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VIII.— *The Genus Hyracotherium. A revision and description of new specimens found in England.*

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[PLATES 49–51].

Introduction and List of Known Specimens.

Professor TEILHARD DE CHARDIN (1927)* has called attention to the need of a revision of the British specimens of the genus *Hyracotherium*. As far back as the year 1901, DEPÉRET† also made a statement that there exist “interprétations diverses et parfois inexactes relativement aux caractères au limites des genres,” and that “ces divergences provenaient soit d’une fausse interprétation des types, soit de l’état encore incomplet des documents sur quelques-unes de ces formes animales.”

The present account of the very few known English specimens of *Hyracotherium* has been undertaken in an endeavour to fulfil Professor TEILHARD DE CHARDIN’S request and, further, to record details of a specimen in the collection of the Sedgwick Museum at Cambridge and some new material recently acquired by the British Museum (Natural History), none of which has been so far described.

I am indebted to Sir ARTHUR KEITH and Mr. R. H. BURNE for permission to examine the type specimen of *Hyracotherium leporinum* in the College of Surgeons as well as for photographs and casts; to Dr. LANG, Mr. M. A. C. HINTON and Mr. A. T. HOPWOOD for permission and help in examining the specimens in the British Museum; to Dr. WALTER GRANGER, of the American Museum, for specimens of *Eohippus* for comparison; to Dr. J. VIRET, of the University of Lyons, for casts of *Pachynolophus maldani* and *Propachynolophus gaudryi* and to Professor O. T. JONES for permission to examine and describe the Cambridge specimen in the collection of the Sedgwick Museum.

* ‘Une révision très précise des restes d’*Hyracotherium* trouvés en Angleterre serait nécessaire pour qu’on puisse donner utilement un nom spécifique à la forme d’Erquelinnes.’

† Doubts as to the correctness of OWEN’S figures had been expressed as long ago as 1874 by KOWALEWSKY, see EARLE (1896).

A careful review of these specimens and a comparison of the types with the published figures has shown that DEPÉRET'S suggestion that interpretations have been mistaken is not devoid of foundation. The earlier figures, and even the published casts* of some of the specimens are in some particulars very misleading and, in consequence, wrong impressions have arisen.†

As far as can be ascertained the following list represents all the known specimens from British deposits.

1. *Hyracotherium leporinum*. (Fig. 1, Plate 49.)

The type specimen in the Collection of the College of Surgeons : from the London clay of Studd Hill, Herne Bay, Kent, consists of a skull with three molars, four premolars and stump of the canine on the left side, and three molars and three premolars on the right. It is described by OWEN (1842, b. Plate XXI) and illustrated by a lithographic plate, and also by a woodcut in his History of British fossil mammals in 1846. This figure is quite inaccurate in those details which modern research has rendered necessary.

2. *Hyracotherium leporinum*. (Fig. 3, Plate 49. Fig. 4, Plate 50.)

From the London clay, Herne Bay, on the foreshore, in the Sedgwick Museum collection, Cambridge.

This specimen shows a palate with the last three premolars and the three molars on the right side, and the same on the left side except that the second premolar has been displaced on to the palate.

3. *Hyracotherium (Pliolophus) vulpiceps*. (Figs. 1, 2, Plate 51.)

Specimen No. 44115 in the British Museum collection : taken from the London clay, "Roman cement bed" near Harwich. This consists of a skull, almost complete, described and illustrated by OWEN (1858) in the journal of the Geological Society as the type of *Pliolophus vulpiceps*. OWEN had the dentition of the left side sectioned off and developed, in which process it appears to have suffered some damage. Afterwards the rest of the skull seems to have been returned to the original discoverer (The Rev. RICHARD BULL) and, as noted by LYDEKKER (1886), subsequently was lost sight of. Since then the specimen has fortunately been rediscovered and added to the collection of the British Museum. I am indebted to the keeper of Geology, Dr. LANG, for

* Owing to certain imperfections of the teeth being masked by paint on the cast.

† DEPÉRET notes that LEMOINE'S figures are not sufficiently accurate. It will appear that DEPÉRET had himself suffered from a like disability in discussing the British forms from the only figures and casts then available.

authorising the further development of this valuable and interesting specimen. The resources of modern instruments and the skill and care of Mr. PARSONS have resulted in an almost perfect palate and lower jaw.

4. *Hyracotherium (Pliolophus) vulpiceps*. (Figs. 1, 2, 3, Plate 50.)

Specimen No. 38801 in the British Museum collection, from the London clay, Sheppey.

This specimen consists of an imperfect cranium with the three molars and the third and fourth premolars on the right side, and the first and second molars on the left side. The teeth are in rather an advanced stage of wear. Illustrated by OWEN by a lithographic plate in the Geological Magazine, 1865.

5. *Hyracotherium (Pliolophus) vulpiceps*. (Figs. 4, 5, Plate 51.)

Blackheath Beds, Abbey Wood : British Museum collection Nos. 13761/2/3.

This specimen consists of a portion of a right maxilla of a young adult with the third and fourth premolars and the first two molars. There is also a third molar of the opposite side and a fragment of a right mandible with the last premolar and the first two molars, all apparently belonging to one individual.

6. *Hyracotherium cuniculus*. (Figs. 6–9, Plate 51.)

The type specimens are two upper molars and an alleged upper premolar. To these may be added two lower molars, a fragment of lower jaw with the third molar and a separate first lower molar.

With the exception of the last two specimens, which are in the collection of the Ipswich Museum, the type and other specimens are in the collection of the British Museum, Nos. 36572 and 36569. All were found in the Suffolk Pebble Beds at Kyson.

The Type Specimen of Hyracotherium leporinum.

The type of the genus *Hyracotherium* and the type of the species *H. leporinum* may now be re-examined together with the specimen in the Sedgwick Museum. These two, when compared side by side, show no perceptible differences. The Cambridge specimen is in rather a better state of preservation, and slight accidents of abrasion or other damage are compensated by one or the other specimen. Unfortunately, in neither case are there any teeth in front of the second premolars.

The Molar Teeth.

The first and second molars are broader than long, the greatest breadth being in the front half along a line drawn through the protocone and paracone. The metacone lies more towards the middle of the palate than does the paracone, so that lines drawn through the metacone and paracone in each case point outwards at an angle of

30 degrees with the mid line of the palate. The third molar differs in that the posterior half of the tooth is narrower than that of the other molars, owing to the metacone being turned in so that the metacone-paracone line makes a still larger angle (about 40 degrees).

The protocone and hypocone in all three molars are circular at the base, except that there is a pinched-up ridge which joins the cusps with the protoconule and metaconule, respectively. It is not correct, therefore, to say that the two internal cusps are absolutely conical, and the original illustration is misleading in this respect. Thus one of the supposed differences between *Hyracotherium* and certain other genera does not in reality exist.

In all the molars the protoconule is more developed and larger than the metaconule. The protoconule besides being joined to the protocone by a ridge, also sends another ridge antero-externally to a point midway between the protocone and parastyle, but this fades away just before reaching the parastyle, so that the continuity would not be visible until after very considerable wear (see figs. 1, 3, Plate 50, where this condition has almost been reached).

The external cusps, the paracone and metacone, are also circular at their bases, but have distinct fore and aft ridges. Of these ridges the anterior one on the paracone is not much developed, and runs towards the paracone to join it low down. The posterior ridge of the metacone runs to the cingulum. The two ridges between the paracone and metacone run, one down each cusp, slightly outwards to meet each other, the four ribs making a somewhat flat and not quite symmetrical W. At the junction of the middle pair of ribs a small crest runs straight out to the external cingulum, a clear foreshadowing of a small mesostylar loop, whose supposed absence has been considered as a generic character.

The cingulum is well marked, but is thinner on the inner side at the base of the protocone and hypocone. The parastyle is moderately prominent, but the original figures are quite misleading in this respect, owing perhaps to the fact that in the type specimen it has been worn away on all the teeth except the fourth molar of the right side.

The Premolar Teeth.

Of the premolars, neither the type specimen nor the Cambridge one has the first premolar preserved, and of the second it is only possible to say that it was an elongated tooth with a larger anterior and a smaller posterior cusp placed in line with one another on the outer side of the tooth. On the inner side there is a small postero-internal shelf surrounded by a low cingulum.* The third and fourth premolars are, in general appearance, very similar to one another except in size. They have the usual five cusps, of which the two external ones have ribs like those on the para- and metacones

* Shown by the Cambridge specimen only, the type specimen is much worn in this respect.

of the molars, but which form a less noticeable W. Further details of the premolar conditions are given later in this paper, when they are discussed for all the specimens.

The Type Specimen of "Pliolophus" vulpiceps. (Figs. 1, 2. Plate 50.)

The side of the skull and lower jaw which were sectioned off and developed under OWEN'S direction show the dentition in rather a damaged condition. The development of the remainder of the skull with modern instruments has revealed both upper and lower teeth, which are only moderately worn and in perfect condition except that the incisors and canine of the upper set are represented only by stumps and the outer borders of the first premolar and third molar are a little abraded. The lower jaw is complete except for the incisors which, as in the upper jaw, are represented only by the roots.

In the upper jaw the four premolars and the three molars form an unbroken series without diastemata and occupy a total length of 50 mm. There is a diastema of 8 mm. between the canine and the first premolar.

The Upper Molar Teeth.

The upper molars show only very slight points of difference when compared with those of *H. leporinum*. They appear to be a shade more square in outline owing to the parastyle not being quite so prominent, the degree of difference, however, is very small. The ribs of the paracone and metacone run more straight and do not form a W. There is a trace of a mesostyle, but it is less developed than in *H. leporinum*.

The Upper Premolars.

All the premolars are two rooted. The first, which is somewhat damaged, has a single high cusp with a small talon shelf behind. The second has an anterior cusp with a slightly lower cusp just behind and closely appressed to it, anteriorly and posteriorly there is a low cusplet on the cingulum. The cingulum is not strongly marked on the outer side but spreads out on the inner side and gives rise to a low internal cusp. The outline of the tooth is sub-triangular. The double main cusp has not been remarked before in *Hyracotherium* and its supposed absence led WORTMAN (1896) to consider this as a point of difference between *Hyracotherium* and *Eohippus*. The third premolar has also the two external cusps somewhat pressed together into a fore and aft ridge. There is a well-marked internal cusp with another rather smaller one in front between it and the parastyle, thus making the tooth four cusped and rather square in shape. The cingulum is well marked in front and behind. The fourth premolar is a triangular tooth with a well-marked cingulum all round. By the addition of a "metaconule," which is only a little smaller than the "protoconule," the tooth has become five cusped. There is also just discernible a very minute cusp in the position of a "hypocone."

Counting from the first premolar backwards, there is a slight but progressive tendency for the two external cusps, the protocone and tritocone, to become more and more separated from one another, but they never become so separated as in the first molar.

The Lower Molar Teeth.

So far only in this specimen and the more recently discovered fragment from Abbey Wood has a lower dentition of *H. vulpiceps* been obtained, while lower teeth of *H. leporinum* are at present entirely unknown. The fact that the upper and lower dentitions of the form under discussion are in undoubted association adds to their importance.

There is a closed series of teeth from the third molar up to the second premolar, a short diastema of two millimetres divides the second from the first premolar, which, in turn, is divided from the canine by a diastema of ten millimetres. A gap of three millimetres separates the canine from the third incisor.

The first premolar has a single flattened trenchant cusp, the second is similar but with the addition of a small anterior cusp and a posterior talonid : a small diastema separates these two teeth. In the third premolar the antero-internal cusp is the larger and is placed a little in front of an antero-external cusp which is rather lower ; these two cusps are somewhat pressed together. The talonid has a single cusp on the internal side which runs down behind on to a well-marked cingulum ridge : this tooth is submolariform. By the development of an external cusp on the postero-external border of the cingulum the fourth premolar has become fully molariform. The same gradual separation of the two anterior cusps occurs on the lower premolars as has already been noted in the upper premolars.

The molar teeth all show a small reduplication of the antero-internal cusp (the metaconid being the larger and anterior with the smaller mesoconid just behind and closely pressed against it). The ridge of the hypoconid runs forward to a point between the protoconid and metaconid where it dies away. The talonid on the first two molars has only a very small hypoconulid. The third has a well-marked single cusp on the talonid.

In general terms the lower teeth correspond closely with a cast of the teeth of *P. maldani* but differ in certain small details. In *H. vulpiceps* the third molar has approximately the same length as has *P. maldani* but is a broader tooth, the cusps also appear to be less trenchant. These may amount to specific differences but not more.

In the side of the specimen originally described by OWEN the teeth from the second premolar forwards are missing and the last two molars are somewhat shattered and split longitudinally. OWEN'S figure therefore is not only incomplete but misleading. TEILHARD DE CHARDIN (1922) has given an account of a tooth as a third lower molar of a species of *Hyracotherium* which is illustrated, together with diagrams of the third molars of *H. cuniculus*, *Propachynolophus maldani* and a *Lophiotherium* for comparison. He states that there is a general likeness of the fragment to *Propachynolophus* " which

is, however, contradicted by the disposition of the tubercles which are grouped as in *Hyracotherium*, *i.e.*, the hypoconulid with two lobes strongly separated, the internal being smaller than the external; the metalophid crest scarcely reaching between the hypo- and entoconids; the antero-external arm of the hypoconulid abutting on the middle of the hypoconid instead of between the hypoconid and entoconid." This statement, which is similar to one made by DEPÉRET (*loc. cit.*) is not correct for *H. vulpiceps*, and can only be due to OWEN'S figure, because up to the present the only described and figured specimens are those of *H. vulpiceps* and the third lower molar of the form originally described as *Macacus eocænus*, subsequently transferred to *H. cuniculus*. The figure of *H. vulpiceps* is misleading, owing to a longitudinal split through the whole tooth which gives a false appearance of two lobes on the talonid which, as is shown by the perfect and scarcely worn tooth newly developed from the opposite side of the same specimen, is really quite different. The talonid is broad and rather flat, the hypoconulid is a little crescentic with the crescent arms running fore and aft so that the anterior arm (the antero-external arm of TEILHARD) runs to a point midway between the entoconid and hypoconid. TEILHARD figures three crests on the hypoconulid and mentions one as the antero-external; this appears to be the central one in his figure corresponding to what is here called the anterior arm in text-fig. 2. The outer one in his figure which runs down to the outer base of the hypoconid cannot be traced in the present specimen. The posterior arm curves round to the inner side and is flat and not well marked, but on its way down to the base of the entoconid shows a very small corrugation of the enamel which is all that can be said to represent the second talonid cusp. It can hardly be seen with the naked eye and the statement therefore that a double talonid cusp is a generic character of *Hyracotherium* is not correct. As for the rest of the tooth it is only necessary to state that the anterior crest of the hypoconid runs down to a point midway between the protoconid and mesoconid as in TEILHARD'S figure of *Propachynolophus*, which the present specimen resembles more than it does his figure of *Hyracotherium*. A comparison of the two lower molars in fact helps to show that there is very little, if any, difference between these two genera. The molars of *H. cuniculus* which are described later are a little different.

Hyracotherium vulpiceps. (Figs. 4, 5, Plate 51.)

The Abbey Wood specimen.

This specimen is, on the whole, nearer *H. vulpiceps* than *H. leporinum*, but differs from both in its rather smaller size in length of the tooth row as well as in the breadth of the teeth. The lower teeth show a similar reduction in length and breadth.

The third upper premolar is interesting in that it has more the shape of the corresponding tooth in *H. vulpiceps* while the cusps are nearer to those of *H. leporinum* and so is, in a sense, intermediate. DEPÉRET has given it as his opinion, following LYDEKKER, that not only is OWEN'S genus *Pliolophus* not valid, a view that everyone must agree

with, but that there is hardly any specific difference between the two forms. The present specimen tends to confirm this view. A final answer must, however, await until more than single and incomplete specimens are available for study.

In the same beds as this specimen were found a tooth of *Coryphodon*, one of a small Creodont and also of a small lemuroid as yet unnamed. TEILHARD notes that in France *Hyracotherium* occurs associated with *Coryphodon* in levels that are considered as Sparnacian; the London clay is usually regarded as Cuisian, and the "Macacus eocænus" deposits—the Kyson Pebble Beds—as Thanetian. The third lower molar from Erquelinnes figured by TEILHARD (1927) seems to be in the same stage of evolution as that of *H. cuniculus*, which, as far as we can tell from the few fragments that are known to us, is not only the smallest but the most primitive Hyracothere in existence. We are faced with the difficulty therefore of having a form occurring in deposits which are considered one as Sparnacian and the other as Thanetian and, further, as far as the second level is concerned, we have *H. cuniculus* living contemporary with the more advanced *H. leporinum*. This point has already been clearly appreciated by TEILHARD.

Hyracotherium cuniculus.

OWEN described and figured a certain number of separate upper teeth as *H. cuniculus* and later added to the species the fragment of the lower jaw originally described by him as *Macacus eocænus*. These fragments, with two lower molars added later, are unfortunately all that have so far been discovered of an animal that should be very interesting.

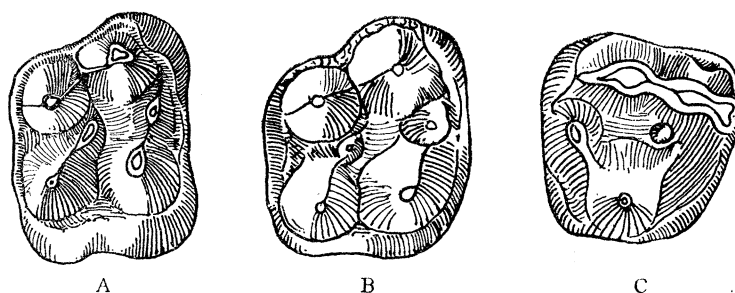
There can be little doubt as to its being properly described as a *Hyracotherium* of which genus it forms the smallest species known. Except for the lower jaw, which is in the Ipswich Museum, all the teeth are in the collection of the British Museum.

The co-types are a right and left upper molar and one premolar. To these were added the two third right lower molars which seem never to have been figured or described. OWEN pointed out the general resemblance of the teeth to those of *H. leporinum*, stating at the same time that a difference in the transverse crests prevented the idea that the animal was merely a small variety of the larger form. The alleged premolar presented, and still presents, a difficulty in its unusual small size.

Of the upper molars that of the left-hand side appears, from its shape, to be a third molar and is in absolutely unworn condition (text-fig. 1 and fig. 6, Plate 51). In size it is actually smaller than the first molar of *H. leporinum* and measures no more than 8 mm. in its greatest breadth and 7 mm. in greatest length. A strong cingulum surrounds the whole tooth and bears a small but clearly defined parastyle; the paracone is perfectly conical, and the metacone nearly so owing to the very slight development of the fore and aft ridges. These ridges are, however, present to a small degree, and with the low rib which joins the two cusps form a straight line without any trace of the W formation.

The protocone and hypocone, on the other hand, are much less conical and with the proto- and metaconule form well marked cross crests. It was on this character that OWEN laid stress in his comparison of the two species, saying that "the true molars of these two species further differ in a point not explicable on the supposition of their having belonged to a smaller individual or variety, for the ridge which passes transversely from the inner to the outer cusp is developed midway into a small crateriform tubercle in the teeth of the *Hyracotherium leporinum*, but preserves its trenchant character in the *H. cuniculus*, even in molars which have the larger tubercles worn down." This description is not quite correct, because *H. cuniculus*, in spite of the crests being sharper and more clearly defined, has a well-marked protoconule and an equally well-marked, but rather smaller metaconule. On the second specimen, a well-worn tooth which is a shade larger and possibly a second molar, the proto- and metaconules cannot be seen, but this applies equally to worn teeth of any Hyracothere.

The upper premolar presents more than one difficulty. In the first place, it is not easy to be certain of the actual tooth in the collection to which OWEN is referring because



TEXT-FIG. I.—Sketch diagrams of an upper molar of *Hyracotherium cuniculus* (fig. A) and an upper molar of *Eohippus* sp. (fig. B) showing a similar stage of development. *Hyracotherium cuniculus* third upper premolar.

there are seven teeth to choose from labelled "upper and lower premolars," all from the same locality, and to several of them OWEN'S description could apply, while his figure is too small and inaccurate to be of any help. Two of them are five-cusped teeth of the right shape for a third premolar, but neither of them fits OWEN'S figure, which agrees better with a specimen that is more properly to be referred to *Protodichobune*, (FORSTER COOPER, 1932). It shows a large internal and two moderately sized external cusps and two intermediates and to this extent is like *Hyracotherium*. A closer examination shows, however, that the ridge from the posterior intermediate cusp runs to the outside of the posterior external cusp instead of to a point between the two external cusps; this, together with the fact that the tooth is much too small even for the small molar, makes it almost impossible to believe that it belongs to *Hyracotherium* at all.

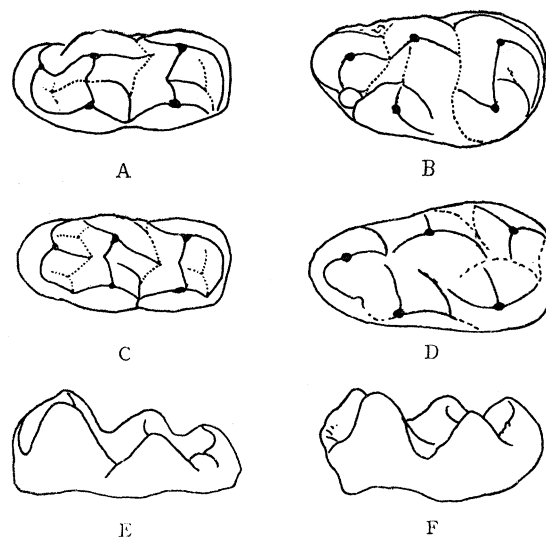
There are, however, two teeth in the collection which in size and pattern are very possibly the third premolars of this species. Both are of the left side, and may have been added to the set after OWEN'S time. (The catalogue number for all these specimens "several detached upper and lower premolars purchased in 1853" is 36572.) Both

teeth are the same in pattern (text-fig. 1C, and fig. 7A, Plate 51). In size they are small but in correct proportion to the upper and lower true molars. In shape they agree moderately well with those described for *H. leporinum*. The two external cusps are slightly elongated and flattened and a low parastyle is present. The large internal cusp is conical but with two low arms, the anterior runs forward towards the parastyle and produces a well-marked anterior intermediate cusp (the "protoconule"), the posterior arm is shorter and points towards, but by no means reaches, the posterior external cusp. Anterior to the end of this arm and separate from it is a minute cusp (the "metaconule"). Behind this point the tooth forms a large basin which, in proportion, is perhaps rather larger than usual, so that while the cusp distribution is more like that of *H. leporinum*, the more square shape approaches that described for *H. vulpiceps*. The cingulum is unusual in that it is absent from the exterior face of the tooth and at the centre of the inner face being well marked on the posterior face only.

The lower molars are certainly like those of a Hyracothere (text-fig. 2 and figs. 8 and 9, Plate 51), and are definitely third molars both of the right-hand side. Moreover, as they fit the upper teeth they are the more easily to be accepted, and in addition, support the contention that the upper teeth are true molars and not, as might otherwise be suggested, milk teeth. The left third molar in the Ipswich Museum, which Owen originally described as a *Macacus*, and which came from the same locality, is without much doubt of the same species as the two teeth just mentioned. There are, however, certain small differences, the Ipswich specimen is a shade larger, with a length of 9 mm., while the breadth remains practically the same. A much more noticeable ridge runs along the anterior border of the tooth from the protoconid to the paraconid, instead of dying away at the base of the paraconid, as it does in the other two specimens, but these are slight variations of no importance.

The other two molars in the British Museum also present small variations in the height of the cusps and in the details of the talonid. In one the protoconid and metaconid are distinctly higher than the hypoconid and entoconid, which again are higher than the talonid. The parastylid ridge running from the protoconid round the front of the tooth is very well marked, and in this specimen there is a small rounded secondary tubercle on the inner arm of the hypoconulid—the only case known to me in which anything amounting to a duplication of the talonid cusps occurs. This tooth seems to resemble in this respect the fragment of a rather larger molar figured by TEILHARD and attributed by him to *Hyracotherium*. In the second tooth, all the main cusps are approximately of equal height, instead of decreasing from in front backwards, the parastylid ridge is less marked, and the inner arm of the talonid has a small wrinkling of the enamel, but nothing approaching a secondary cusp. It must be remembered that these specimens are not known to belong definitely to *Hyracotherium*, and their attribution to that genus, while quite possible, is still provisional. On the whole, *Hyracotherium cuniculus*, from its considerably smaller size, and in the rather more pronounced roundness of the cusps of the teeth, may be considered as

the most primitive known stage of the European Hyracotheres. But so far as can be judged from the very small amount of material, it comes within the range of the genus, and the upper molar pattern can be paralleled in simplicity by a form of *Eohippus* which is in a similar stage of development (text-fig. 1).



TEXT-FIG. 2.—Diagrams of the pattern of the third lower molar in various Hyracotheres. Figs. A and C are after DE CHARDIN.

A *Hyracotherium cuniculus*.

B *Hyracotherium cuniculus* from a specimen in the British Museum.

C *Propachynolophus maldani*.

D *Hyracotherium vulpiceps* British Museum No. 44115.

E *Hyracotherium cuniculus* side view of B showing a small secondary cusp on the talonid.

F *Hyracotherium cuniculus* side view of D.

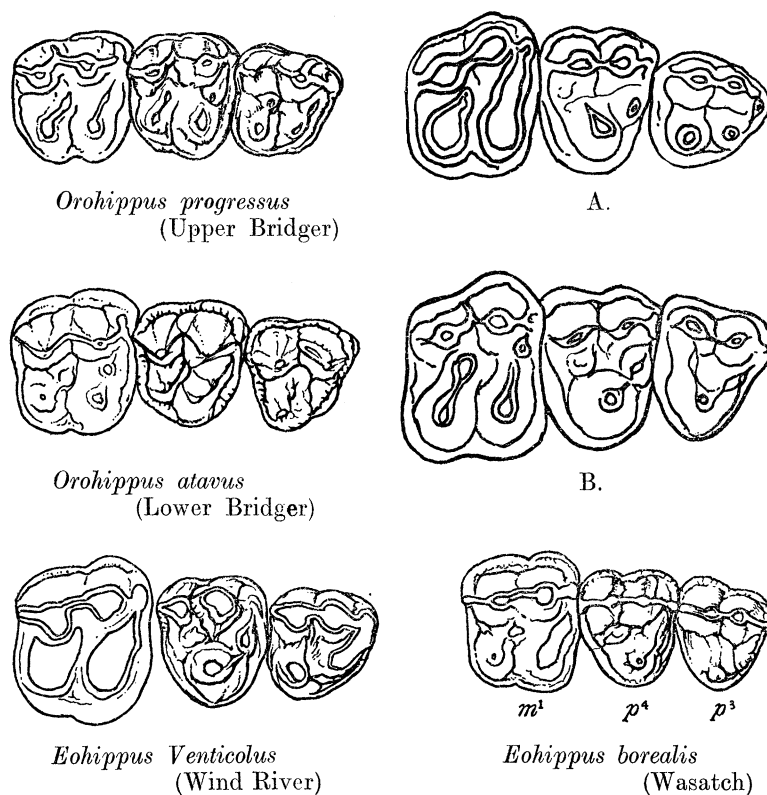
TEILHARD'S convention has been slightly altered in that the lines representing the vallies between cusps are dotted while those representing crests are complete, these latter are somewhat emphasised in the diagrams to show their position, actually the cusps are more rounded. Figs. E and F are drawn reversed and so appear to be from opposite sides to B and D.

Comparison of the Premolar Evolution of Hyracotherium and Eohippus (TEXT-FIG. 3).

GRANGER (1908) has given a very clear account of the evolution of the premolars in the Eocene horses and of the gradual molarisation that takes place as we proceed from the genus *Eohippus* to *Orohippus*. The characters of *Eohippus* are :—

1. The third and fourth upper premolars in the less advanced forms have two external and one internal cusps. In the more advanced forms a fourth cusp is clearly indicated, and the third premolar shows more progression than the fourth.
2. The second upper premolar has two external cusps and an internal ledge.
3. There is a diastema between the first and second upper premolar.
4. The premolars have no mesostyle.
5. In the fourth lower premolar a small entoconid may be present or absent.
6. The second lower premolar usually has two anterior cusps and one posterior.

On comparing *Hyracotherium* with *Eohippus* as regards their premolar condition it is seen that all the specimens of *Hyracotherium* agree very closely with GRANGER'S description of *Eohippus* and, further, that they can be divided into two forms on the state of evolution of the third premolar. In the type specimen of *H. leporinum*, text-fig. 3 B



TEXT-FIG. 3.—The last two upper premolars and first molar of certain species of *Eohippus* after GRANGER with the addition of *Hyracotherium vulpiceps* (A) and *H. leporinum* (B).

(College of Surgeons), and in the Cambridge specimen, the third premolar has two external cusps and one internal one. Two ridges run from the internal cusp to the external cusps, forming a V. On the anterior arm is a well-developed intermediate cusp, but a corresponding cusp is not formed on the posterior arm. These specimens therefore rank in this respect as the "less advanced forms." In the type of *H. vulpiceps*, text-fig. 3 A and in the second specimen assigned by OWEN to this species, the third premolar is distinctly more advanced. Instead of being triangular it has become more nearly square, the two external cusps are as usual, though closer together than they are in the fourth premolar. On the inner side, however, instead of a single cusp, there is a pair of well-developed cusps, the posterior being rather the larger. There is as yet no great sign of intermediate cusps on the cross crests, which are themselves barely in evidence, but the anterior inner cusp runs forward as a swelling, which gives the impression that a cusp is forming. The tooth, therefore, is on the way towards molarisation, but has not fully reached that condition.

The fourth upper premolar of *H. leporinum* is a triangular tooth with two external cusps joined, as in the third premolar, by a low ridge and one large somewhat crescentic internal cusp. The anterior horn of the crescent runs forward to a parastyle, and on its way gives rise to a moderately well-developed anterior intermediate cusp. The corresponding cusp on the posterior arm of the crescent is much less developed, as is the arm itself.

In all forms, the parastyle is present on the premolars, and there is a well-developed cingulum.

The condition, therefore, in *H. leporinum* appears to be almost identical with the figure given by GRANGER for *Eohippus borealis*, while the specimens ascribed to *H. vulpiceps* appear to be closer to his figure of *E. venticolus*. The material of *Hyracotherium* is at present too scanty to allow of a definite judgment, but it would appear likely that the European Hyracotheres were undergoing a similar kind of molarisation of the premolars as the American Eohippids.

The Genera of Eocene Horses.

While a general practice seems to have arisen, as a *modus vivendi*, to give the American forms the name *Eohippus* and the European forms *Hyracotherium* or other names, the question of their relationships has been left as a moot point. Authorities have, none the less, been divided on the question as to whether *Hyracotherium* differs from *Eohippus* or not. The view that there is no difference between the European and American genera is not a new one; COPE used the term *Hyracotherium* for the American forms, and later WORTMAN, *loc. cit.*, investigated the problem with some care, and came to the conclusion that "one is in a measure justified in considering *Eohippus* and *Hyracotherium* as referring to one and the same group of species." He goes on to state that "there is, however, a constant and important difference between the European and American genera seen in the structure of the second superior premolar. In all the American forms which I have seen, this tooth has two external cusps, whereas in the European species it is always single, and is therefore more primitive." What European species WORTMAN here refers to I do not know. As far as the British specimens are concerned, there was none at the time he wrote that had the second upper premolar in a condition fit to show this particular character. At the present time, the Cambridge specimen and the redeveloped *H. vulpiceps* in the British Museum both show that this tooth is distinctly divided at the top into two closely appressed external cusps. WORTMAN'S sole distinction therefore fails, and his view as to the identity of the two genera is thereby the more strongly supported.

EARLE (1896), in a short paper which seems to have attracted too little attention, and which is referred to again below, came to the same conclusion.

On the other hand, there is the view, held by DEPÉRET and others, which still seems to be supported, that *Hyracotherium* is the more primitive form, and separable as a

genus. DEPÉRET, *loc. cit.*, in his revision of the family of the Hyracotheriidae, states that the limits of the genus *Hyracotherium* appear to him to have been too much widened (“singulièrement exagérées”). He notes, however, that the various species of *Eohippus* have a general resemblance in many points to *Hyracotherium* but differ, and thereby approach *Pachynolophus*, in the less conical form of the tubercles in the upper molars, the greater compression of the external cusps and the greater development of the parastyle. While this is true of some of the forms it is not true of all, and part of the alleged differences are due to a mistaken reading of the true conditions found in *Hyracotherium*.

According to DEPÉRET the important points on which the generic distinction rests lie in the structure of the teeth, and these are,

1. On the upper molars the six cusps are almost regularly conical in shape and the two well-developed intermediate cusps show hardly any tendency to form crescents.
2. A thick cingulum is present.
3. A mesostyle is completely absent.
4. The parastyle is but little developed.
5. The third and fourth upper premolars are triangular with five conical tubercles.
6. The lower molars have four distinct cusps arranged in two rows, the internal cusps are conical, and the external sub-crescentic. The third molar has a strong bicuspid talonid.

Several of these points are incorrect as to fact, and appear to have arisen from a consideration of OWEN'S figures rather than from a close examination of the actual specimens. The cusps are certainly conical in shape, but not more so than can be seen in some specimens of *Eohippus*. It has been shown above that there is at least the beginning of a mesostyle in *H. leporinum*; while the parastyle is quite as well developed as in *Eohippus* or in *Pachynolophus*, its alleged absence being due to damage as has already been described. Such differences, then, as have been observed to exist between the British and American forms amount to no more than specific variations and in no instance are of sufficient magnitude to enable them to be described as different genera.

It remains therefore to consider the relations of *Hyracotherium* to various European genera. *Pachynolophus* (the genotype *P. duvali*), according to DEPÉRET, differs from *Hyracotherium* in that the external cusps are compressed, the intermediates (protoconule and hypoconule) are subconical and compressed into transverse crests and the internal (protocone and hypocone) are subconical and compressed from front to back. In other words, they are elongating into the line of the loph or cross crests of which they form an integral part. The cingulum has become thin and is almost absent on the inner side, while the parastyle is strongly developed.

EARLE, *loc. cit.*, after a study of the actual specimens in European museums pointed out that the original drawings of *Hyracotherium* were misleading (quoting KOWALEWSKY to the same effect), and after giving his opinion that *Hyracotherium* and *Eohippus* are

the same generically, proceeded to consider the difference between *Hyracotherium* and *Pachynolophus*. His conclusions were much the same as those of DEPÉRET, and further he could find no generic differences between the genera *Propalæotherium* and *Pachynolophus*.

These differences, it may be noted, are of degree only—often of very small degree—and the genus *Propachynolophus*, which is supposed to be intermediate, makes any sound generic differentiation all the more difficult. TEILHARD follows the lead given by DEPÉRET in considering *Hyracotherium* as separable from other genera. In a discussion on the systematic position of *Propachynolophus*, he states that it is altogether separable by the characters of its molars, but this becomes questionable when the true characters of the molar teeth of *Hyracotherium* are considered. It is interesting to note that a mesostyle may be present or absent in various specimens, or perhaps species, of *Propachynolophus*. I am unable to detect any character denoting a generic difference between *Hyracotherium leporinum*, *Propachynolophus Gaudryi* and *Pachynolophus Maldani*, although the considerable variation in size undoubtedly denotes a specific difference.

In any series of ascending mutations, such as is shown by the Eocene horses, generic distinctions are as much a matter of convenience as anything else. Dividing lines may be drawn and genera provisionally established according to the stage of evolution of some chosen character or combination of characters, or, it may be, because there is some gap in our knowledge of the series as, for example, there is between the genera *Orohippus* and *Epihippus*. When a definite division occurs in a line and the branches progress on different lines of evolution, as for example, *Palæotherium*, a generic name has a still more definite value. To establish genera, on the other hand, on every minimal variation and often on very insufficient material, only leads to confusion. This appears to have been the case with the European horses of the Lower Eocene.*

The European Hyracotheres are so few in number of actual specimens, scattered in various deposits and for the most part fragmentary in condition, that we must turn to the more liberal deposits of the United States for analogous information to throw light on questions of genera and species. My friend, Dr. WALTER GRANGER, has, at my request, kindly answered from his wide experience of the Eocene American fauna, certain questions as to the conditions exhibited by species of *Eohippus*, as follows.

1. What is the range of variation in any given species from a definite level ?

“ This is a matter of personal opinion based on the study of variation in any species of modern mammals in a given region.” Dr. GRANGER is inclined from his experience to grant rather a wide range in size and in “ the more unimportant and less structural characters.” The differences in the characters used to divide the species of *Hyracotherium* are perhaps too narrow in their range.

* Owing to the lack of the necessary material in this country for comparison of the European forms with the British, I am unable to form any sound judgment as to the precise relationship between *Hyracotherium*, *Pachynolophus* and *Propachynolophus* either generic or specific.

2. Do more than one species come from any definite level ?

“This is very certain, there are at least three species in the Gray Bull beds of the Bighorn Wasatch.” It follows, therefore, that such species as *H. leporinum* and *H. vulpiceps* (if indeed they are separable as species) and such forms as *Propachynolophus maldani*, etc., might easily be co-æval, and to base stratigraphic conclusions on their occurrence is unsafe.

3. Is there always an increase in size from lower to higher levels ?

The answer is in the negative. *Eohippus resartus*, for instance, the largest species of Eocene horse in America, comes from the Grey Bull beds and also from the New Mexican Wasatch. In the succeeding Wind River, Bridger and Uinta there is nothing larger than this form and, in fact, most species from these later horizons are smaller. It is not until the Oligocene (*Mesohippus*) that there is a decided increase in size. This sounds a note of warning against using an increase in size as a sure sign of a later level (e.g., *Propachynolophus gaudryi*), although in general the increase in size from *Hyracotherium* to *Equus* is obviously true.

Summary.

1. The British specimens of Eocene horses so far discovered belong to a single genus *Hyracotherium* and can be divided into three species, *H. cuniculus*, *H. leporinum* and *H. vulpiceps*. The last two being very close together.

2. The genus *Hyracotherium* is not more primitive than *Eohippus*, and no clear distinction can be drawn between the two. The species of *Hyracotherium* are at the same stage of evolution as some species of *Eohippus* but less advanced than others.

3. The European genus *Propachynolophus* appears to be the same as *Hyracotherium* and some forms of the genus *Pachynolophus* are hardly distinguishable.

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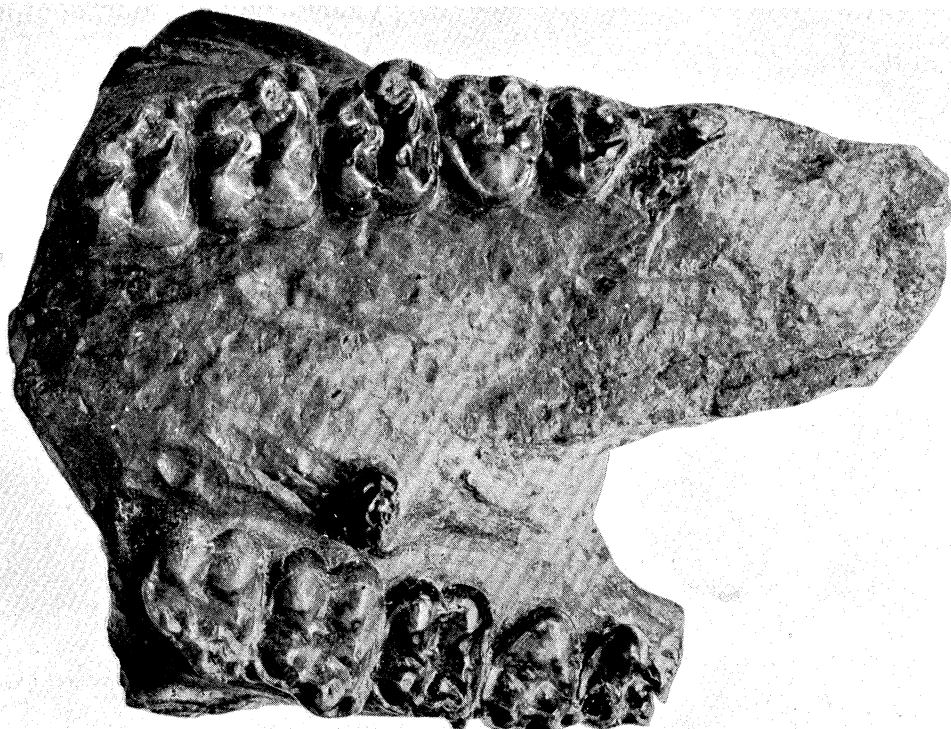
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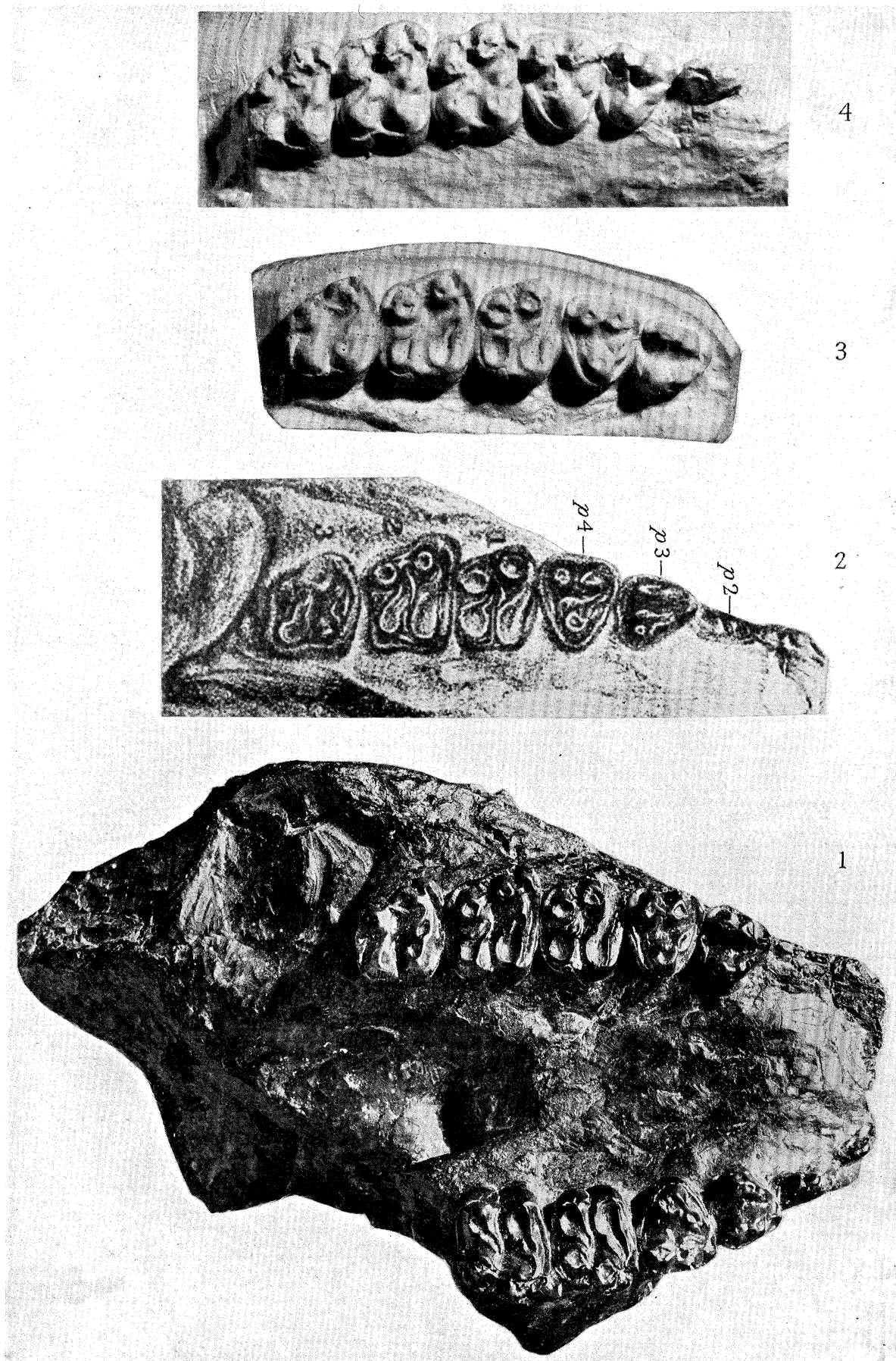
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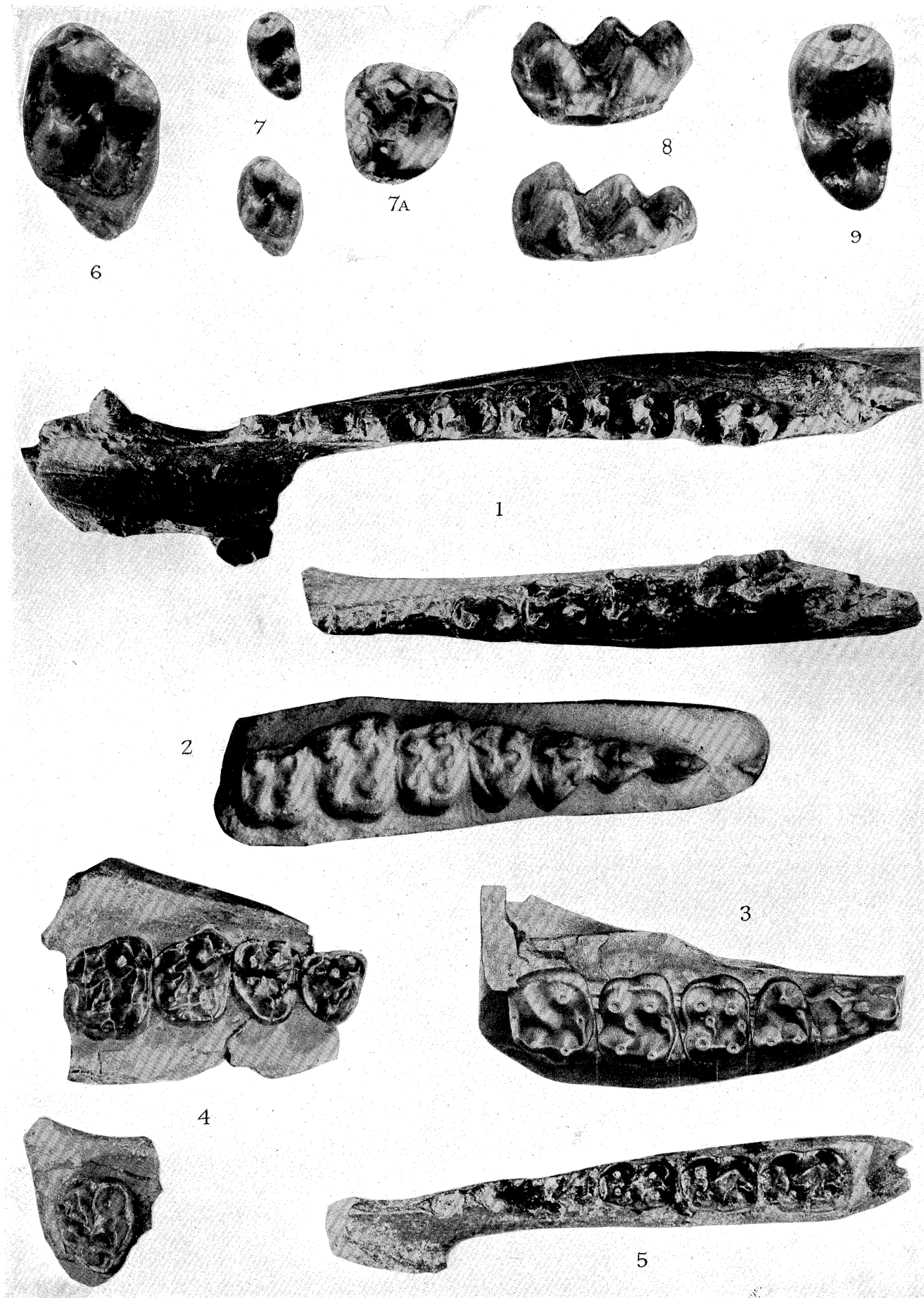


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DESCRIPTION OF PLATES.

PLATE 49.

- FIG. 1.—*Hyracotherium leporinum*—The type specimen in the Royal College of Surgeons. Photograph supplied by the College.
- FIG. 2.—OWEN'S figure of the same specimen.
- FIG. 3.—*Hyracotherium leporinum* the Cambridge specimen.
All the figures are twice the natural size.

PLATE 50.

- FIG. 1.—*Hyracotherium vulpiceps*. B.M. 38801. Photograph supplied by the British Museum.
- FIG. 2.—Part of OWEN'S figure of the same specimen.
- FIG. 3.—Cast of the right maxilla of the same specimen lighted so as to show the condition of the parastyle and incipient mesostyle, and the structure of the premolars.
- FIG. 4.—Cast of the right maxilla of the Cambridge specimen of *H. leporinum* for comparison.
All the figures are twice the natural size.

PLATE 51.

- FIG. 1.—*Hyracotherium vulpiceps* the lower jaw of the type specimen of this species B.M. 44115 as now developed, the smaller section below is the left-hand portion originally developed by OWEN. It shows the accidental splitting of the last molar. Photograph supplied by the British Museum.
- FIG. 2.—Cast of the right maxilla of the same specimen.
- FIG. 3.—*Hyracotherium vulpiceps*, OWEN'S figure of the left maxilla of the same specimen.
- FIG. 4.—*Hyracotherium vulpiceps*? The portion of the right maxilla and third upper molar of the opposite side of the Abbey Wood specimen.

FIG. 5.—Fragment of the left mandible of the same specimen with the last premolar and the first two molars.

FIG. 6.—*Hyracotherium cuniculus* type upper molar B.M. 36569, enlarged about four times.

FIG. 7.—*Hyracotherium cuniculus* upper molar (fig. 6) below and a third lower molar above enlarged to twice the natural size.

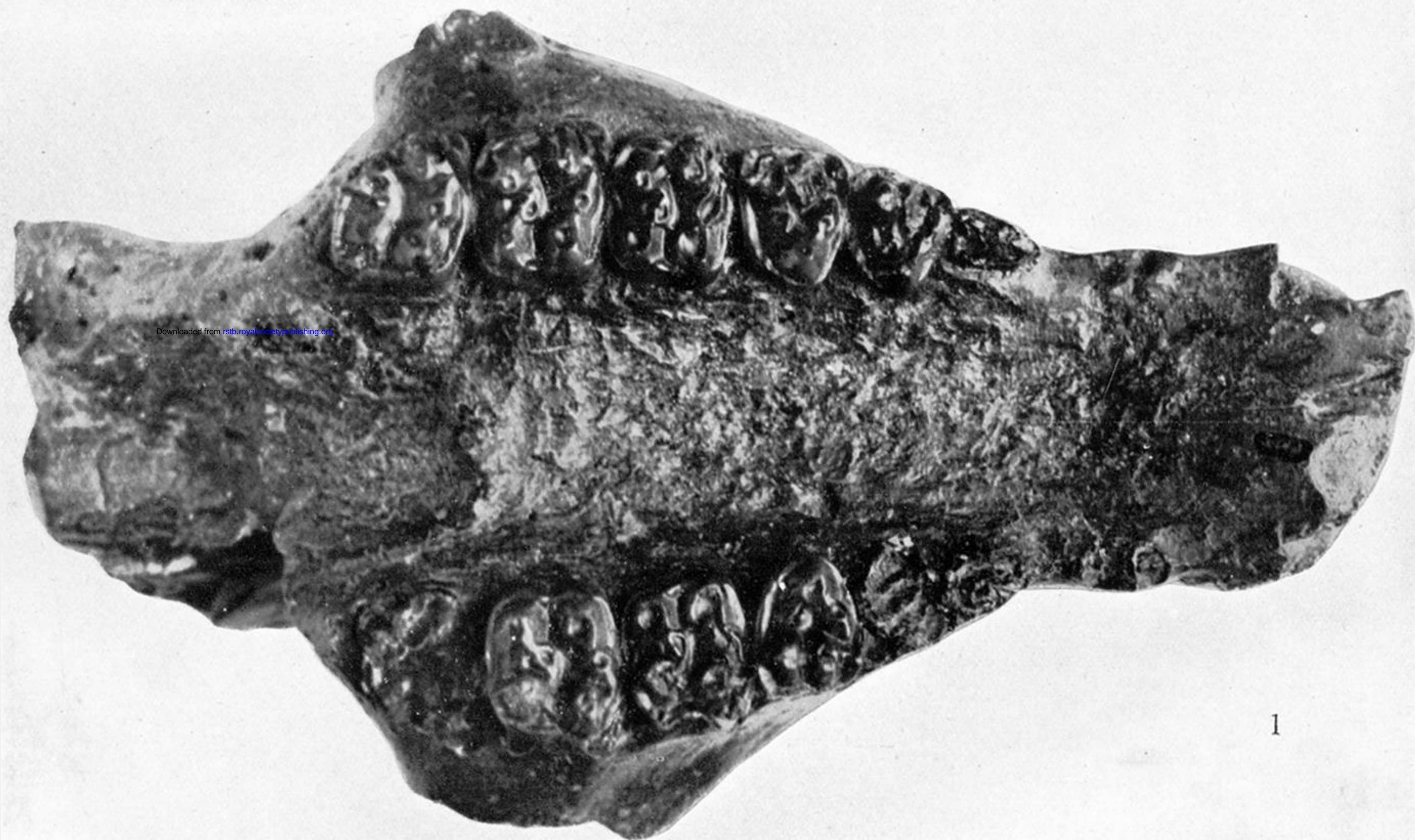
FIG. 7A.—*Hyracotherium cuniculus* third upper premolar, enlarged four times.

FIG. 8.—*Hyracotherium cuniculus* the two third lower molars in side view, the lower figure shows the small secondary cusp in the talonid, enlarged to four times the natural size.

FIG. 9.—*Hyracotherium cuniculus* upper surface of the third lower molar, fig. 8 upper specimen, enlarged to four times the natural size.

Unless otherwise stated all the figures are twice the natural size.

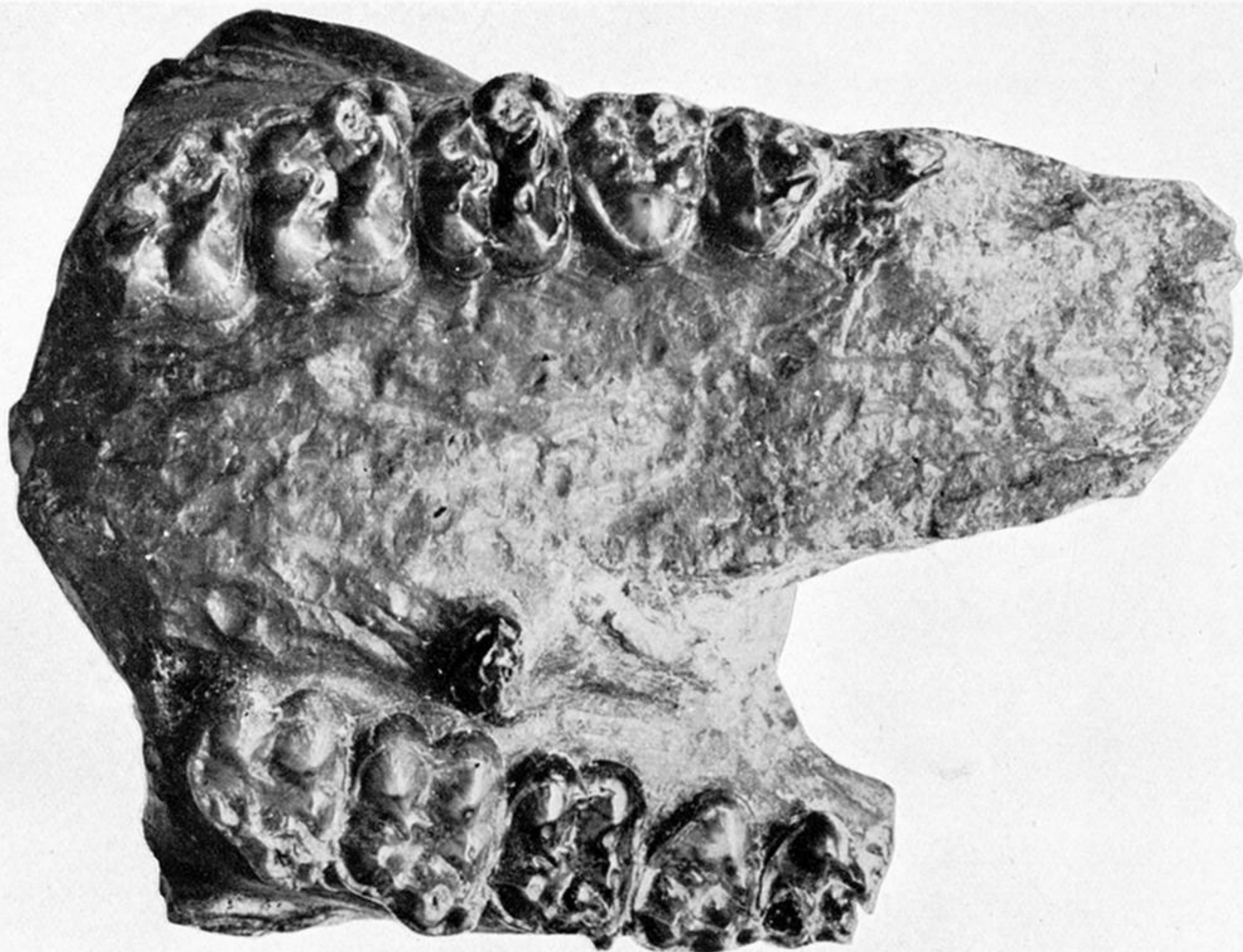




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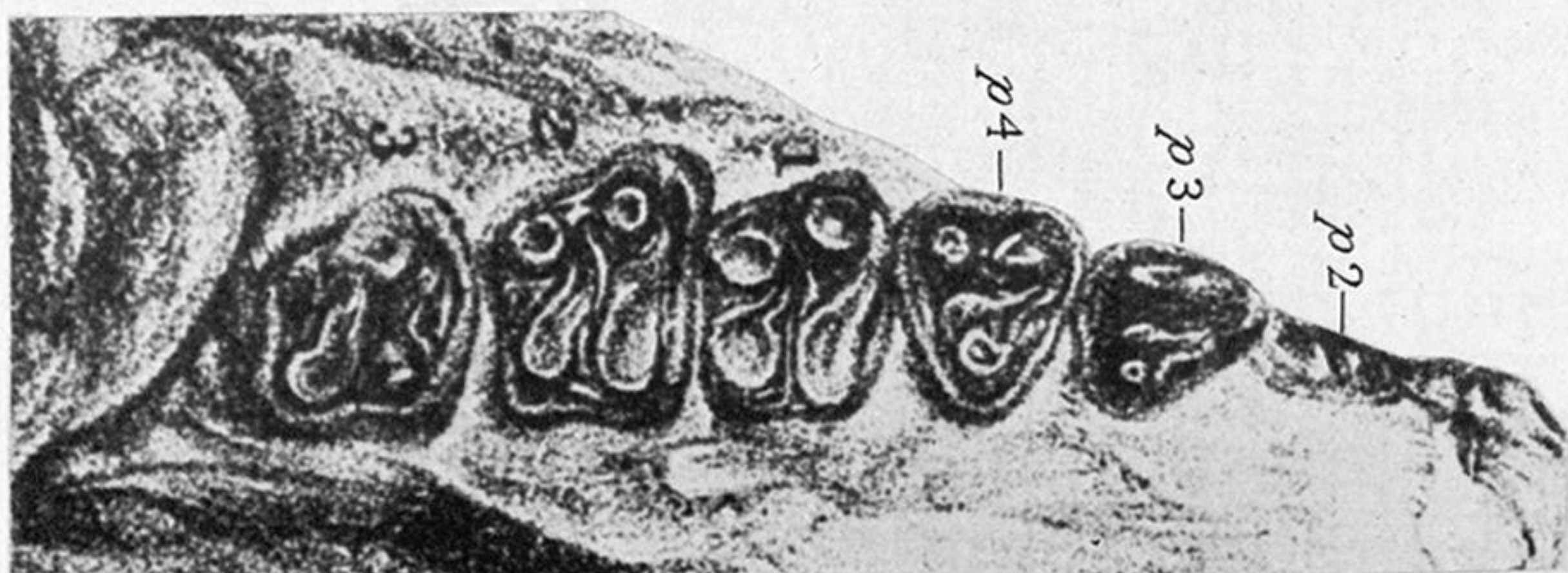
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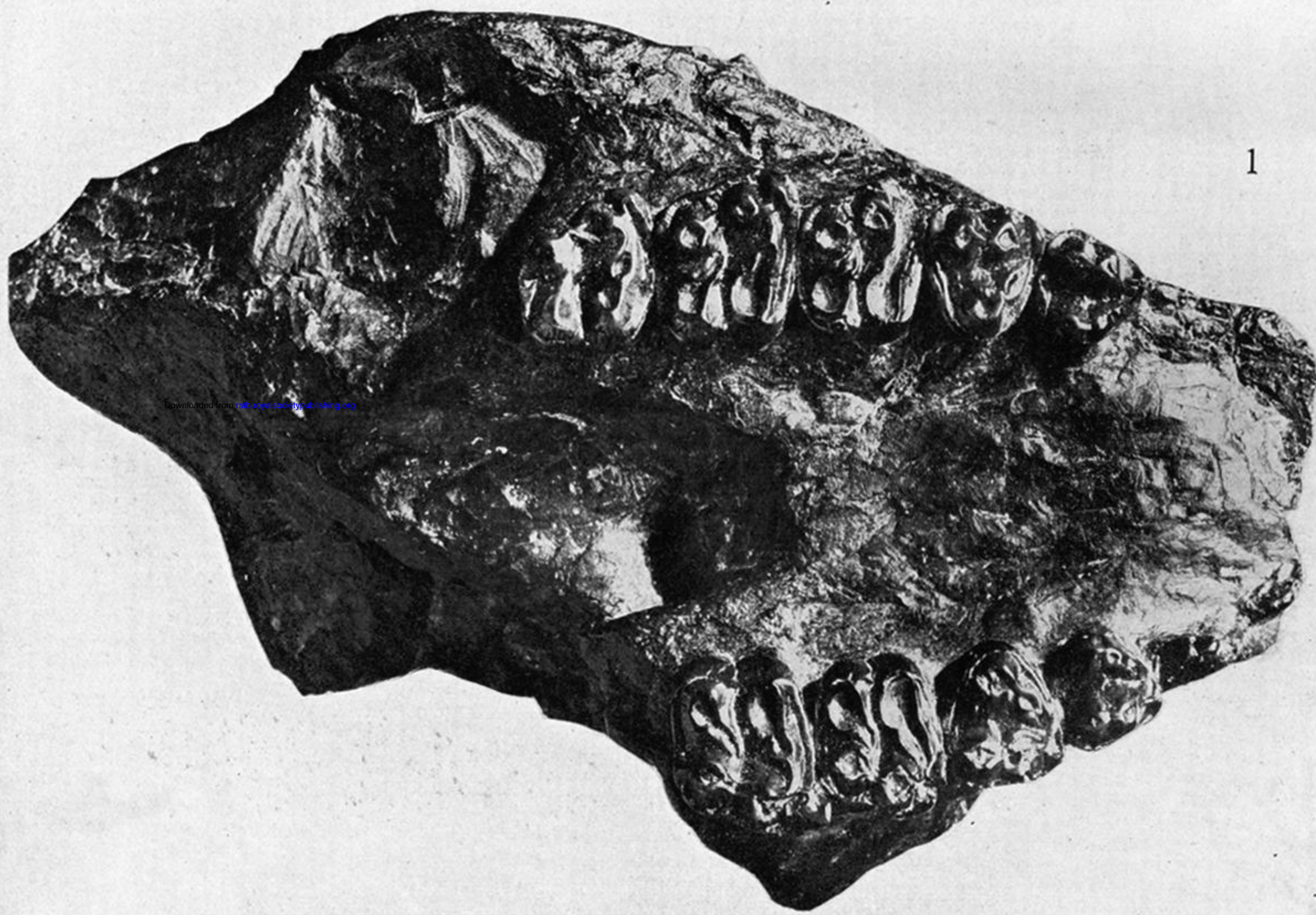
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PLATE 50.

FIG. 1.—*Hyracotherium vulpiceps*. B.M. 38801. Photograph supplied by the British Museum.

FIG. 2.—Part of OWEN'S figure of the same specimen.

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FIG. 4.—Cast of the right maxilla of the Cambridge specimen of *H. leporinum* for comparison.

All the figures are twice the natural size.

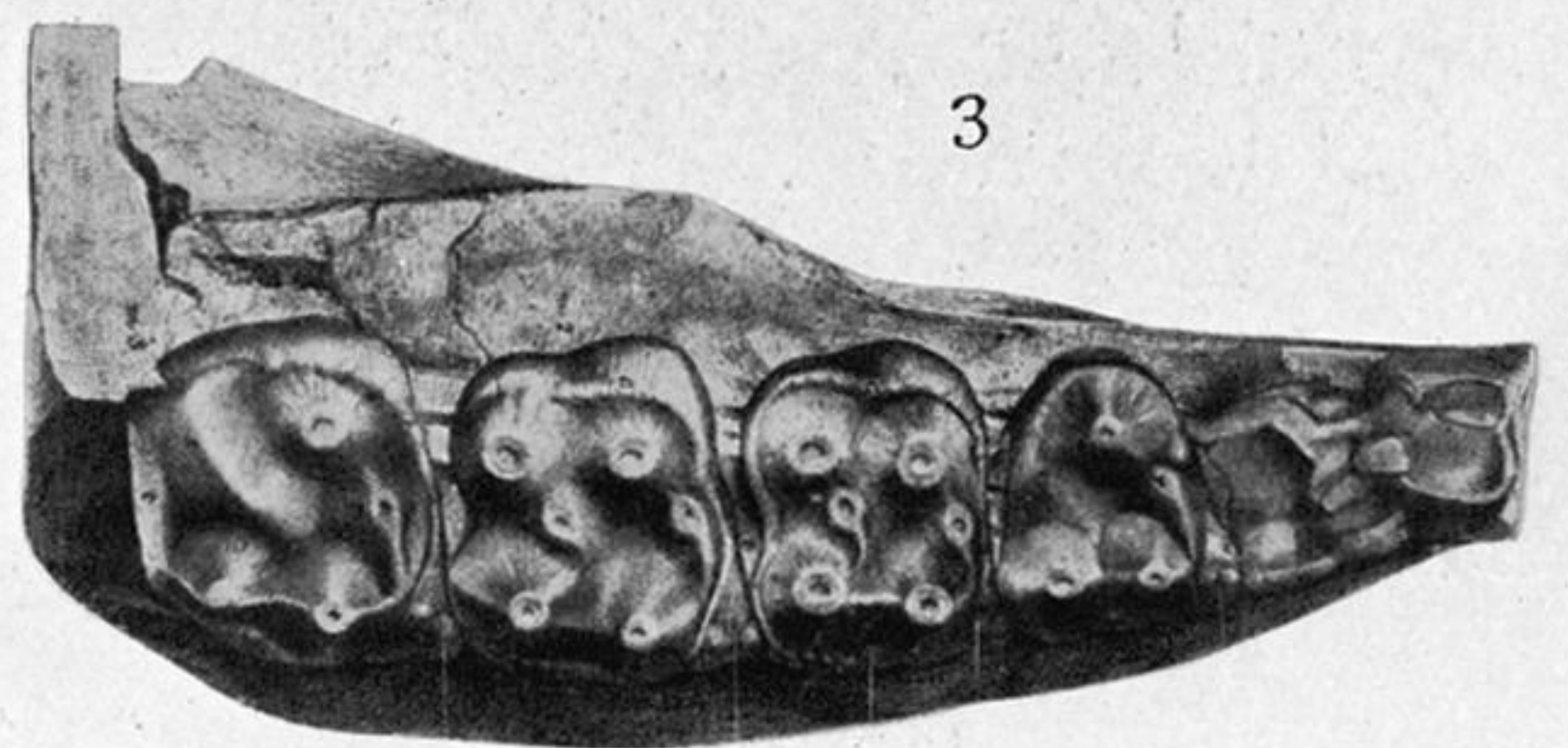
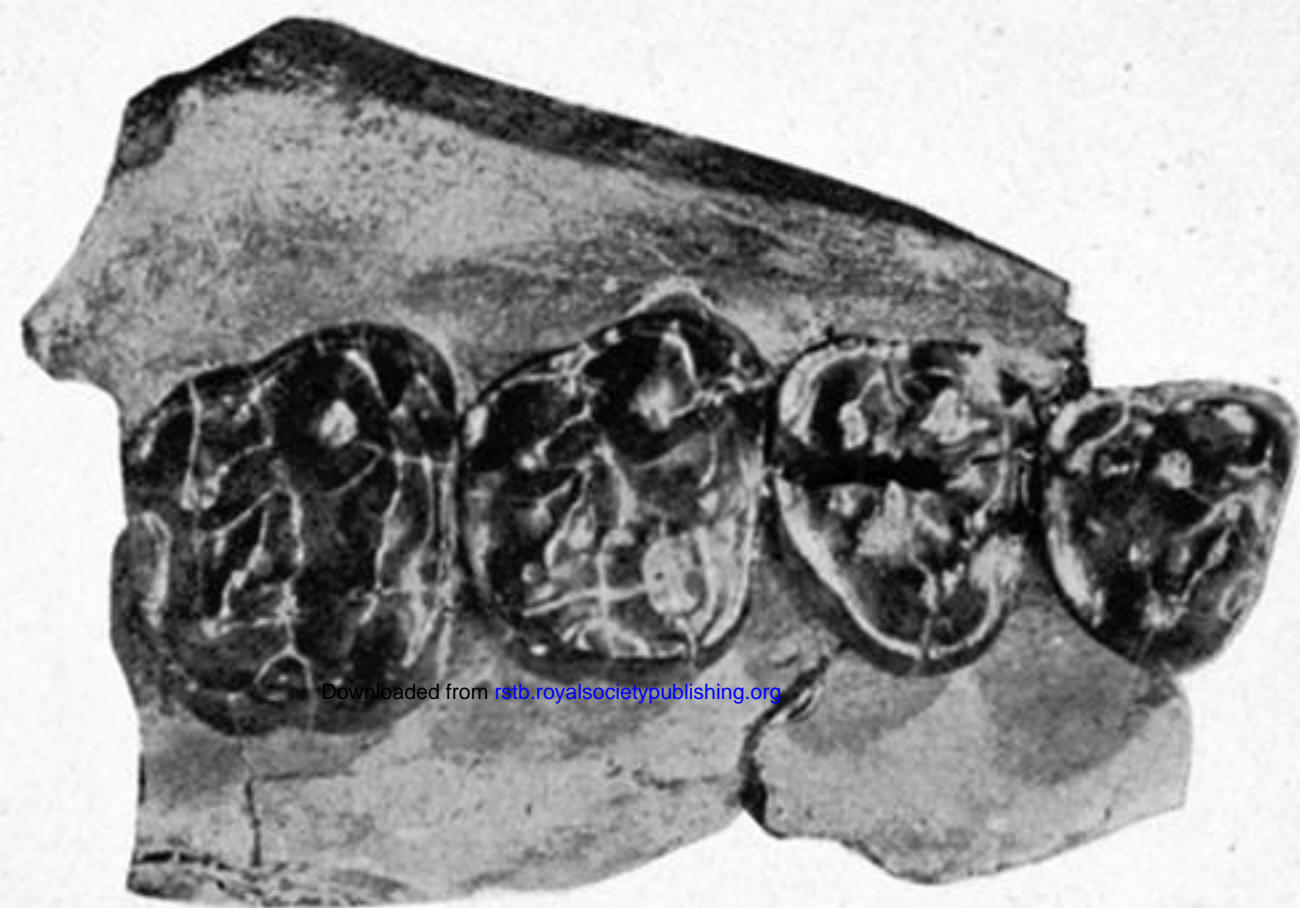
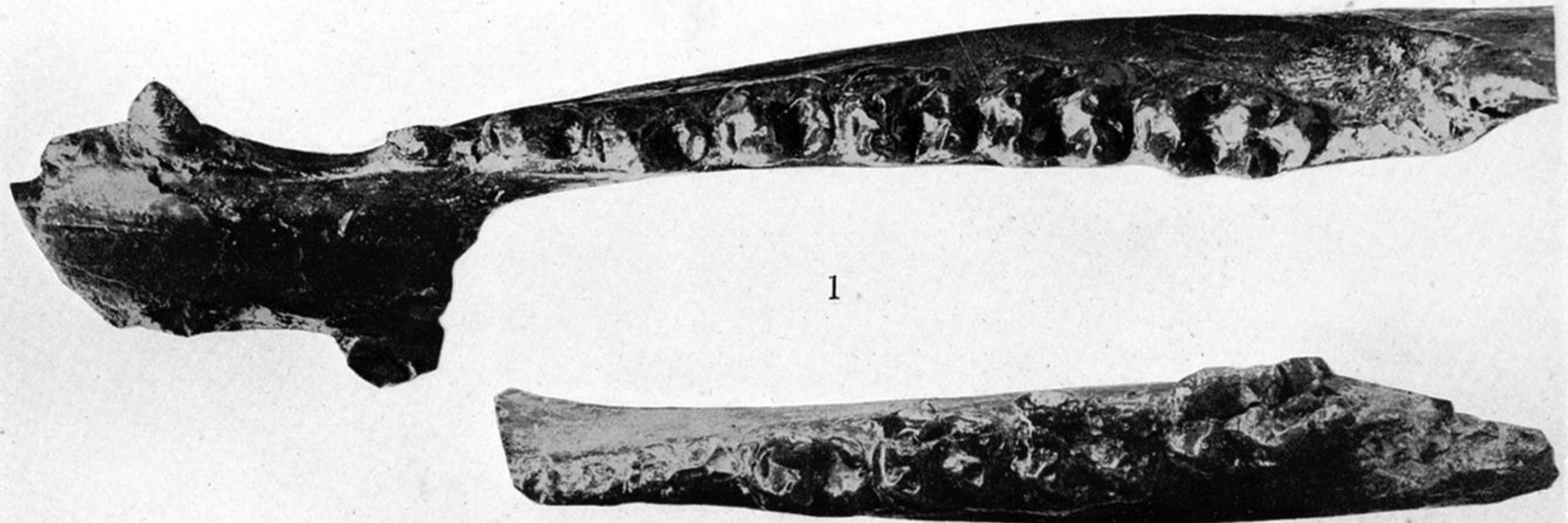
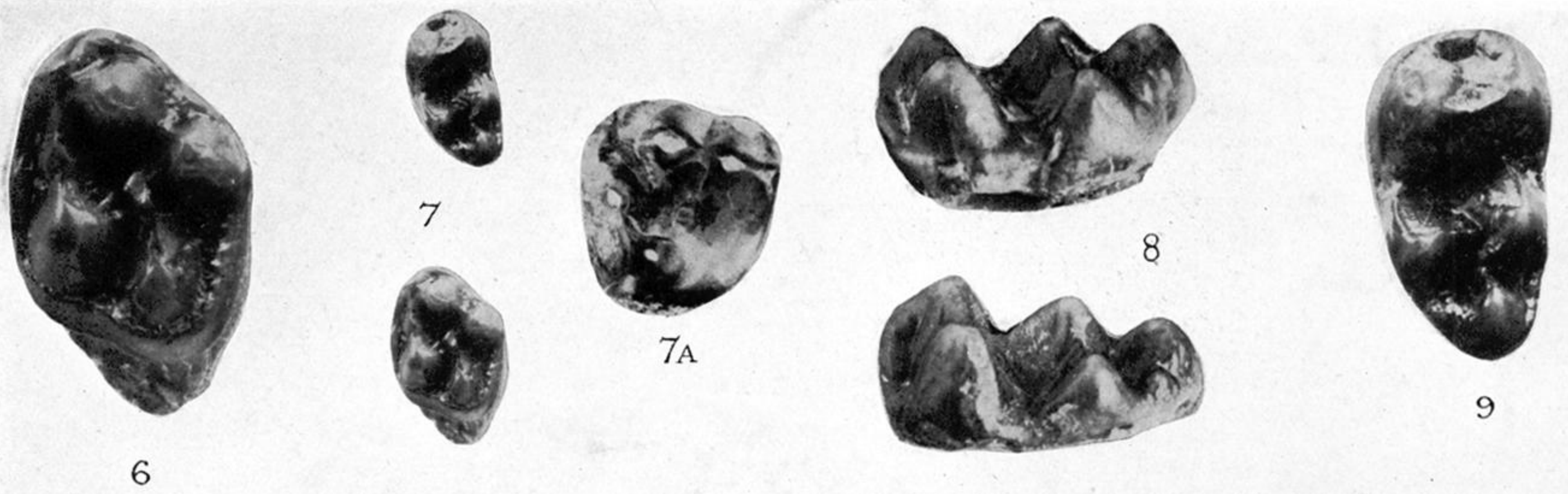


PLATE 51.

FIG. 1.—*Hyracotherium vulpiceps* the lower jaw of the type specimen of this species B.M. 44115 as now developed, the smaller section below is the left-hand portion originally developed by OWEN. It shows the accidental splitting of the last molar. Photograph supplied by the British Museum.

FIG. 2.—Cast of the right maxilla of the same specimen.

FIG. 3.—*Hyracotherium vulpiceps*, OWEN'S figure of the left maxilla of the same specimen.

FIG. 4.—*Hyracotherium vulpiceps*? The portion of the right maxilla and third upper molar of the opposite side of the Abbey Wood specimen.