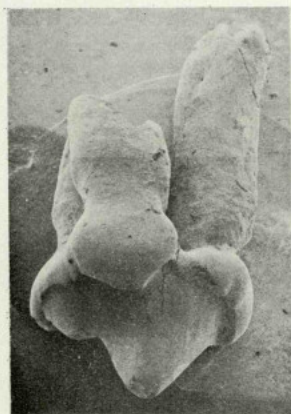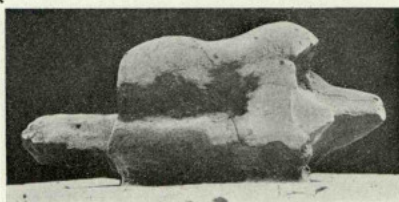
Plate VIII

A: Left Pd_+ VJ 1028 - 155. Buccal view. 55 $\times$ enlarged.

B: As above. Occlusal view. 69 $\times$ enlarged.

C: As above. Lingual view. 55 $\times$ enlarged.

D: As above. Mesial view. 53 $\times$ enlarged.

E: As above. Distal view. 55 $\times$ enlarged.

F: Right Pd^+ VJ 1030 - 155. Occlusal view. 68 $\times$ enlarged.

G: As above. Lingual view. 68 $\times$ enlarged.

H: As above. Distal view. 85 $\times$ enlarged.

I: Right Pd_+ VJ 1041 - 155. Lingual view. 82 $\times$ enlarged.

K: As above. Radical view. 65 $\times$ enlarged.
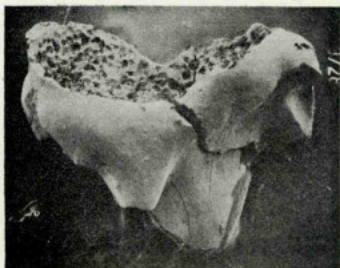
Plate IX

A: Right M$_+$ 1010 - 155. Bucco-radical oblique view. 60 $\times$ enlarged.

B: As above. Radical view. 60 $\times$ enlarged.

C: Right M$_+$ VJ 1021 - 155. Occlusal view. 50 $\times$ enlarged.

D: As above. Lingual view. 50 $\times$ enlarged.

E: Right M$_+$ VJ 1015 - 155. Buccal view. 45 $\times$ enlarged.

F: As above. Occlusal view. 47 $\times$ enlarged.

G: As above. Lingual view. 36 $\times$ enlarged.

H: As above. Mesial view. 45 $\times$ enlarged.

I: As above. Linguo-occlusal oblique view. 36 $\times$ enlarged.
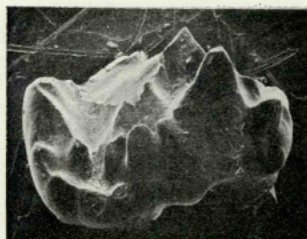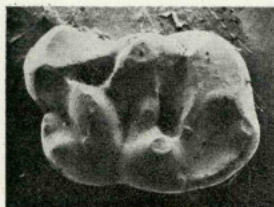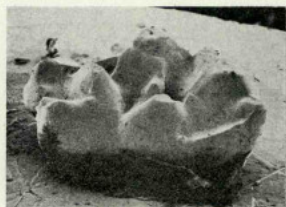
K: As above. Distal view. 45 $\times$ enlarged.
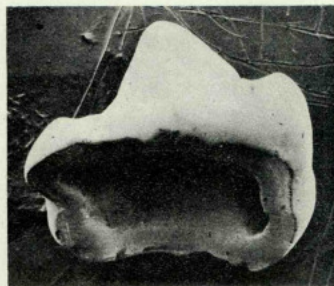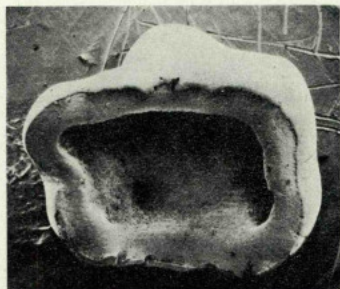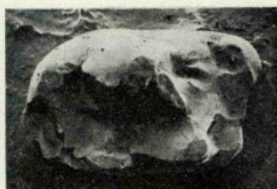
Plate X

A: Left M_+ VJ 1016 - 155. Lingual view. 42 × enlarged.
B: Left $M_{5?}$ VJ 1046 - 155. Lingual view. 45 × enlarged.
C: Right $M_{5?}$ VJ 1017 - 155. Occlusal view. 50 × enlarged.
D: As above. Lingual view. 50 × enlarged.
E: Right M_+ VJ 1026 - 155. Occlusal view. 52 × enlarged.
F: Aberrant left M_+ VJ 1018 - 155. Occlusal view. 52 × enlarged.
G: As above. Linguo-occlusal oblique view. 52 × enlarged.
H: Worn down left M_+ VJ 1047 - 155. 64 × enlarged.
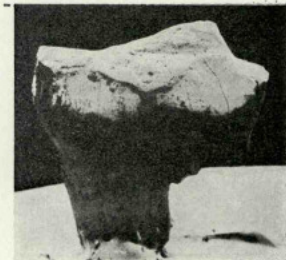I: As above. Linguo-occlusal oblique view. 64 × enlarged.
K: As above. Lingual view. 64 × enlarged.
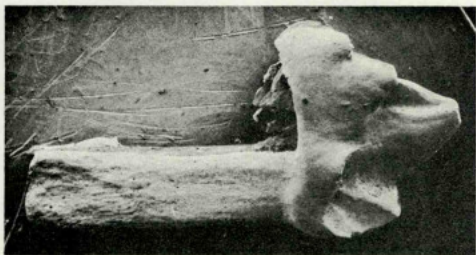
Plate XI
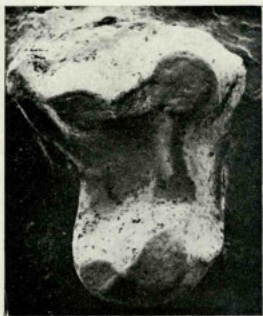
A: Worn down right M_+ VJ 1045 - 155. Occlusal view. 54 × enlarged.
B: As above. Linguo-occlusal oblique view. 54 × enlarged.
C: Right M^+ VJ 1048 - 155. Occlusal view. 79 × enlarged.
D: As above. Lingual view. 79 × enlarged.
E: As above. Distal view. 79 × enlarged.
F: Right $M^{3?}$ VJ 1014 - 155. Occlusal view. 53 × enlarged.
G: As above. Linguo-occlusal oblique view. 48 × enlarged.
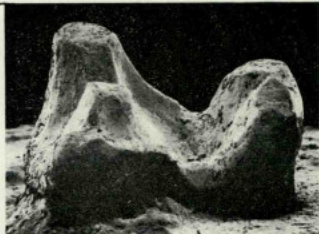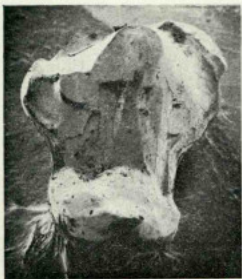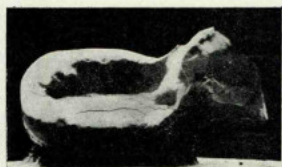H: As above. Lingual view. 48 × enlarged.

Plate XII

A: Right $M^{3?}$ 1014 - 155. Occlusal view. 44 × enlarged.
B: Right M^+ VJ 1050 - 155, lingual half. Occlusal view. 37 × enlarged.
C: As above. Disto-occlusal oblique view. 37 × enlarged.
D: As above. Distal view. 37 × enlarged.
E: Left M^+ VJ 1051 - 155, lingual half. Occlusal view. 58 × enlarged.
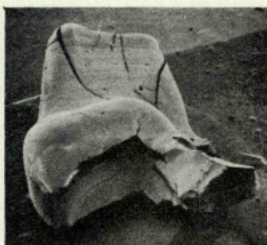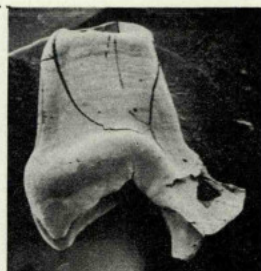F: As above. Lingual view. 52 × enlarged.
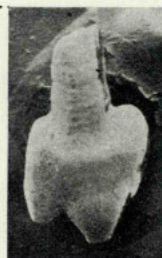
A

B

C

D

E

F

MEMÓRIAS DA COMISSÃO GEOLÓGICA DE PORTUGAL (1857-1869)

1865 — GOMES, B. A. — *Vegetaes fosseis;* — *Flora fossil do terreno carbonífero das visinhanças do Porto, Serra do Bussaco e Moinho d'Ordem, próximo de Alcacer do Sal.* 46 p., 6 est. (Com tradução em francês). Esgotada.

1865 — PEREIRA DA COSTA, F. A. — *Da existencia do homem em epochas remotas no valle do Tejo;* — *Noticia sobre os esqueletos humanos descobertos no Cabeço da Arruda.* 40 p., 7 est. (Com tradução em francês). Esgotada.

1866 — RIBEIRO, C. — *Estudos geologicos;* — *Descripção do terreno quaternário das bacias hydrographicas dos rios Tejo e Sado.* 164 p., 1 carta (com versão francesa por Dalhunty). Esgotada.

1866-67 — PEREIRA DA COSTA, F. A. — *Molluscos fosseis;* — *Gasteropodes dos depositos terciarios de Portugal.* 2 fasc. 263 p., est. (Com versão francesa por Dalhunty). Esgotada.

1867 — NERY DELGADO, J. F. — *Estudos geologicos;* — *Da existencia do homem no nosso solo em tempos mui remotos provada pelo estudo das cavernas;* — *Notícia ácerca das grutas de Cesareda.* 133 p., 3 est. (Com versão francesa por Dalhunty). Esgotada.

1867 — RIBEIRO, C. — *Estudos geológicos;* — *Memória sobre o abastecimento de Lisboa com águas da nascente e águas de rio.* 119 p. Esgotada.

1868 — PEREIRA DA COSTA, F. A. — *Monumentos prehistoricos;* — *Descripção de alguns dolmens ou antas de Portugal.* 97 p., 3 est. (Com tradução em francês). Esgotada.

MEMÓRIAS DA SECÇÃO DOS TRABALHOS GEOLÓGICOS DE PORTUGAL (1869-1886)

1871 — RIBEIRO, C. — *Descripção de alguns silex e quartzites lascados encontrados nas camadas dos terrenos terciário e quaternário das bacias do Tejo e Sado.* 57 p., 10 est. (Com tradução em francês). Esgotada.

1876 — NERY DELGADO, J. F. — *Terrenos paleozoicos de Portugal;* — *Sobre a existencia do terreno siluriano no Baixo Alentejo,* 35 p., 2 est., 1 carta (Com tradução em francês). Esgotada.

1878 — RIBEIRO, C. — *Estudos prehistoricos em Portugal;* — *Noticia de algumas estações e monumentos prehistóricos,* 1.º vol. 72 p., 21 est. (Com tradução em francês). Esgotada.

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1880 — CHOFFAT, P. — *Étude stratigraphique et paléontologique des terrains jurassiques du Portugal;* — *Le Lias et le Dogger au Nord du Tage.* (XII + 72) p.

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