IX.—*On the Skull and Dentition of* Paraceratherium bugtiense: *a Genus of Aberrant Rhinoceroses from the Lower Miocene Deposits of Dera Bugti.*

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(*Communicated by* A. Smith Woodward, *F.R.S.*)

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Contents.

Introductory and Historical.

In 1911 a preliminary notice* was published of a rhinocerotine lower jaw from the Bugti deposits of Baluchistan. This specimen shows a very peculiar feature of the front teeth, which instead of being procumbent, or even upturned, as in other rhinoceroses, are formed into a pair of downwardly turned tusks. On the strength of this well-marked character a new genus *Paraceratherium* was formed for the species. The posterior part of the lower jaw and loose upper and lower teeth had already been discovered in the same locality by Dr. Pilgrim, who, being without the anterior parts of the jaw, described† the form as *Aceratherium bugtiense*. The same investigator had already described some curious teeth, which he had found lying separately, as possible incisors of a skull which he named *Bugtitherium grandincisivum*, an animal which is possibly an Entelodont, but is still insufficiently known. These teeth are now known to be the lower incisors of *Paraceratherium*.

The lower jaw, on which the genus was founded, was obtained during an expedition by the present writer to Baluchistan in 1910, together with such other specimens of rhinoceroses as showed the presence of several forms of small, medium and large size, and one of an exceeding size since described as *Baluchitherium osborni*.‡ The last named animal has again to be considered in connection with the present species.

During a second expedition in the following year was obtained by good fortune

* C. Forster Cooper, 'Ann. Mag. Nat. Hist.,' vol. viii, p. 711.

† G. E. Pilgrim, 'Mem. Geol. Surv. India,' vol. iv., No. 2, 1912.

‡ C. Forster Cooper, 'Ann. Mag. Nat. Hist.,' vol. xii., p. 376 (Thaumastotherium) and 'Phil. Trans.,' Series B, vol. 212, pp. 35–66.

not only a skull, which from its position a little further in the cliff and from the similar condition of tooth wear, undoubtedly belongs to the jaws already obtained, but also parts of three other skulls and further fragments of lower jaws and separate teeth. The skull and dentition can therefore be described with fair accuracy, excepting only the front upper part. This lacuna in our knowledge is unfortunate as, owing to the aberrant shape of the corresponding part of the lower jaw, it is not possible to do more than hazard a guess at the shape of the nasal and premaxillary region.

All these specimens were discovered in a bone-bed at Chur-Lando, of which the first sign was found at the end of the first expedition, when most of the time available had been expended in prospecting in other and less rich parts. A piece of a limb bone was observed projecting from the side of a small nullah and excavation immediately started, and for the short remaining period of the expedition all its members* worked hard to obtain as much as possible. During the second expedition the bone bed was further laid open and showed a layer of bones covering many square yards. From the false bedding of the sands, gravels and clays there was the appearance of some eddy or backwash of a flooded river and here was found a quantity of bones of various animals (fig. 1) for the most part much disturbed and mixed together by the action of the water, gnawed and broken by contemporary crocodiles and to some extent dislocated by the subsequent faulting of small earthquakes, which are still a common occurrence in these parts of Baluchistan.

It is convenient to describe here one specimen of which the illustration given (fig. 2) is the only record. At the extreme corner of the bone-bed, as far as excavated, a pelvis of large size was uncovered. It was apparently in good condition as far as the external surface was concerned, and was carefully hardened and plastered for transport. A box was ordered from Jacobabad to hold it and another of equal size to be loaded as a counterpoise for the camel. They arrived in camp only at the end of the expedition, when the temperature was much over 100 degrees in the shade and a steamer at Karachi had to be caught. On loading up it was found that while the camel could rise it was unable to step down a ledge of rock a few inches in height. In view of a three days' journey to Jacobabad and the short time at disposal, the specimen was hurriedly unpacked and placed on a folded tent on top of the camel, a load it could easily manage. Owing, however, to the peculiar gait of these animals the specimen became cracked, and finally was ground to powder and reluctantly had to be abandoned. It is not certain whether this pelvis is that of *Baluchitherium* or *Paraceratherium*, possibly the former on account of its considerable size.

The fauna of this particular bone-bed is most interesting. In addition to remains of *Paraceratherium* and *Baluchitherium* other rhinoceroses occur, representing the genera

* Dr. W. M. JEFFREYS accompanied me on the first expedition and gave the most valuable help. The other workers were the native butler and cook, the interpreter Nathoo Ram, and an excellent Baluchi duffadar Abderrahman Khan. On the second expedition, knowing better the kind of work in hand, four native workmen were brought from Jacobabad.

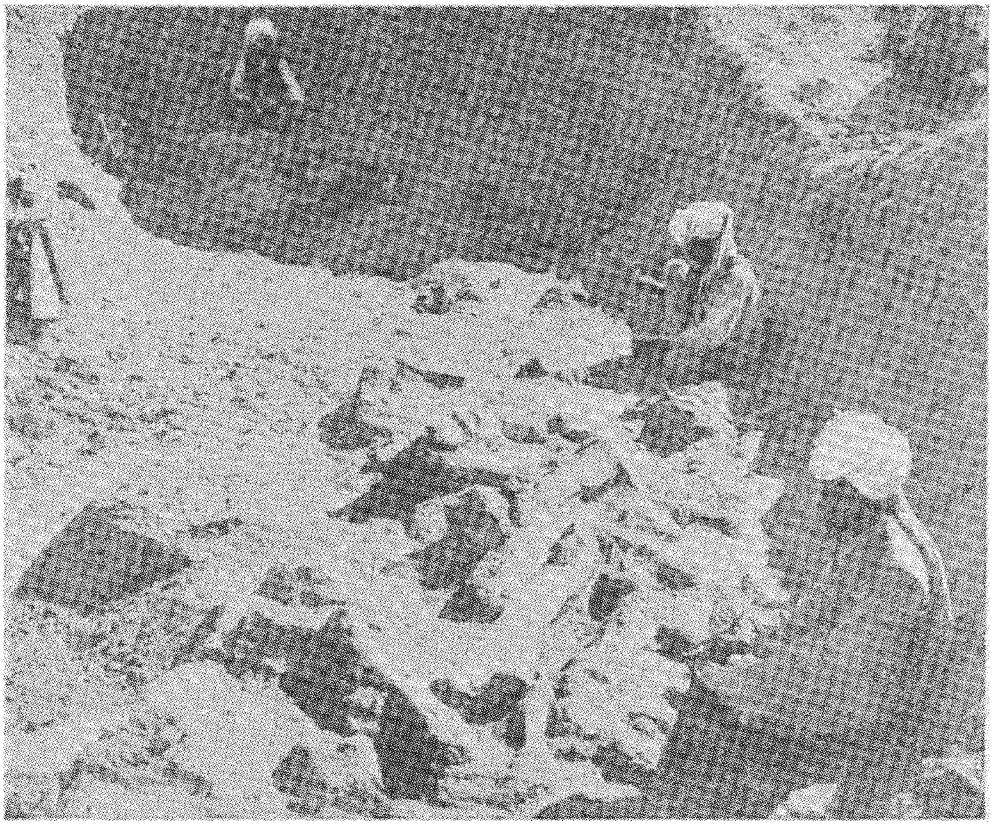

FIG. 1.—Bone bed at Chur-Lando, showing bones of *Baluchitherium* and *Paraceratherium* in situ.

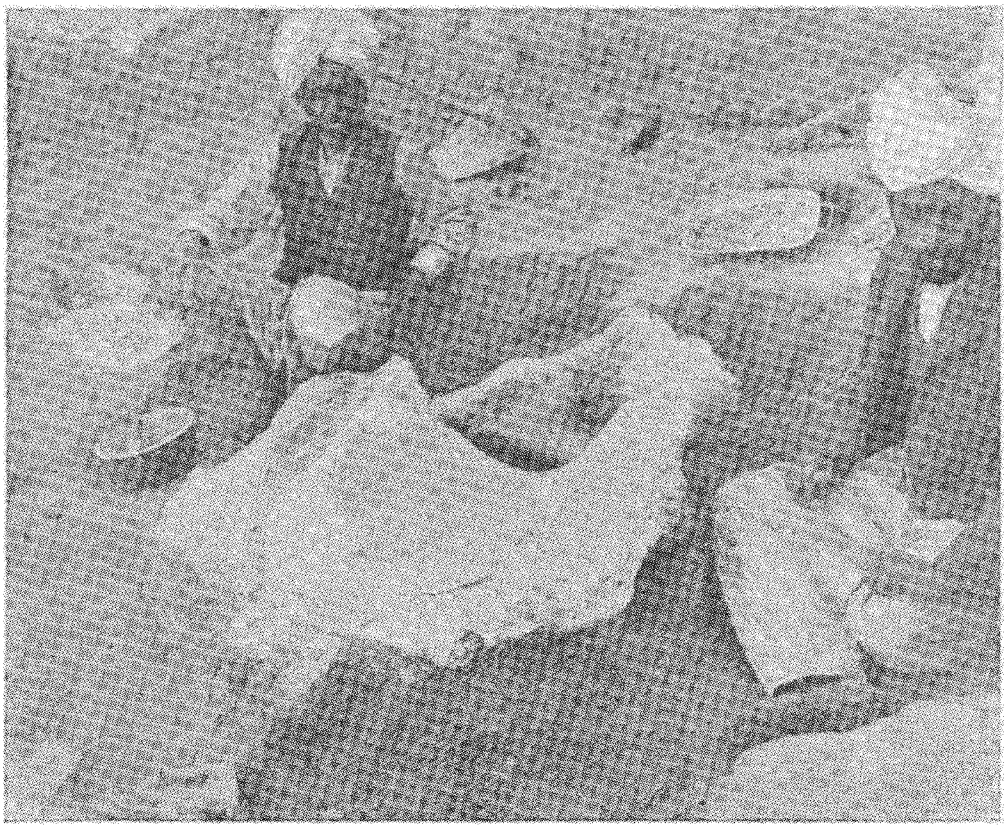

FIG. 2.—Pelvis of ? *Baluchitherium*.

Diceratherium, *Teleoceras*, and *Aceratherium*, which have not yet been described. The remaining forms are chiefly *Anthracotheres* of an advanced type such as *Gelasmodon*, *Hemimeryx*, etc., and a problematic Hippopotamus, *Aprotodon*.*

The whole fauna is a peculiar one, and at the time was unknown elsewhere; but more recently two of its forms—*Paraceratherium*, the subject of the present paper, and *Baluchitherium*—have been found in other places. Both species were discovered in Turkestan by Borissiak, who regards them as one form and has described them under the name *Indricotherium*, while *Baluchitherium* has still more recently been discovered in Mongolia by Granger of the American Museum. These two forms, then, had a wide range over Asia, and although the Anthracothere fauna seems at present peculiarly an Indian one its range may yet be found to be wider.

Skull of Paraceratherium.

Of the skull of this species there are four specimens, of which none is perfect and two only have any teeth, the remaining two consisting of no more than the fairly complete occipital region as far forward as the posterior parts of the zygoma. The best specimen is complete along the lower surface from the condyles to the second premolar on the left side and to the third premolar on the right. It is an old animal, in that the premolars are much worn and the molars considerably so; it is aberrant, in that the third molars are not developed but are represented in the specimen by shallow depressions in which no trace of tooth can be found. The upper surface is badly crushed on one side but fairly good on the other.

In general shape these skulls, which vary somewhat in size, are rather larger than a specimen of a large white rhinoceros (*R. simus*) in the Cambridge University Museum. The width of the occipital condyles† of the specimen of *R. simus* is 152 mm. In the four specimens of *Paraceratherium* the same measurements are 186, 188, and in two specimens 210 mm. These skulls will be referred to as A, B, C, and D respectively.

A side view (fig. 3) of the best specimen (B) shows a low occiput with only a moderate crest and a rather flat surface as far as the posterior region of the orbit. From here the skull begins to rise to the nasal region, but to what extent cannot accurately be told owing to the absence of that part, and also to the possibility of some crushing. However this may be, the upper surface of the skull seems to have been more level and with less of a saddle than that of *R. simus*. The anterior border of the orbit lies over the middle of the first molar, a position more forward than in primitive rhinoceroses, where according to Osborn‡ it lies over the second molar and occupies a position half-way between the two ends of the skull. To restore the missing front

* C. Forster Cooper, 'Ann. Mag. Nat. Hist.,' 1913, vol. xii., p. 515, and 1915, vol. xvi., p. 404. A complete account of the Anthracotheriidæ is appearing in the 'Palæontologia Indica.'

† This is an important measurement to have in considering the connection with the atlas of *Baluchitherium*. *Cp.* Forster Cooper, 'Phil. Trans.,' *loc. cit.*

‡ Osborn, 'Mem. Am. Mus. Nat. Hist.,' vol. i., part 3.

part of the present skull (specimen B) on this basis would make it disproportionately long in the premaxillary region and out of keeping with the lower jaws. The facial region, therefore, is not long, and in this respect is not primitive.

The zygoma, considering the large size of the skull, is thin and weak when compared with the corresponding part of *R. simus*.

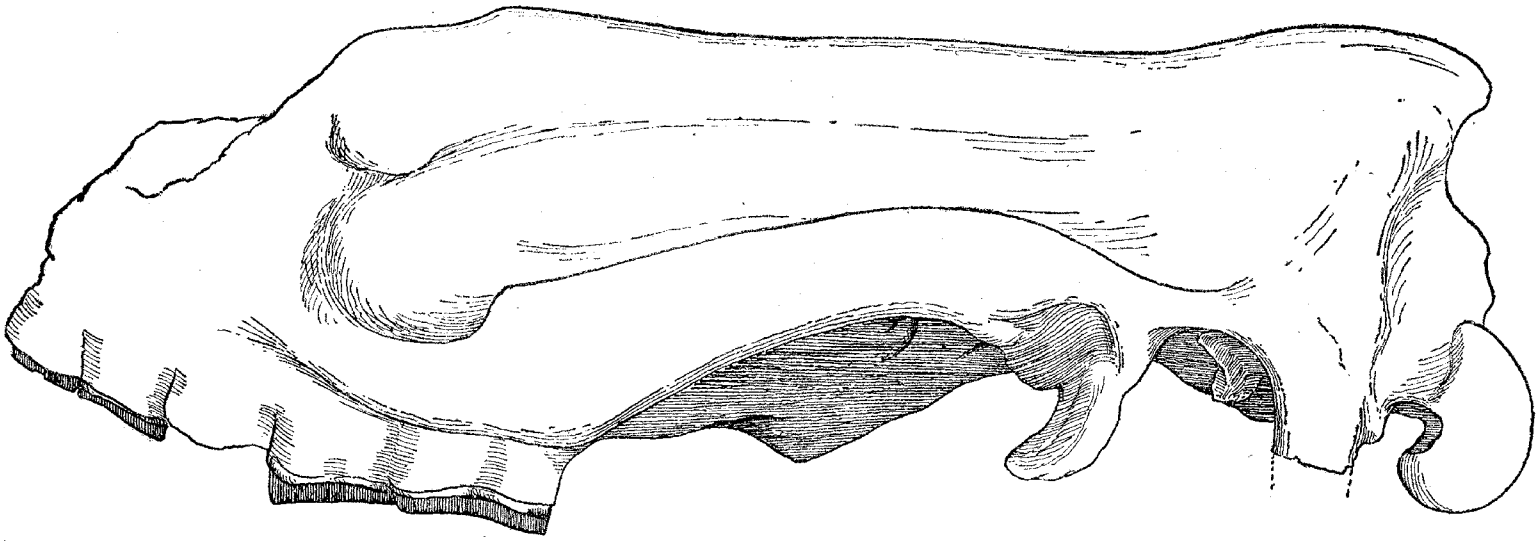

FIG. 3.—Skull B, side view. $\times \frac{1}{4}$.

FIG. 4.—Skull D, side view, showing the broad tympanic process. $\times \frac{1}{4}$.

Characters that can be observed in a side view of the skull (figs. 3 and 4) are the prominence of the condyles and, more particularly, the conformation of the parts connected with the ear region. A reference to modern rhinoceros skulls* shows that the external auditory meatus tends to become closed below by the expansion forward of the post-tympanic process, which may abut on, or even (*R. sondaicus*) become

* Figured by OSBORN from papers by FLOWER and HATCHER, *loc. cit.*, figs. 28–32.

fused with, the post-glenoid process. As far as modern forms are concerned the most open condition is found in *R. sumatrensis*, though even here the post-tympanic process runs forward to a considerable degree. Of extinct forms the "Aceratheres" show a wide range, some being open and others closed, while *Hyrachyus*, one of the oldest rhinoceroses known, though not considered to be on the direct line of ancestry of any later forms, has, according to OSBORN'S figure,* the post-tympanic and par-occipital processes pressed together, but with the line of junction still clearly marked, and in front a rather narrow ∩-like space between them and the post-glenoid process of the squamosal.

In the four skulls of *Paraceratherium*, while attention must be called to the considerable variation in size and shape of all these processes, the condition of this region is different from those described above. The post-tympanic and par-occipital processes, unlike *Hyrachyus* and like modern forms, are closely fused and without any trace of this original separation, but, like *Hyrachyus*, there is no forward extension of the post-tympanic to separate off the auditory meatus. The width between the post-tympanic and post-glenoid processes is a very striking feature, and results in a wide bay in some portion of which ran the auditory meatus, but whether straight out or in an upward direction there is no evidence. The variation in size of these parts from the comparatively slender formation of skull B, to one nearly twice the size in skull D, is shown in fig. 4.

The base of the skull (fig. 5) shows some features worthy of notice: the occipital

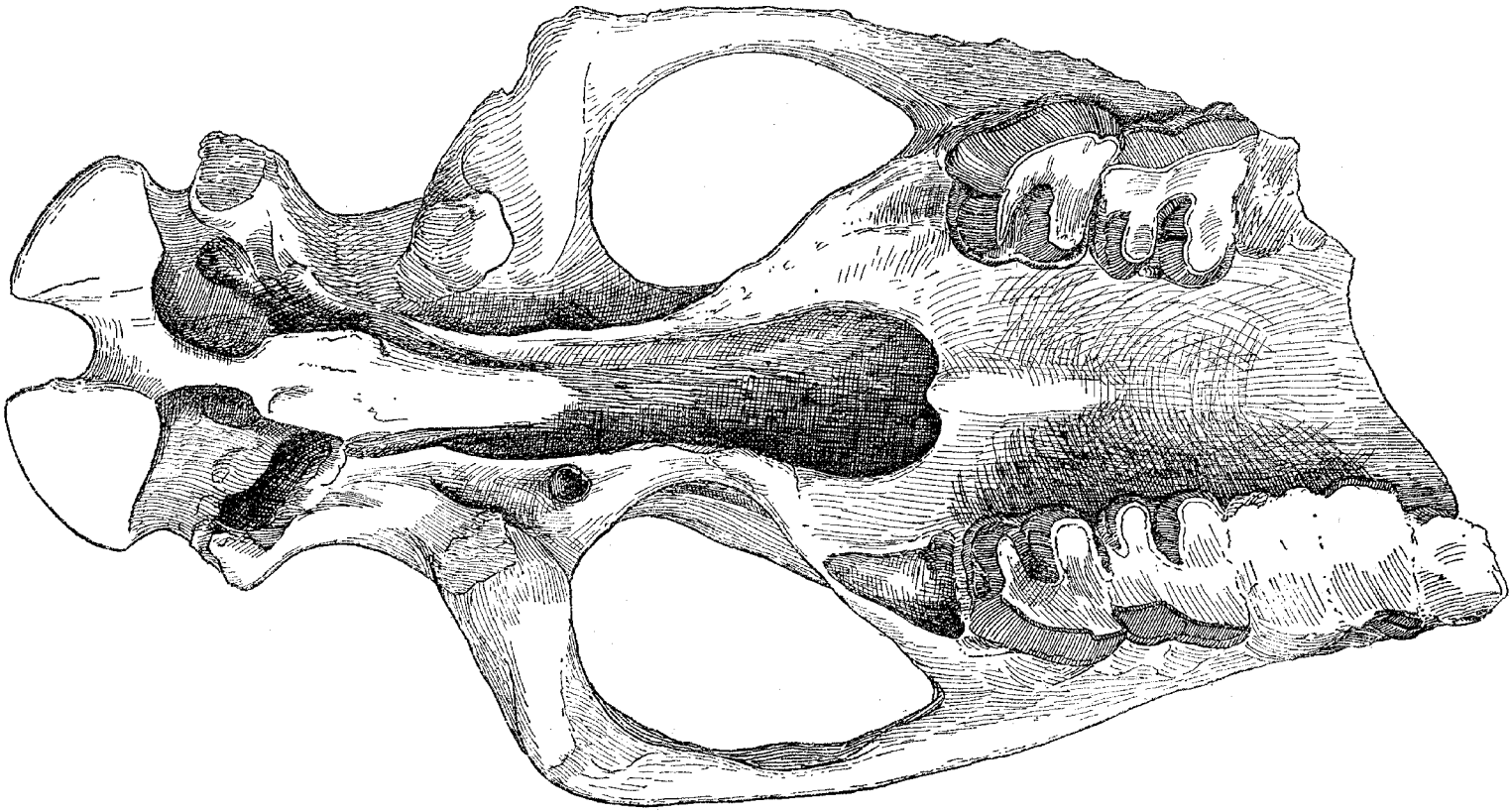

FIG. 5.—Skull B, palatal surface. × ¼.

* *Loc. cit.*, Plate XIIA.

condyles are deeply undercut along their ventral borders as also is the forward process of the basi-occipital, which instead of being a plain basilar ridge is further accentuated by a marked depression on each side.* These spaces are presumably for the insertion of the rectus capitis muscles which would require strong insertions to flex the heavy and long head. The basisphenoid swells out into an elongated boss, rather more pronounced than in modern rhinoceroses,† which flattens out towards the presphenoid but which has well marked grooves from the foramen lacerum medium in which ran the palatine nerve and artery.

The region of the vomer is flat and extends forward to a great length so that the posterior borders of the choanæ lie more forward than, and are overhung by, the posterior border of the palate, and there is no trace of the bony septum dividing the nares. This condition is very different from modern Perissodactyles, where the choanæ are always visible and the septum large. What the condition was in extinct forms it is not possible to state with certainty, but in a small skull (apparently a species, as yet undescribed, of *Diceratherium*) from the Bugti beds, the condition of these parts is more like the modern one.

The figures published by Osborn‡ appear as though *Hyrachyus* and most of the Aceratheres approached more the specimens under discussion, but it is not always certain from the illustrations that the skulls have been fully developed in these parts from the matrix. The forward position of the choanæ seems to be the more usual in mammalia generally, but the smallness or absence of the dividing septum is unusual. The posterior border of the palate shows a comparatively small tubercle, and the palate itself is a deep concave dome, whose deepest part is at a level between the first and second molars. The tympanic bullæ and connected parts are not well preserved and have mostly fallen out. In one specimen (D) it is in place on one side, but is in too poor a condition for description except to say that it seems quite comparable to that of modern rhinoceroses.

Of such foramina as can be observed, the condyloid is quite large and close to the foramen lacerum posterius but separated therefrom by a bony septum. The jugular and carotid sections of the foramen lacerum anterius are separated by a bridge of bone, and the postglenoid, unlike that of the rhinoceros, is very large and is situated at the base of the postglenoid process. An alisphenoid canal is present. A post squamosal foramen situated between the squamosal and the ex-occipital bones, a foramen which is of variable occurrence in modern forms,§ is here present.

The dorsal surface (fig. 6) has a flat sagittal crest which spreads out gradually to its greatest width over the orbits. There is no observable sign of a horn having been

* This is least marked, curiously enough, in the largest of the skulls (D).

† Comparisons unless otherwise specified are with modern rhinoceroses.

‡ 'Memoir,' *loc. cit.*

§ This foramen is particularly well marked in the tapir, where it is bounded in part by an exposure of the mastoid.

present on these parts of the skull, and from the general smoothness of all the skull-bones it is probable that horns were entirely absent on the nasal bones as well.*

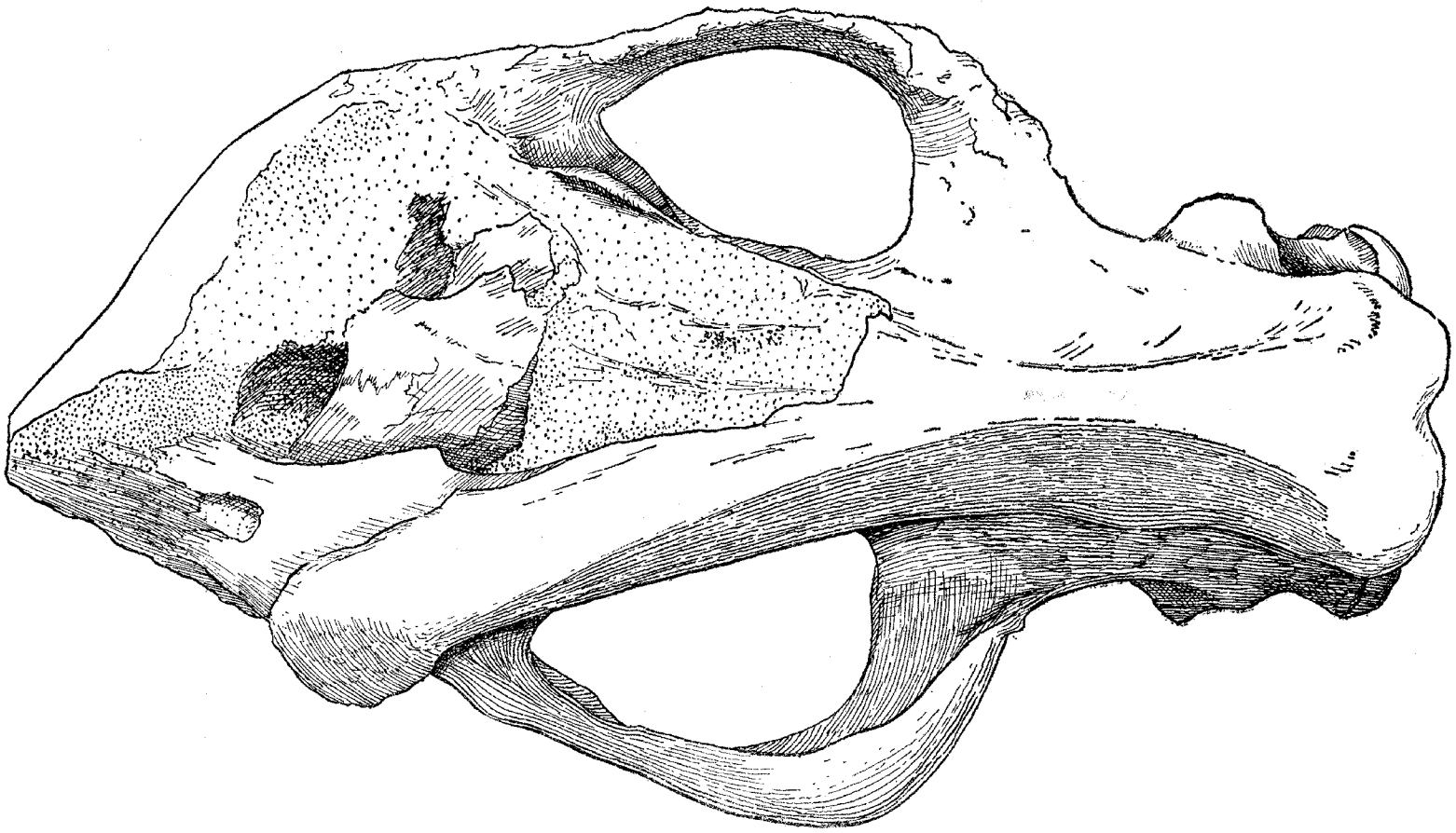

FIG. 6.—Skull B, upper surface. × ¼.

The skull as a whole is clearly rhinocerotine in character, dolichocephalic, with the antorbital portion of the face rather shorter than the postorbital. The total length of the skulls may be estimated at not less than 900 mm. (No. B), while the largest (No. D) may have been a little longer. These measurements have to be considered when comparing the relationships of this form with the elephantine rhinoceros *Baluchitherium osborni*, whose skull, though not found in the Bugti deposits, has now fortunately been discovered by Granger in Mongolia.†

* This test, the presence of exostoses on parts of the skull other than the actual horn bases, such as on the zygoma and around the orbit in horn-bearing animals, and *vice versa*, was pointed out to me by Baron VON NOPSCA. It is a useful, if indirect and perhaps not absolute, criterion which seems to be supported by an examination of the skulls of recent horn-bearing animals. The exostoses are supposed to be due to a superabundance of horn-forming hormones.

† This Chinese skull, a separate species *B. grangeri* (OSBORN), measured on the cast is nearly 4 feet 3 inches long (= say 1300 mm.). See note in 'Natural History New York,' vol. xxii., No. 6, p. 569.

Dentition of Paraceratherium.

Jaws and Lower Teeth.

With the exception of the as yet undiscovered front part of the skull, the dentition is fairly completely known and is of great interest. The formula may provisionally be written :—

$$\text{I. } \frac{?}{1} \text{ C. } \frac{?}{0} \text{ PM. } \frac{3}{3} \text{ M. } \frac{3}{3}.$$

The chief generic distinction rests on the shape and position of the lower incisors, and these together with the bone parts of the jaw may be described first. Of lower jaws there is one specimen (the type of the genus) almost complete, of a very aged animal; a right ramus of a less elderly but also adult animal; and a fragment with first three premolars of a young form, together with other fragments, notably two symphyses, and a large number of loose teeth; enough in all to give a complete picture of the lower dentition.

The jaws themselves have already been described and figured,* and the only correction necessary to the original description concerns the lower border of the ramus, which was stated to be concave owing to crushing and probably flat. In the young adult specimen here figured (fig. 7) the lower border is seen to be slightly convex, there being a regular

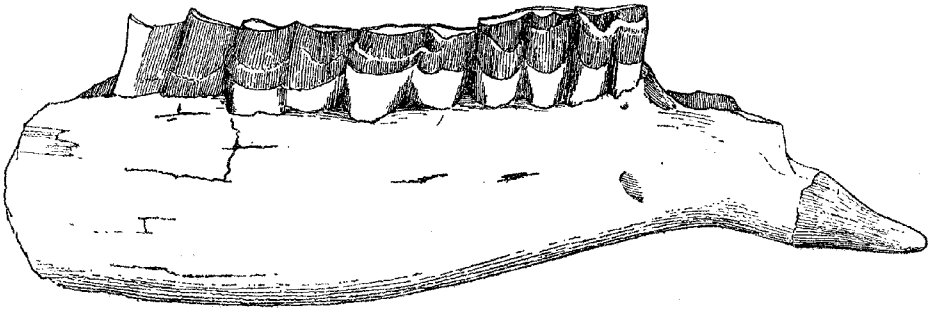

Fig. 7.—Lower jaw, outer view of right side of a small adult. × ¼.

curve under the whole molar-premolar series and a downward bend at the region of the incisors, the greatest depth being beneath the first and second molars.† This jaw, though not so old as the larger type specimen, is fully adult and with fairly well worn cheek teeth; in spite of this, however, the incisor shows no sign of use.

The two fragments of symphyses (fig. 8, A–B) mentioned above require some comment, they are larger and more massive than the other specimens as the comparative measurements show.‡

It is unfortunate that in each case the teeth have all been splintered off leaving only the roots, but as far as can be seen from the measurements of the teeth sockets, they were not larger than the other specimens. Both specimens have a slight swelling

* C. Forster-Cooper, 'Ann. Mag. Nat. Hist.,' Series 8, 1911, p. 711, Plate X.

† In this specimen the first premolar is absent through loss.

‡ See table of measurements, p. 390.

underneath the symphysis, which in one case amounts to a distinct boss. It is possible that these fragments represent the jaws of males and point to the males being a little more massive but not so noticeably large as to give them the size of a *Baluchitherium*.

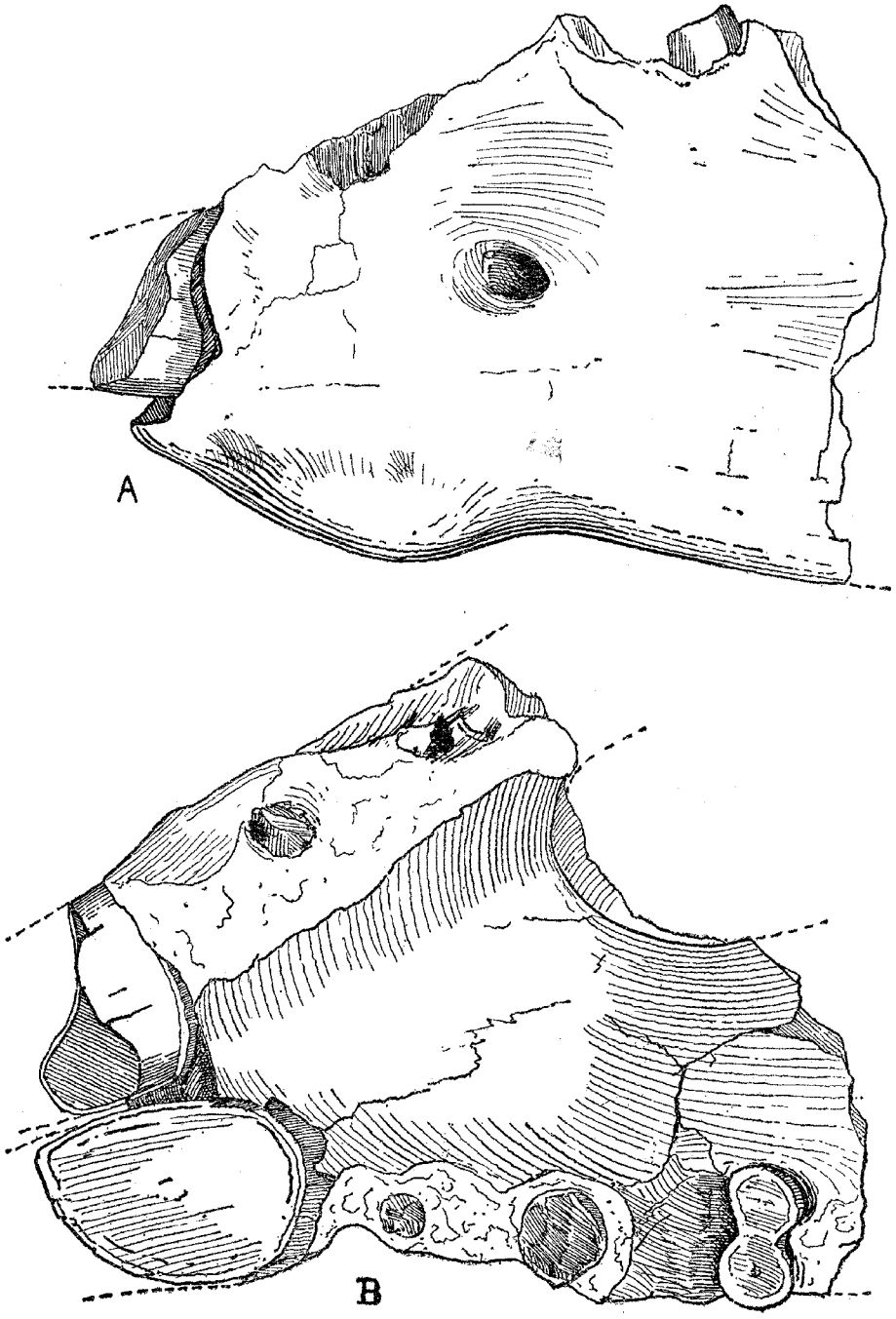

FIG. 8.—Mandibular symphysis. A side view; (B) upper surface. × ½.

A large number of lower incisors and anterior premolars have been found. Of the former there are in the present collection altogether ten specimens and PILGRIM* has figured

* PILGRIM ('Rec. Geol. Surv. Ind.,' vol. 37, pl. 4) figured as the incisors of *Bugtitherium grandincisivum*. BORISSIAK found similar teeth at Turgai ('Imp. Akad. Sci., Petrograd,' 1918) which he described as upper incisors and canines of *Indricotherium* (= *Baluchitherium*). One of the two teeth figured by BORISSIAK is more curved than the other and is generally a little different. It certainly is canine-like in

two more. Six of them show no signs of wear whatever and the remainder have no more than a slight abrasion just at the tip, which in some cases is produced a very little way along the dorsal surface. In shape, these teeth consist of a sharp cone averaging from 2 to $2\frac{1}{2}$ inches supported on a stout root about 4 inches long.

These teeth lie as a pair at the front end of the jaws pointing forward and downward, they are slightly divergent at their tips but closely opposed at the base of the crowns, where they are produced into an internal ridge on which is a pressure mark where their bases touch one another. There is some variation in the size and thickness of the crowns which is sufficiently shown in the illustration (fig. 9). The roots vary

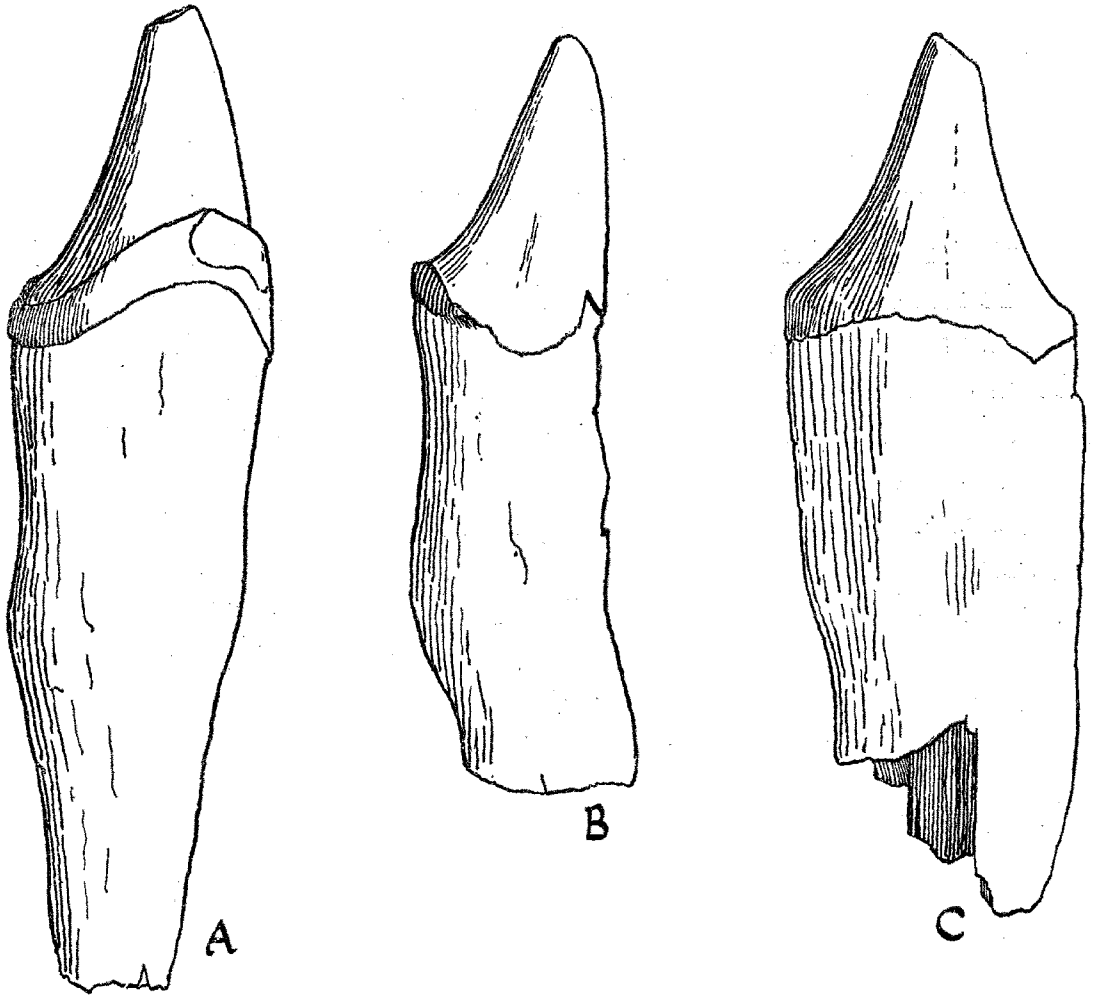

FIG. 9.—Three left lower incisors: (A) internal; (B) lower; (C) external faces. $\times \frac{2}{3}$.

rather more, some being quite straight, others a little curved, while in section they are usually oval but occasionally nearly round.

What was the function of the lower incisors it is hard to tell, since they show so little signs of use; evidently they were not used for digging and it is not easy to see any offensive or defensive value in them. In the earlier history of the genus they may

appearance. The presence of these two strange genera both in Turkestan and in Baluchistan is very curious, and their relationships require elucidation. See note at end of this paper.

have had any of these functions but in this, apparently the last stage, they seem to be functionless relics.

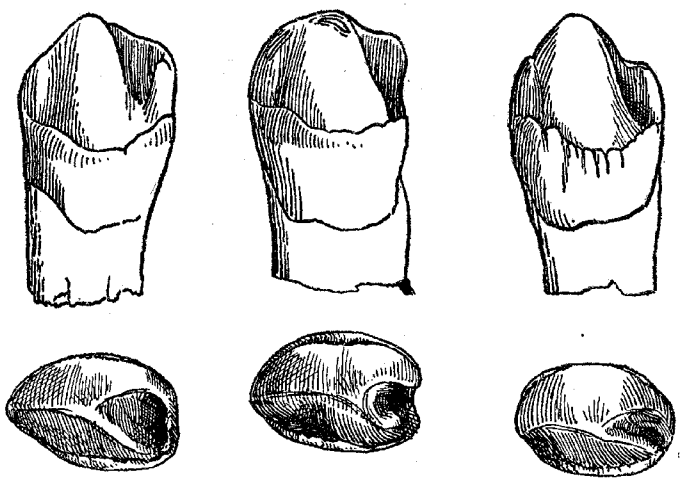

FIG. 10.—Three first lower premolars, internal and crown surfaces. × ⅔.

Of the anterior premolar (*pm*2) there are nine specimens, of which five show no wear at all and the rest only a little on the posterior edge (fig. 10). Even in the old jaw where the molars have been worn down to the level of the gum this tooth shows hardly any wear. From these facts it seems most probable that the anterior part of the upper jaw was edentulous, or, at any rate, the anterior upper teeth whether incisors, canines, or front premolars were not opposed to the corresponding lower teeth.* In shape this tooth consists of a well developed protoconulid from which run three ridges, one straight forward, which has a small column developed on its front border but only to a slight degree, being in some specimens hardly observable. The remaining ridges both run backward, the outer one goes straight back and swells out into an internal buttress which shows posteriorly the pressure mark of the next premolar; the other or inner ridge runs inward as well as backward. The root is either single or a little constricted. The third premolar is pointed in front and, together with the fourth premolar and the molars, is similar to the ordinary Acerathere pattern. The cingulum is strongly marked on the premolars, both on the inner and outer sides; on the molars, though present, it is less noticeable.

Upper Teeth.

The upper teeth, especially the premolars, present more points of interest than do the lower. The premaxillary region of the skull is not known, but it may be stated with fair certainty that there were not more than six cheek teeth, three premolars and three molars.

* A condition somewhat analogous is figured by OSBORN ('Mem. Am. Mus.,' vol. i., part III) in *Aceratherium platycephalum* (Plate XVIII), where the lower premolar, in this case the first, is out of use although balanced by the second upper premolar. The first upper premolar is present but could not have been used having no lower tooth to work against. A very different condition is that shown in *Aceratherium tridactylum* on Plate XVII.

The general pattern of the upper teeth is rhinocerotine, and as far as the molars are concerned very much in the stage of development of an Acerathere, such as *A. platycephalum*,* with which form there is also an additional resemblance in the remains of the post-sinus in the third molar. The premolars, however, are in a considerably more primitive condition. Of the anterior premolar of the series (pm^2) the specimen figured (fig. 11) is the only one in the collection that is not too abraded for description. It shows a curved ectoloph composed of the protostyle, protocone, and tritocone, which cusps are marked by slight undulations of the external surface. On the inner side of the tooth the deuterocone and tetartocone in the actual stage of wear of the specimen are united, but from the comparative narrowness of the connection were probably separate at the upper part of the unworn tooth. In front the protocone and deuterocone are separate, so that there is no protoloph formed, while, behind, the tritocone and tetartocone are joined to form a metaloph. The tooth is triangular, the metaloph slopes a little backward from the outer to the inner side of the tooth, while the front ridge, as far as it exists as the elongated deuterocone, slopes more sharply backward.

The third premolar is still somewhat triangular and differs from the second chiefly in the presence of a complete protoloph connecting the anterior inner and outer cusps. There are two absolutely unworn specimens of this tooth, which show the cusps in their complete state (fig. 12, A and B). The ectoloph is higher than the

* Osborn, 'Mem. Am. Mus. Nat. Hist.,' vol. i., part 3, Plate XVIII.

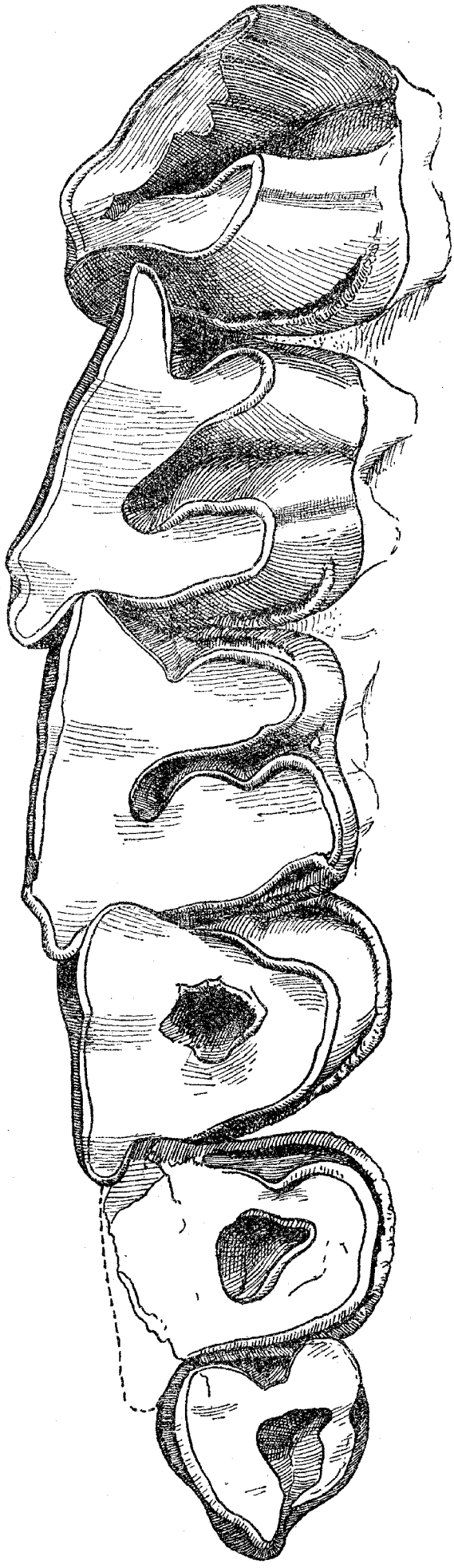

Fig. 11.—Upper premolar and molar series. The first two teeth are from one specimen, the rest from another. × ⅔.

internal cusps and the protostyle, protocone, tritocone and metastyle form a line very slightly bowed outward, with the cusps but faintly marked off the one from the other.

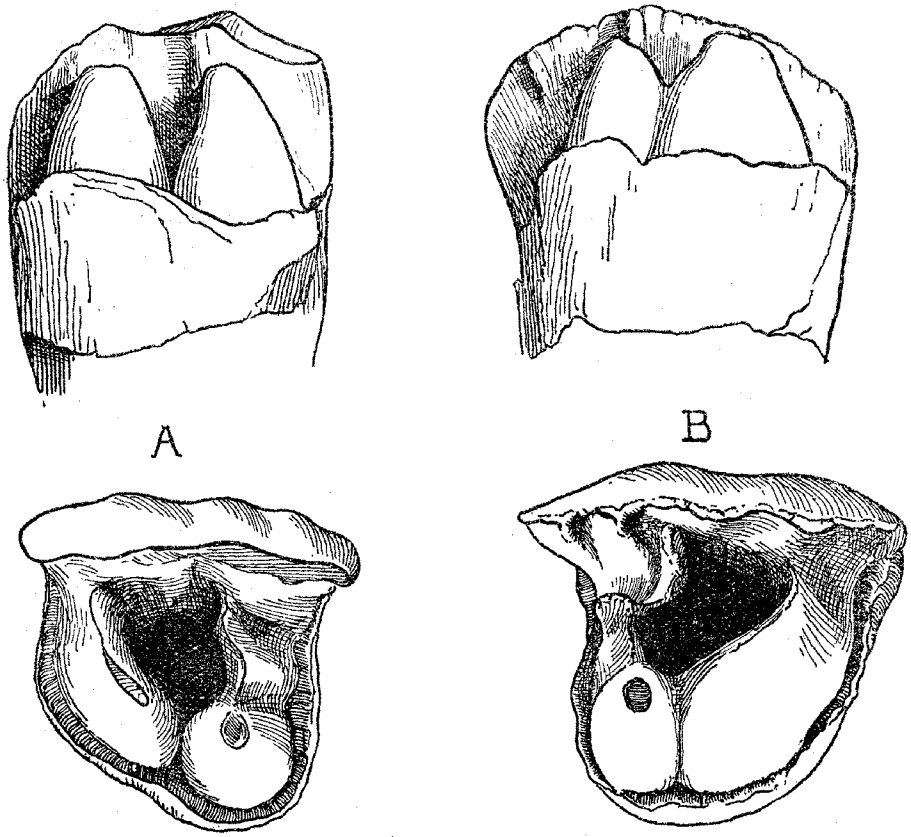

Fig. 12.—Two third upper premolars, internal and crown surfaces, showing different stages from (A) the complete division of the tetartocone and protoloph; and (B) an incomplete division. × $\frac{2}{3}$.

The deuterocone and protoconule which make the protoloph form a single sharp ridge, whose upper edge curves down to join the ectoloph. The tetartocone stands more isolated, and the metaconule likewise preserves more of its individuality in not joining the tetartocone on the one side, or the ectoloph on the other, till a level considerably below its upper surface; it is also marked by distinct grooves on the posterior face which run from the top to the bottom of the cusp.

There is some variation in different specimens in the extent to which the two internal cusps, the deutero- and tetartocones, are separated from one another. In one moderately worn specimen (fig. 11) they are confluent, in another, worn to a similar degree, they are still separate; and of the unworn specimens in one they are separate as low as to the cingulum (fig. 12, A), in which case the specimen would show them separate even if more worn than the first example, while in the other they are joined high up and would become confluent with very little wear (fig. 12, B). These teeth therefore show various conditions leading up to the separation of the protoloph and metaloph, and so the third premolar is shown to be the most advanced of the series.

Of the fourth premolar there is a good unworn specimen *in situ* with a portion of the third in front and with the first molar behind (fig. 13), so that its designation as the

fourth premolar is certain. It differs from the other premolars in that the protoloph sweeps round and includes the tetartocone, which is only differentiated from the ridge by the shallowest of depressions. This, according to OSBORN,* is the primitive condition

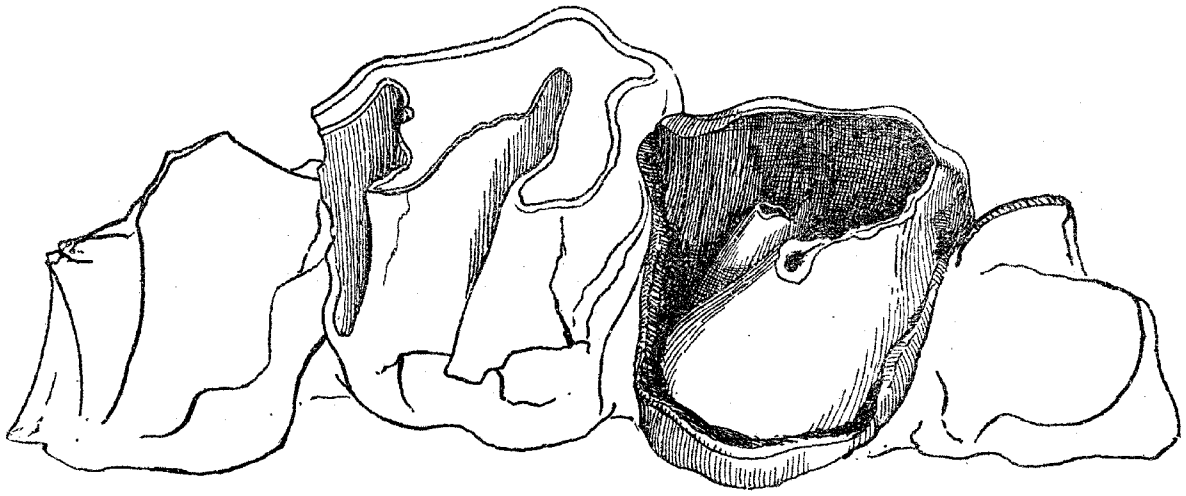

FIG. 13.—A fourth upper premolar and first molar with fragments of third premolar and second molar, viewed from the inner side and partly from above. × ⅔.

for typical Aceratheres, and thus the fourth premolar is the least molarised of the series. The metaconule stands entirely separate and only joins the ectoloph and tetartocone at or near the level of the cingulum. It is a compressed cusp or ridge, which runs forward to join the ectoloph low down at a point midway between the protocone and tritocone. A second specimen of the fourth premolar (fig. 14) shows as an additional and unusual feature a buttress from the lower part of the tritocone, which runs halfway towards the base of the metaconule.

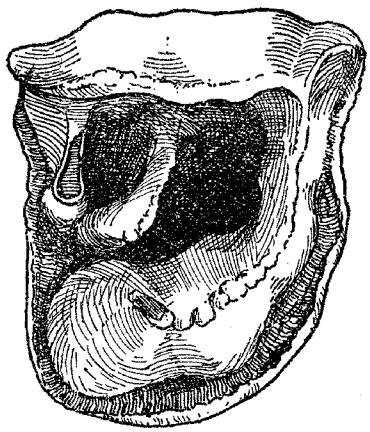

FIG. 14.—A fourth upper premolar, crown surface showing the small metaloph and an additional buttress. × ⅔.

All the premolars have a well-marked cingulum round the inside of the tooth, and a less well-marked but still distinct one along the base of the ectoloph. All of them when worn show a flat and roughly triangular area of dentine, with a central depression in which the enamel remains unabraded.

It will be seen from the figures and description just given that the process of molarisation has proceeded to a very slight degree and in this respect *Paraceratherium* is still very primitive.

The third premolar appears to be the one that has progressed the most, although still rather triangular in shape. The condition of the second premolar is difficult to decide owing to lack of suitable material, but to judge from Borissiak's figure here reproduced (fig. 15), it was

* OSBORN, *loc. cit.*, p. 89, fig. 8A.

about the same as the third, but as it has become the anterior tooth of the series the possibility of some secondary alteration in shape must be borne in mind. The fourth premolar is, at any rate, the least molarised of the series.

As, in the attempt to discover the lines of evolution, considerable account is taken of

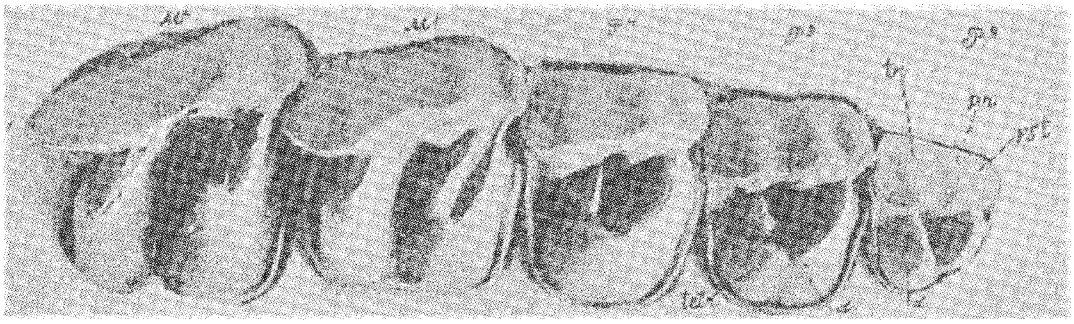

Fig. 15.—*Indricotherium* three premolars and two molars (after Borissiak). Much reduced.

the progressive molarisation of the premolar teeth and of the sequence in which they change, these points are of interest in the present case, and the condition shown by *Paraceratherium* may be compared briefly with that shown by other forms.

Osborn,* writing chiefly of American forms, has shown that in the Aceratheres it is the second premolar which is the first tooth to take on the molar pattern followed in order by the third and then the fourth.

In the Hyracodontidæ, Amynodontidæ and a few "atypical" Aceratheres the order of change is different, the fourth premolar being the first to alter, followed by the third and then the second, which is the order for the Perissodactyls generally. Abel† has stated that some, apparently the majority, of European rhinoceroses differ from the American Aceratheres in that the fourth premolar is the first to change. In one genus, however, *Epiaceratherium*, the change is after the pattern of the American Aceratheres.

Paraceratherium at any rate agrees more with the American Aceratheres than with the European forms. In spite of the size of this form, of the loss of the anterior premolar, of the specialisation of its lower incisors and of the presumably later age we have to look back to so early a form as *A. filholi* to find a parallel primitive condition of the premolars, from whose pattern it has changed only in the slightly more molarised condition of the second premolar. It has not progressed as far as, *e.g.*, the Oligocene form *Aceratherium platycephalum*.‡

With the exception of the third, the molars do not require much detailed description. They are "Aceratherine" in general structure and, of the secondary folds, the ante-

* Osborn, *loc. cit.*, p. 90, footnote.

† Abel, 'Palæogenen Rhinocerotiden Europas,' 'Abh. der K.K. Geol. Reichsanstalt,' 1910. Both Osborn and Abel in all cases leave the first premolar out of account, as being from some cause or other too variable. *Paraceratherium* has no first premolar, and, as suggested in the text above, the second, and now the leading, premolar may likewise have become modified.

‡ Osborn, *loc. cit.*, fig. 40.

crotchet alone is at all developed, a feature in keeping with the primitive condition of the premolars. The protoloph as, *e.g.*, in *Teleoceras* and certain other rhinoceroses, is wide at its inner end owing to the partial constriction off of the protocone. In addition to this expansion there is another feature, not to be seen in the other rhinoceroses, in the form of a groove, sometimes very strongly marked, which runs vertically down the lingual side of the protocone, as though it was attempting to divide it into two.*

In the third molar (fig. 16) the antecrotchet is present, though less developed than in the others, and in some cases is barely observable. A small crotchet can just be made out in one unworn specimen. The chief feature of the tooth is the presence of a cusp rising on, or just above, the cingulum at a place where the continuation of the ectoloph would have been originally. This tubercle is usually accompanied by a depression which represents the remains of the post-fossette. These features are very variable, and in some specimens the tubercle, which varies very much in size, may be present without the depression and *vice versa*. In no case are they as strongly marked as in the figure of *Aceratherium simplicidens* (*platycephalum*) given by Osborn.† The line down the protocone is present in some teeth, absent in others, and never so clearly marked as in the anterior molars.

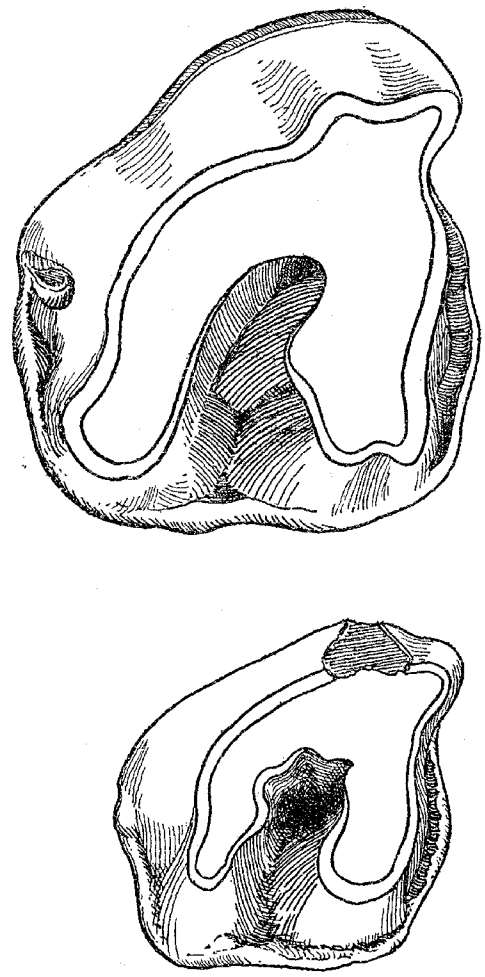

Fig. 16.—Two third upper molars showing range in size and variation in the posterior cusp. × ⅔.

The cingulum is well developed along the front, outer and hinder borders of the teeth, but is variable on the inner side.

The teeth of *Paraceratherium* show a wide range of variation in size as the table of measurements shows. A similar range has been observed by Borissiak‡ in *Indricotherium*.

Comparison with Indricotherium, Baluchitherium and Aceratherium.

As mentioned in the introduction to this memoir the skeleton of *Indricotherium* is undoubtedly the same as that of *Baluchitherium*,§ and Borissiak has described teeth

* This groove can be seen slightly marked in the second and third molars of fig. 12.

† Osborn, *loc. cit.*, fig. 43, p. 115.

‡ Borissiak, 'Imp. Akad. Sci. Petrograd,' 1918.

§ C. Forster Cooper, 'Phil. Trans.,' B, vol. 212.

also found by him in the Turgai deposits as belonging to *Indricotherium*. These teeth appear to be identical with those described in the present paper.

As Russian works are at present difficult to obtain, a reproduction of one of BORISSIAK'S figures (see fig. 15 above), together with some notes* on his paper are here given. The teeth are described as of a very primitive structure, like those of *Epiaceratherium* but " of an entirely different type." The animal is represented by forms of three different sizes. The measurements of the one given by the author, and stated by him to be " in all probability " of a medium-sized animal, are incorporated in the table of measurements in the present paper (see p. 390).

The anterior teeth he describes as canines and incisors with the statement that the canines " in opposition to the most ancient of the known rhinoceroses are stouter than the incisors," and that they are more like those of the Lophiodontidæ than anything else. As is mentioned in the footnote to p. 378, one of the teeth figured by him is certainly caniniform in appearance, while the others exactly resemble the lower tusks of *Paraceratherium*, a form which certainly has no lower canines and whose anterior parts of the upper jaw are unknown.

He states further that " In all probability, as a primitive form, *Indricotherium* had all three pairs of incisors," and that " it is possible that the first pair of upper incisors was stouter than the other two, the incisors having the appearance of teeth from an upper jaw." If this should prove to be the case then *Indricotherium* and *Paraceratherium* are undoubtedly different genera. It is, however, more probable that he has mistaken lower tusks for upper ones.†

The upper canine certainly raises a problem. Prof. OSBORN informs me that it is present in the Mongolian skull of *Baluchitherium*. It is impossible, as yet, to say whether it was present or not in *Paraceratherium*, owing to lack of direct evidence. The indirect evidence of the lower jaw is worth little, but is against the presence of an upper canine, which certainly did not work against the lower tusks, as for instance it does in *Amynodon*, because these turn down and show no signs of wear, though it is conceivable that it was present as a defensive weapon without a corresponding lower tooth.

Of the premolars and molars he describes an unworn set which, as can be seen from the figure here reproduced (fig. 15), are very similar to those described in the present paper as belonging to *Paraceratherium*. The second premolar appears to have the deuterocone partially separated from the protoloph. The third and fourth come within the range of variation of *Paraceratherium*. Of the third molar, his figure‡ and description show that it had the posterior cusp and post-fossette rather more strongly

* BORISSIAK, " Dentition of *Indricotherium*," paper presented at the session of the ' Physico-mathematical Sciences,' Petrograd, February 3, 1916. (I have, once more, to thank Mrs. BERKELEY HALLÉ for a translation of this paper.)

† See note at end of this paper.

‡ Not here reproduced.

marked than in those here described. On the whole, there is no doubt of the identity of some of the Turgai and Baluchi teeth.

The specimens of *Aceratherium bugtiense* obtained by PILGRIM* in Baluchistan likewise show no differences from those described in this paper. But the more complete material of the present collection shows that his notation of the anterior teeth in Plate VIII, fig. 6, as PM 1–3, must be amended to PM 2–4, and further light can be thrown on parts of the milk dentition of which he figures DM 2–3 and DM 3–4,† which renders their attribution to *Paraceratherium* doubtful. The new material consists of two specimens of the right and left upper first and second milk molars, in absolutely unworn condition, showing minor variations but in all probability belonging to a single animal, and with them the corresponding part of a right lower jaw. Of the upper teeth DM1 shows an ectoloph much curved along the outside border and much bent over at the top (fig. 17, A, B, C), and springing from it in front there is a strongly marked ridge or "protostyle" while the ridge itself bends sharply round to join the anterior cross ridge. Of these cross ridges there are, in the specimen of the right side, three of which the anterior one just mentioned remains thin, the middle ends internally in a moderately stout cone-like cusp and the posterior is thin and short. The left-side specimen (fig. 17, D) has the first two ridges much the same while the third ridge arises lower down the inner border of the ectoloph and instead of remaining free turns in abruptly and joins the second ridge on the inner side of the cusp. The second deciduous tooth has the same well marked protostyle and an interior ridge which curves right round and in general shape somewhat resembles the fourth true premolar. In the right-hand specimen the ridge is fused to a cusp which represents the premolar tetartocone in position. From the anterior inner edge of the cusp a small ridge projects a little backwards and towards the ectoloph which, however, it does not reach. There is also a small projection (damaged in the specimen) in the reverse direction from the posterior part of the ectoloph.

In the other specimen the anterior ridge and tetartocone are separate, and the posterior ridge, which is thin, irregular and denticulated, runs to join the ectoloph low down, the little ectoloph ridge here being absent. Both first and second milk molars have a very strongly marked cingulum on all sides except the outer, where it is present but less noticeable. The maxillary border in each case is continued for a short way beyond the anterior tooth without signs of any other being present, so that there is no doubt that these teeth really represent the first two deciduous teeth.

On comparing these specimens with PILGRIM'S figures of the milk dentition,† it will be seen that the specimens figured as the second and third milk molars agree roughly in size with those figured here as the first and second; but that there are some con-

* PILGRIM, *loc. cit.*

† PILGRIM, *loc. cit.*, Plate IX., figs. 2 and 3.

siderable discrepancies in the structure of the two, especially in the anterior tooth, of which the front ridge in PILGRIM's specimen curves backwards instead of pointing

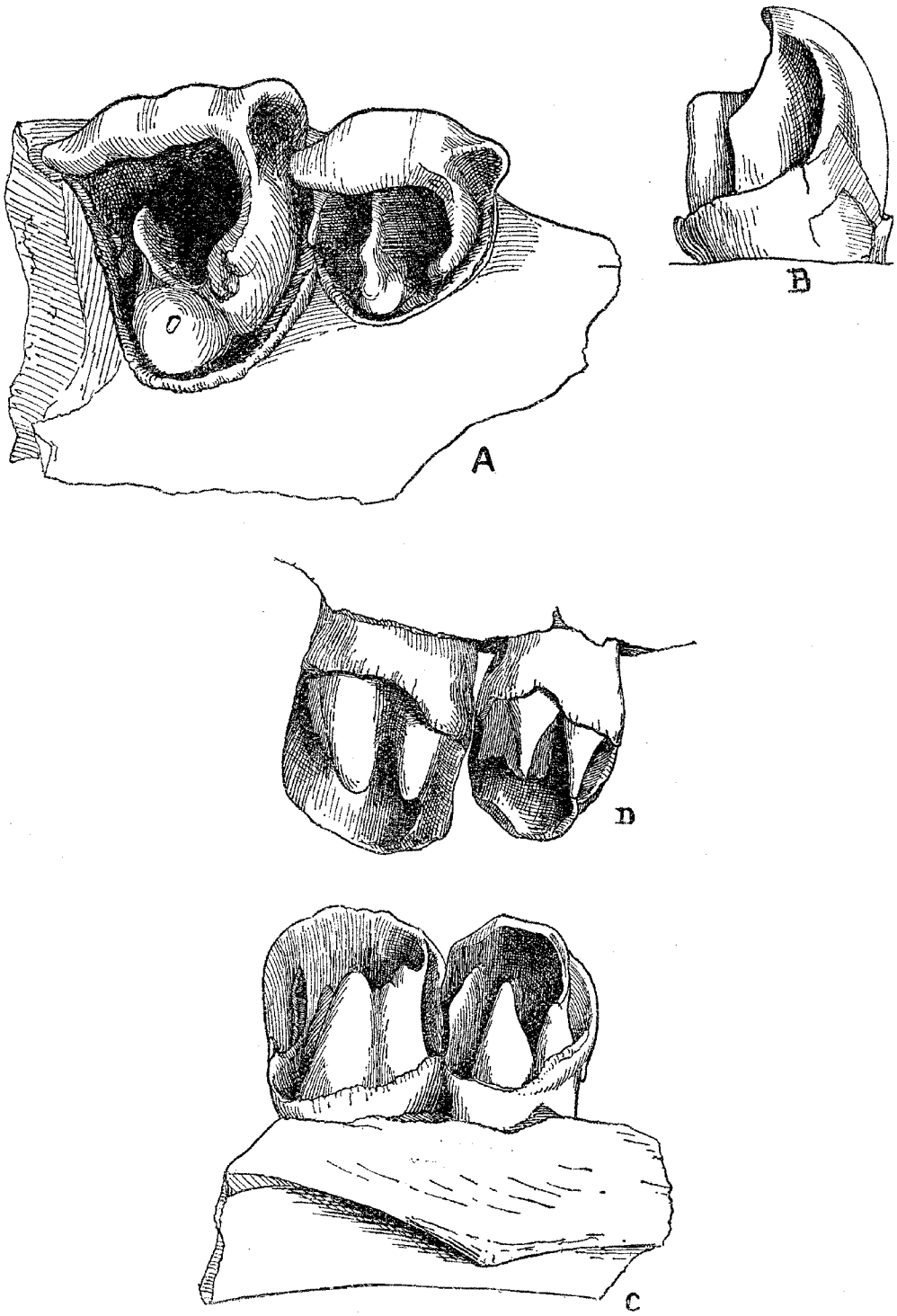

FIG. 17.—First and second upper milk teeth. (A) crown surface of a specimen of the right side; (B) front surface of (A); (C) inner surface of (A); (D) inner surface of a specimen of the left side showing differences in the divisions of the cusps and crests. × $\frac{2}{3}$.

sharply across, while there is no third ridge at all. As there is in the present collection a milk dentition which agrees better with PILGRIM's figures, and which the present writer

attributes to a doubtful form, provisionally, and probably erroneously,* placed by him with the "Amynodontidæ," it is more than likely that PILGRIM's specimens belong here and not to *Paraceratherium* at all.

The lower fragment (fig. 18) calls for little comment. It is a slender bone with part of the symphysis (with a curious little ligamentary pit just behind it which is not

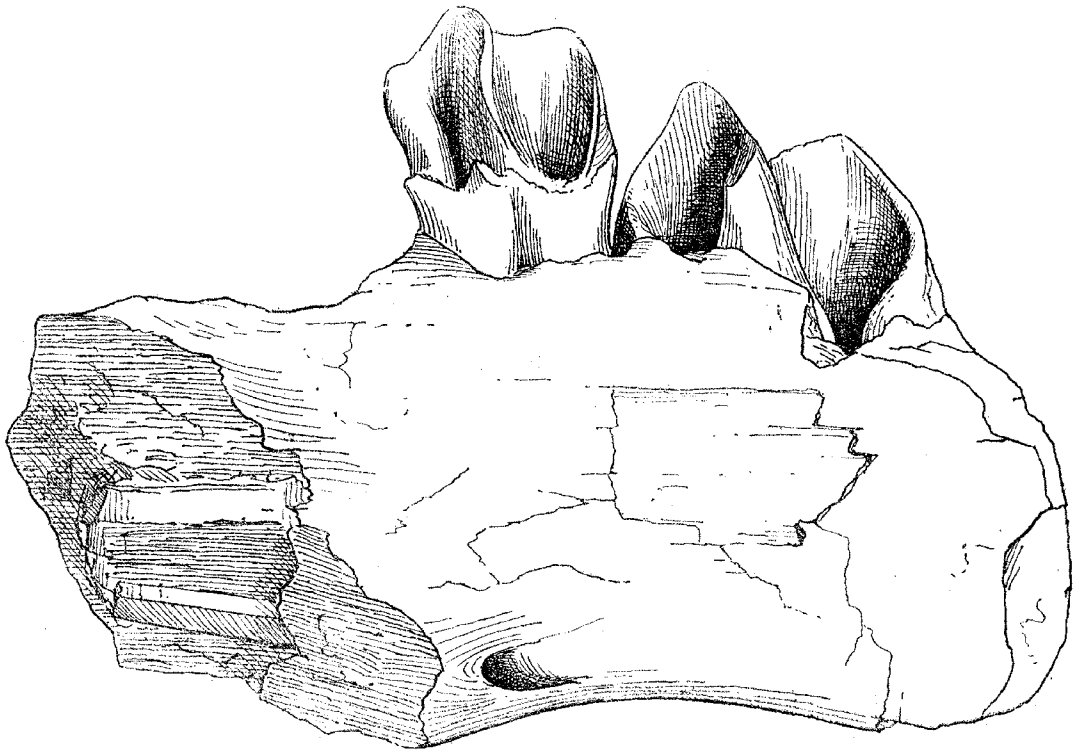

FIG. 18.—Part of a lower jaw with the first two milk teeth, inner view. × ⅔.

observable in any of the adult jaws), the root of the tusk is present, which shows the specimen to be referable to *Paraceratherium*, together with the first deciduous tooth and the second one half erupted. The tooth is typically rhinocerotine.

The question now arises as to the relation of the teeth of *Paraceratherium* to the large forms described as *Baluchitherium* and *Indricotherium*. Some of the teeth described in the present paper are *in situ* in a skull and there are remains of three other skulls for comparison. The atlas of *Baluchitherium* is known and likewise, thanks to the American Museum expedition to China, a complete skull of a size to fit the atlas. The articulating surfaces for the condyles in the atlas of *Baluchitherium* show that they have an area of more than 100 per cent. greater than the area of the condyles of the *Paraceratherium* skulls, the linear measurements of the two being 188 mm. (skull B) to 288 mm. Making the presumption, which is not necessarily warrantable, that there is a correlation between the size of the condyles and the size of the teeth a second molar length of 74 mm. (skull B) in *Paraceratherium* would imply a corresponding length of

* C. FORSTER COOPER ('Ann. Mag. Nat. Hist.,' vol. ix, May, 1922). This form is now certainly not an Amynodont (November, 1923).

Measurements in Millimetres of the Upper Teeth of Paraceratherium.

	PM 2		PM 3		PM 4		M 1		M 2		M 3	
	Length.	Breadth.	Length.	Breadth.	Length.	Breadth.	Length.	Breadth.	Length.	Breadth.	Length.	Breadth.
Skull A	?	44	53	64	59	66	68	73	84	75	78	70
Skull B	—	—	—	—	62	75	80	82	74	76	not developed	
A left series	—	—	—	—	62	75	80	77	92	81	87	72
A right series	—	—	—	—	62	66	73	63	—	—	—	—
A left series	?	43	53	64	61	73	—	—	—	—	—	—
A right series									88+	98	97	92
A left series									82	79	80	70
A left series									82	77	80	70
Separate teeth	48	45	57	61							92	74
			59	58	57	60					89	71
			63	59							83	70
			70	64					96	77		
Dr. PILGRIM's Measurement							90	81	93	88	74	79
Indricotherium.												
BORISSIAK's Measurement	43	51	55	70	61	78	78	86	94	93	96	88

Length of tooth series of skull A.—PM 2—M 3, 330.

Breadth of palate of skull B measured from the inside borders of M 1, 110.

Symphysis of lower jaws. Length and width. Type 138, 85. Fig. 7. 127, 78. Fig. 8. 140+, 110.

110 mm. in *Baluchitherium*. The largest specimen in the present collection has a length of 96 mm., which somewhat approaches the figure. The largest condylar width of any of the skulls is, as has already been stated, 210 mm., a measurement still far short of those of the atlas.

The skull (skull B) moreover, the extent of whose missing anterior portion beyond the second premolar can be estimated, could not have been much longer than 36 inches, a measurement far shorter than that of the Mongolian skull, which is 4 feet 3 inches in length.

The question remains whether such a discrepancy in size is, or is not, within the range of sexual or other variation. If it is, and should the lower jaw of *Baluchitherium* when found prove to have the same disposition of the lower incisors as tusks, then *Baluchitherium* must be merged into *Paraceratherium*. Should it prove otherwise then the genera will have been well founded. There are very few large series of comparative measurements of skulls and teeth, so that it is difficult to get information as to individual and sexual variation.* SCHLOSSER† has calculated, from a study of the teeth of bears, that there can be a difference in the size of a species up to a maximum of 30 per cent. ABEL‡ has applied this criterion to distinguish two forms of rhinoceros, and finding the difference as much as 35 per cent. concluded them to be different. Applying the same rule to the difference in length of skull B and the Mongolian skull the difference is 40 per cent., and the difference of condyles is 33 per cent., both over the border line, while the greatest difference of the teeth measurements is not more than 25 per cent. and so just within the border line. As far therefore as the teeth are concerned they could still be reckoned as of one species.

Until further discoveries are made—and much is to be hoped for from the American Museum's expedition in China—the question of the identity or not of the genera *Baluchitherium* and *Paraceratherium* must remain in suspense.

Note, added November, 1923.

Since the manuscript of this paper left my hands, three important publications, two by OSBORN,§ on *Baluchitherium*, and one by BORISSIAK,‖ on *Indricotherium*, have appeared. Moreover, by the kindness of Prof. OSBORN I have received a cast of the magnificent Mongolian skull. With these new documents I am able to add some further remarks upon their bearing upon the genus *Paraceratherium*.

* The largest sexual variation recorded seems to be that of the elephant seal, where the male is twice the bulk of the female. Whether this applies to such measurements as those of the condyles is not certain (see MURPHY, 'Bull. Am. Mus. Nat. Hist.,' vol. 33, Art. 2, 1914).

† M. SCHLOSSER, 'Abh. der Kgl. Bayr. Akad. d. Wise,' 1909, quoted by ABEL.

‡ ABEL, in "Palæogenen Rhinocerotiden Europas," 'Abh. der K.K. Geol. Reichsanstalt,' 1910.

§ OSBORN, 'American Museum Novitates,' No. 78, 1923. *Baluchitherium grangeri;* and 'Natural History,' New York, vol. 23, No. 3, 1923, pp. 208-28. 'The Extinct Giant Rhinoceros (Baluchitherium) of Western and Central Asia.'

‖ BORISSIAK, 'Mem. de l'Acad. des Sciences de Russie,' Petrograd, vol. 35, No. 6, 1923.

There is a *general* similarity in appearance between the two genera, but at the same time some differences which may not be without importance.

The Teeth.

There are still some points which lack of material for comparison leaves undecided; *Baluchitherium* has a very small upper canine; whether *Paraceratherium* had it or not cannot, at present, be told. Nor, from the absence of most of the lower jaw, can we say what were the lower incisors of *Baluchitherium*, though OSBORN'S restoration, however, on the lines of *Paraceratherium* is at all events perfectly reasonable.

About the upper premolars more can now be added, and OSBORN'S tabular statement is here contrasted with one for *Paraceratherium*.

Baluchitherium.	*Paraceratherium.*
The second premolar "Protoloph distinct, with large postero-internal tetartocone and rudimentary metaloph."	Protoloph not distinct from metaloph when the tooth is moderately worn Tetartocone well formed and joined by the metaloph, which is, however, very thin and rudimentary. The shape differs in being more triangular.
The third premolar. "Protoloph forming a long hook-like crest continuous with the tetartocone; metaloph slender, not connected with the tetartocone."	A variable tooth (see p. 382 and fig. 12 A and B), but the protoloph is less continuous with the tetartocone and sometimes not at all, while the metaloph is well developed and is connected with it.
The fourth premolar. "Very prominent metaloph* curving in to tetartocone, within this a slender metaloph."	A very similar tooth with a prominent protoloph running into the tetartocone with little sign of division. The metaloph is extremely slender and somewhat irregular in different teeth (see fig. 16).

The premolars of *Paraceratherium* while quite as long (measurements along the maxilla) as those of *Baluchitherium* are considerably less wide (measurements across the maxilla). Considering the great differences in size between the skulls of the two genera the comparative sizes of the teeth are interesting. The premolars (*pm* 2–4) are almost the same length, 150 mm. in *Baluchitherium* and from 140–150 mm. in *Paraceratherium*. The

* This must be a misprint for protoloph.

molars, on the other hand, show a less close agreement, the length of the three in *Baluchitherium* being approximately 240 mm., in *Paraceratherium* from 200 to 220.*

Osborn† states that the premolar transformation of *Baluchitherium* differs from that of the two Oligocene Aceratheres, *A. occidentale* and *tridactylum*, and that it approaches, but is more advanced than, that of *A. platycephalum* (with which it has already been compared in the present paper), and that it resembles most closely of all the condition of the European *A. filholi*. *Paraceratherium* agrees in differing from the first two forms, in fact in them the premolars are so molarised as to make a comparison barely possible. It agrees more with *A. filholi* except that the third premolar of *Paraceratherium* is a little more advanced in the division between the protoloph and tetartocone.

As for the comparison with *A. platycephalum* that form seems itself to have been in a variable state. On p. 384 I have given an opinion that *Paraceratherium* is *less* advanced. This is so if Osborn's figure of *platycephalum* as reproduced by Zittel‡ is used for comparison, on the other hand the figures of other specimens in Osborn's Memoir§ show stages which are much closer and possibly not as advanced, so that here again is a small point of difference between the two genera in question.

Skull.

Beside such differences as have been noted in the teeth there are others, perhaps more important, in the skull proportions. The condyles in *Baluchitherium* are more upright and are about half as high as they are wide; in *Paraceratherium* they lie flatter

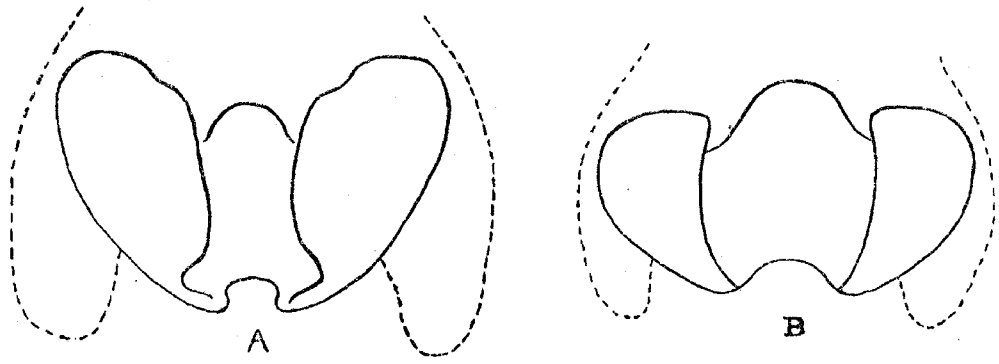

Fig. 19.—Diagrams of the condyles of *Baluchitherium* (A) and *Paraceratherium* (B) drawn to a common width. Much reduced.

and the height is only one-third of the width. The figure (fig. 19) shows this difference in absolute proportion.

* Certain loose molars in the collection, almost as large as those of *B. grangeri*, probably belong to *B. osborni*. Except for their large size they show little difference from *Paraceratherium*, beyond the presence of a small posterior cusp on the third molar and the groove on the protocone (p. 385), characters probably of trivial importance.

† 'Novitates,' *loc. cit.*

‡ Zittel, edition 1911, fig. 627, p. 453.

§ Osborn, "The Extinct Rhinoceroses," 'Mem. Amer. Mus.,' 1900, Plate XIII, figs. 8 and 9.

The opening between the post-zygomatic and the tympanic processes, mentioned on page 373, is in all four skulls of *Paraceratherium* not only relatively but actually wider than in the much larger skull of *Baluchitherium*, and another reversal of proportions is in the orbit, which is a little larger in *Paraceratherium*; and here its front border lies over the first molar instead of over the second.* Finally, the skulls of *Paraceratherium*, as far as can be seen from their condition, show no signs of the great swelling over the frontals which is such a feature in *Baluchitherium*.

BORISSIAK'S memoir on *Indricotherium* contains material of the greatest interest, especially with regard to those teeth which he names first and second incisors and canines. Some of his figures resemble the lower incisors of *Paraceratherium* fairly closely. The others bear no resemblance at all. While the upper incisors and canines, if present, of *Paraceratherium* are still unknown, it is absolutely certain that there were no lower canines, and equally certain that in *Baluchitherium* the upper canines were comparatively minute, so that the canines of BORISSIAK'S collection cannot be placed in either genus. Moreover, Dr. BORISSIAK has been good enough to write to me that he "has reasons to suppose, *from new material*, that the lower jaw of *Indricotherium* had four and not two incisors." If this is the case BORISSIAK'S genus is separate from *Paraceratherium* beyond all doubt.

From the comparisons given in this note it seems that there is additional evidence for its separation from *Baluchitherium*.

* This particular skull, it must be remembered, is abnormal (p. 372 and fig. 5).