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On the Skull, Mandible, and Milk Dentition of Palaeomastodon, with Some Remarks on the Tooth Change in the Proboscidea in General

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IX. *On the Skull, Mandible, and Milk Dentition of Palæomastodon, with some Remarks on the Tooth Change in the Proboscidea in general.*

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[Plates 31 and 32.]

The structure of the skull and mandible and of the teeth of *Palæomastodon* has been described in a number of papers published during the last few years,* and all the information available up to the end of 1905 is summarised in the 'Catalogue of the Tertiary Vertebrates of the Fayûm,' published early in 1906; in that volume a list of all the other papers dealing with this subject will be found. In the spring of 1906 a further expedition to the Fayûm was undertaken, and among the specimens collected were some which add considerably to our previous knowledge of *Palæomastodon*, more especially of the species *P. wintoni*, remains of which are by far the most abundant.

In the present paper it is proposed to give a description of this new material, so far as it supplements the accounts already published. The most important specimens found are: (1) the skull, mandible, atlas, anterior dorsal vertebræ, a left humerus, parts of the radius and ulna, and an imperfect tibia, all belonging to a single individual. This is one of the very few cases in which it is possible to be reasonably certain that a number of bones are really associated, since in these deposits, as a rule, the skeletons seem to have been completely scattered. The skull is complete, except that some of the dorsal surface above the level of the zygomatic arch has been worn away by drifting sand; in both skull and mandible the whole dentition is in perfect preservation. (2) The nearly complete mandible of a very young individual of *P. wintoni*, in which the two posterior milk-molars (m.m. 3 and 4) are in wear, while the second milk-molar (m.m. 2) is represented by its alveolus. The first true molar (m. 1) is also in wear while the crown of the uncut second molar lies in the jaw behind. The germs of the third and fourth premolars (pm. 3 and 4) are found in the jaw beneath the milk teeth which they are about to replace. The incisors are of great interest; in general form they are similar to those of the adult, but their outer edges bear a number of serrations like those described as occurring in the incisors of the imperfect mandible which was made the type of *Phiomia serridens*, Andrews and Beadnell.† It now appears that the genus *Phiomia* must be abandoned, since it is founded on the lower milk-dentition of a species of *Palæomastodon*, as in fact has

* See "On the Evolution of the Proboscidea," 'Phil. Trans.,' B 196, p. 99.

† 'A Preliminary Note on some New Mammals from the Upper Eocene of Egypt,' pp. 1–5, figs. 1, 2 (Survey Department, Cairo, 1902).

already been suggested by SCHLOSSER.* This species must have been much smaller than *P. wintoni* and may, perhaps, be *P. parvus* or *P. minor*, probably the latter.

The adult skull (Plate 31, figs. 1, 3) agrees very closely with the one figured on Plate 12 of the 'Catalogue of the Tertiary Vertebrata of the Fayûm,' and referred provisionally to *P. beadnelli*, though it is now clear that it belongs to the smaller species *P. wintoni*. The only points in which the present specimen differs are, that the condyles are a little wider owing to their greater extension outwards, and the paroccipital plate of the exoccipital is not so closely applied to the post-tympanic region of the squamosal. This latter peculiarity is, however, the consequence of a slight dislocation which has also led to the fracture of the basi-cranial axis (see Plate 31, fig. 3).

The most important points upon which this skull completes our knowledge are: (1) The structure of the zygomatic arch; (2) the form of the premaxillæ and their relations to the maxillæ and to the tusks.

The form of the zygomatic arch is shown in figs. 1, 3, Plate 31. It will be seen that the zygomatic process of the squamosal (*sq.*) is stout and arched strongly outwards, its antero-inferior surface being continuous with the articular surface for the mandible. Beneath it as far as the level of the anterior border of the glenoid surface the jugal (*ju.*) sends back a stout process which posteriorly is produced downwards into a prominent process (*p.* in figs. 1, 3). The middle part of the jugal arches strongly outwards and is very slender, the reduction of the zygomatic arch so noticeable in the later Proboscidea having already begun. Anteriorly it widens out again and unites with the zygomatic process of the maxilla (*mx.*), its antero-superior angle forming a postorbital prominence in the manner shown in the figure. The form of the zygomatic process of the maxilla and of its suture with the jugal has been described elsewhere.

The other part of this skull which is of importance is the anterior end of the snout, here well preserved. The palatine processes of the maxillæ (*mx. p.*, Plate 31, figs. 1, 3) extend forwards as tongue-like processes which diverge from one another anteriorly, and are there separated by a V-shaped notch. Externally they form the inner border of the alveoli of the tusks, this arrangement being particularly characteristic of the group and already well marked in *Mœritherium*. Laterally the maxillæ extend on to the face, the premaxillo-maxillary suture (*sut.*) running upwards and backwards from opposite the posterior angle of the tusk, and following the crest of a sharp ridge which seems to have extended up towards the anterior border of the orbit. The premaxillæ extend only a little way in front of the palatine processes of the maxillæ, from which they are separated between the tusks by a sort of fossa (*foss.*). In the middle dorsal line they are separated anteriorly by a small notch, on either side of which each terminates in a bluntly-rounded anterior border. Above they join one another in a long straight median suture which is raised on a slight ridge, running back on to the floor of the nasal cavity. On either side of this median ridge is a slight

* 'Neues Jahrbuch f. Mineralogie,' 1905, vol. 1 (*Referate*), p. 157.

concavity, external to which again are the long and prominent convexities caused by the alveoli of the incisors, the anterior and outer sides of which alone are formed by these bones. The alveoli themselves appear to be much too large for the comparatively slender and strongly compressed tusks projecting from them, but probably with advancing age the tusks became thicker and more rounded in section, so that they filled the alveoli more completely; at the same time it should be noted that this specimen was fully adult, all the molars being in wear. In *Tragulus* the alveoli always are much larger than the tusks they lodge, and in this case it appears that these teeth are not firmly fixed, they being described as being movable, the motion probably being caused by pressure of the lips; perhaps in the present case some such condition may have existed, though this does not seem probable.

The tusks themselves (i. 2) are separated from one another by a considerable interval (about 9·5 cm.) (Plate 31, figs. 1, 3, 4). They are strongly compressed laterally, and their posterior edge is sharp; they curve downwards and a little outwards with a slight spiral twist, terminating in a sharp point. On the outer face there is a broad band of enamel which extends back to the posterior edge, which it tends to keep sharp in wear. The roots of the tusks extend back at least to the level of the second premolar. When the jaws are closed the tusks passed down on either side of the narrowest part of the symphysis of the mandible, which with the lower tusks must have projected about 29 cm. in front of the extreme anterior end of the skull. The remainder of the upper dentition agrees closely with the description already published, but this specimen shows that the anterior upper premolar (pm. 2) is separated a little from pm. 3, and projects considerably below it, being raised on a prominence of the alveolar border; in fact, this tooth appears to some extent to have assumed the characters of a canine, and may have performed the functions of one.

The mandible (Plate 31, figs. 1, 2) associated with the skull just described is quite complete and differs in no important respect from the mandibles of *Palæomastodon wintoni* described in the 'Catalogue of the Tertiary Vertebrata of the Fayûm,' p. 157. About the anterior 18 cm., or, including the lower tusks, 29 cm. projected in front of the anterior end of the skull, when the mouth was closed. The dimensions of this specimen are given below. The incisors are separated in the middle line at their base by an interval of about 1·4 cm., but are in contact at their tips. They are rather broad, and their upper surface is concave from side to side. The convex ventral face is marked by the characteristic shallow longitudinal fluting described in the Catalogue. The cheek teeth are similar to those already described.* The dimensions of the above-described skull and mandible are given below:—

Skull—	cm.
Extreme length (occipital condyles to end of premaxillæ) . . .	70·0
Length from foramen magnum to end of premaxillæ	70·5
Length from posterior border of palate to end of premaxillæ .	43·0
Length from posterior border of palate to end of condyles . .	34·0

* See Catalogue, p. 142.

Skull (*cont.*)—

	cm.
Width of foramen magnum	8·6
Width between outer angles of occipital condyles	20·0
Width just behind auditory opening	37·0
Width at zygomatic arch (widest part)	44·7
Width of glenoid surface for mandible	9·7
Width of palate between hind lobes of M. 3	8·8
Width of palate at narrowest point	6·9
Width of palate at diastema in front of Pm. 2	7·8

The measurements of the upper teeth (in centimetres) are :—

Tusk (i. 2)—

Length in straight line from middle of the alveolar border	16·0
Width at alveolus	3·8
Width of enamel band at alveolus	3·0

	Length. cm.	Width. cm.
Pm. 2	4·0	2·3
Pm. 3	3·3	3·0
Pm. 4	3·75	3·3
M. 1	4·5	3·6
M. 2	6·0	4·4
M. 3	7·0	5·1

	cm.
Length of molar series	16·7
Length of premolar series	10·6
Length of molar and premolar series together	27·5

Mandible—

	cm.
Length from condyle to tip of incisors	89·0
Length from condyle to tip of symphysis	76·5
Length from angle to tip of symphysis	45·8
Length of symphysis	27·3
Depth beneath condyle	23·8
Depth beneath coronoid process (approx.)	22·0
Depth of mandibular ramus beneath last molar	10·0
Width of middle of ascending process	18·5
Width of narrowest part of symphysis (approx.)	9·0
Width between outer angles of condyles	34·4
Width between outer angles of coronoid processes	28·0
Greatest width in straight line between outer edges of incisors	13·5
Width of each incisor at base	8·3
Length of protruded portion of the incisors measured along the inner border	11·0

Cheek teeth—	Length. cm.	Width. cm.
Pm. 3	3·3	2·0
Pm. 4	4·1	2·9
M. 1	4·2	3·0
M. 2	5·7	3·9
M. 1	7·1	4·5

	cm.
Length of premolar series	7·1
Length of molar series	17·3
Length of molar and premolar series together	24·6

Accompanying the skull and mandible described above, a number of other bones were found which almost certainly belonged to the same individual. These include the atlas and two dorsal vertebræ, the left humerus, the imperfect right radius and ulna, and the right tibia wanting the epiphyses. These specimens, which confirm the determinations of isolated examples made in the Catalogue, may now be briefly described and their dimensions given.

The atlas in its structure closely resembles those described in the Catalogue, more especially that figured on Plate 15, fig. 3, as belonging to *Palæomastodon beadnelli*, but at the same time it is considerably smaller. Its chief dimensions are :—

	cm.
Width between the outer ends of the transverse processes	28·0
Width of neural canal	8·0
Height of canal, including that for the odontoid process (at posterior end)	9·0
Width of surface for skull	15·5
Width of surface for axis	19·3
Length of dorsal bar	5·6
Width of ventral bar	5·9

The anterior dorsal vertebra is remarkable for the great height of the neural spine, which rose about 38 cm. above the top of the neural canal, curving slightly backwards. At its base the spine is strongly convex from side to side anteriorly, while the comparatively narrow posterior surface is concave. Above, it becomes strongly compressed from side to side at least in front, the anterior edge being thin and sharp while the posterior face is flattened.

The dimensions of this vertebra are :—

	cm.
Height to top of neural spine from lower border of centrum	47·3
Width of anterior face of centrum	7·3
Height of anterior face of centrum	6·1
Width between ends of transverse processes	20·5
Width of neural canal (approx.)	4·0
Height of neural canal (approx.)	2·8

A nearly complete left humerus (text-figs. 1, 3), belonging to this skeleton agrees closely in its general form with that described and figured in the Catalogue (p. 164) as belonging to *Palæomastodon parvus*, but is considerably larger and also differs in several important details. The greater tuberosity is very large and rises high above the head; it is continued downwards as a prominent crest, which above forms the outer border of the deep bicipital groove, and below dies away in a slight ridge joining the lower end of the deltoid crest. This latter is very well developed and is strongly deflected outwards; it terminates in a roughened surface which is continued up on to the outer face of the greater tuberosity, the lesser tuberosity, forming the inner border of the bicipital groove, is fairly prominent. The head bears a nearly cylindrical articular surface, being only slightly convex from within outwards; its inner face is truncated by a flat surface. The distal end of the bone differs from that of *P. parvus* in having the inner condyle a little less developed, while on the other hand the outer condyle and the supinator ridge running up from it are much more prominent. In the size of this ridge, which is such a strongly marked character in the later Proboscidea, an interesting series of gradations can be traced from *Mæritherium* through the different sized species of *Palæomastodon* and *Tetrabelodon* up to the recent elephants, the degree to which it is developed apparently depending on the bulk of the animal. This series is illustrated in text-fig. 1. It will be seen that in *Mæritherium* the supinator ridge can scarcely be said to exist at all, while the inner condyle is well developed. In *Palæomastodon parvus* the inner condyle is greatly reduced while the supinator ridge is fairly strongly developed; this is carried still further in *P. wintoni* and *P. beadnelli*. In *Tetrabelodon* it is still longer, and finally it seems to attain about its maximum degree of development in *Elephas maximus*, where its length may equal nearly a third of the total length of the humerus.

The dimensions of the humerus (in centimetres) are:—

	cm.
Total length	56·0
Width of upper end (approx.)	14·0
Width of shaft at narrowest point . .	7·2
Width of distal end at condyles . . .	14·5
Width of distal articular surface . . .	12·4
Length of supinator ridge	12·2

Of the right ulna only the proximal half is preserved. This, so far as it goes, closely resembles the ulna of *P. parvus* figured in the Catalogue, p. 166, fig. 57. The upper lobe of the triradiate articular surface is, however, perhaps a little shorter and the contact of the radius with the inner half of the articulation a little more extensive. The associated radius has a transversely elongated proximal articular surface which is bluntly angulated posteriorly, the angle fitting into the notch between the two lobes of the articular surface of the ulna. This proximal radial

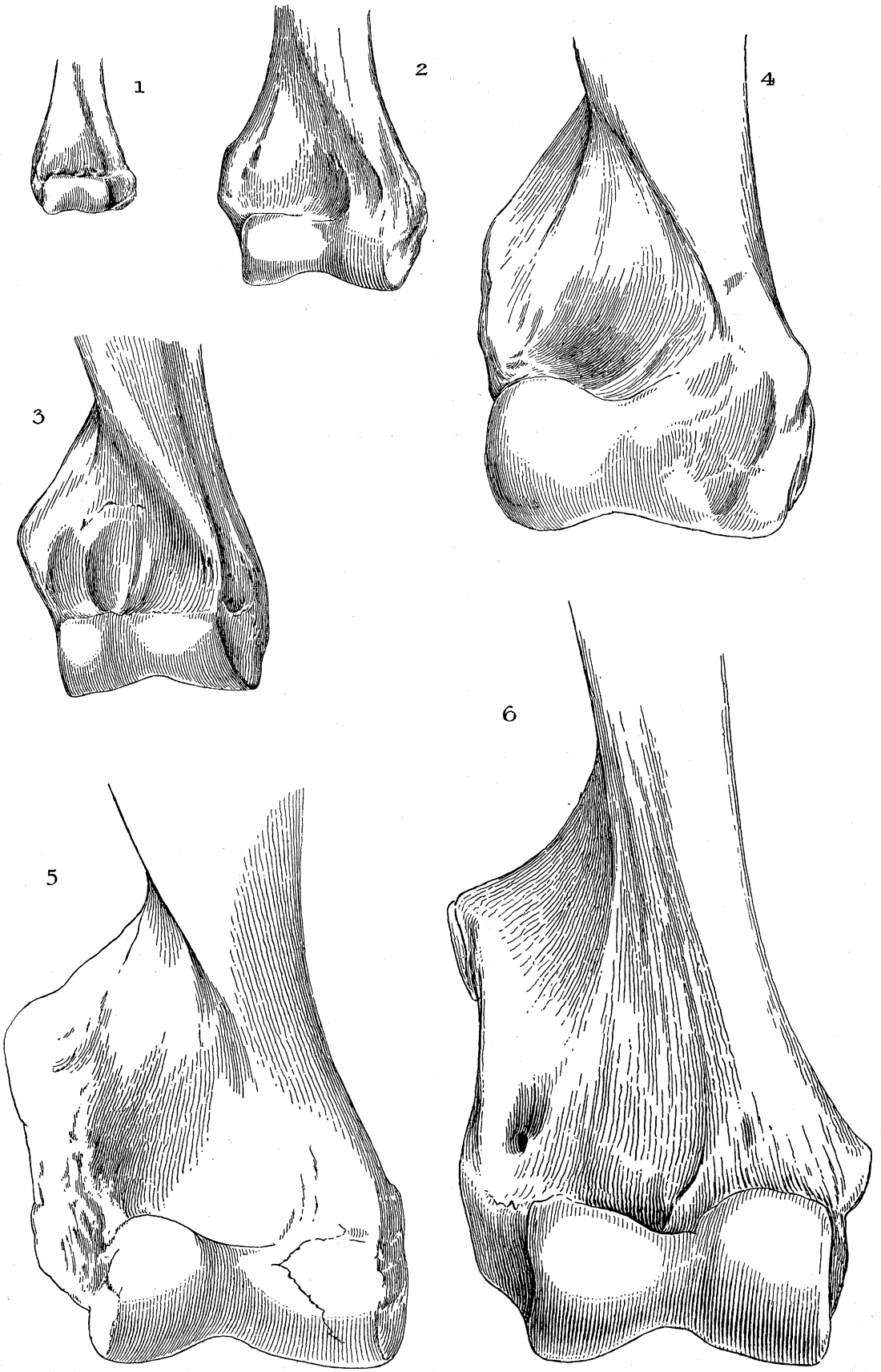

FIG. 1.—Distal End of the Right Humerus of various Proboscidea, showing the increasing size accompanied by the lengthening of the supinator crest.

1. *Mœritherium.* 2. *Palæomastodon parvus.* 3. *P. wintoni.* 4. *P. beadnelli.* 5. *Tetrabelodon angustidens.* 6. *Elephas maximus* (a small individual).

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articular surface is concave in its outer half and convex, especially from side to side, internally. On the posterior surface immediately beneath the articulation there is a deeply ridged surface for union with the ulna; beneath this the shaft is compressed laterally. The distal half of the bone is much crushed, so that its form cannot be determined with certainty; it can, however, be seen that it expanded considerably, and that its postero-external surface is deeply concave and no doubt fitted closely against the ulna; the antero-internal face was convex. The distal epiphysis has been lost, so that the form of the lower articulation cannot be determined. The dimensions of this ulna and radius are:—

	cm.
Ulna—	
Width of articular surface for humerus from side to side	11·6
Width about middle of shaft	7·3
Radius—	
Length without distal epiphysis	38·0
Width of proximal articulation from side to side	6·8
Width of proximal articulation from front to back	4·1
Width of shaft at narrowest point	2·6
Width of distal end above epiphysial surface	8·5

A right tibia wanting both articular surfaces was also found. This bone agrees with the tibia of *P. parvus* figured in the Catalogue, p. 167, text-fig. 58. The upper end is considerably expanded and its posterior face is gently convex from side to side. The cnemial crest is only slightly developed; below and on its inner side is a deep groove for the attachment of a muscle or ligament. The absence of the extremities makes it difficult to be quite certain of the proportions of this bone, but it seems to have been relatively stouter than the tibia of *Palæomastodon beadnelli*, figured in the Catalogue, Plate 16, fig. 4.

Perhaps the most important specimen collected in 1906 is the almost complete mandible (Plate 32), of a very young individual of *Palæomastodon wintoni*, in which the milk-molars are still in wear, the germs of the replacing premolars lying in the jaw below them. The only portion of this mandible that is wanting is the ascending ramus on the right side; the whole is slightly distorted by the pressure to which it has been subjected. The teeth in use were the incisors (i. 2), three milk-molars (the anterior one represented by its alveolus only), and the first true molar. In the jaw beneath the penultimate and last milk-molars are the well developed crowns of the third and fourth premolars, while behind the first molar is the crown of the second molar just ready to be cut. The form of the jaw itself does not differ in any important respect from the adult mandible of *P. wintoni*, the posterior border of the symphysis being only a little in front of the anterior end of the anterior of the two premolars.

The incisors (i. 2, Plate 32, figs. 1, 2) are long procumbent teeth projecting to a very

considerable extent from their alveoli. At their base they are separated in the middle line by an interval of about 9 mm., but their inner borders converge, and the points are in contact. The inner border is slightly concave, the outer towards the point is strongly convex, and is serrated, bearing about eight denticulations, the summits of which are worn so that the dentine is exposed there (Plate 32, fig. 1). The upper surface of these teeth is concave from side to side, and towards the tip is covered by a rather thin coat of enamel, which extends further back along the outer and inner borders than along the middle of the crown. The ventral surface is convex from side to side, and is completely covered with a fairly thick coat of enamel. These incisors appear to grow from persistent pulps, the anterior enamel covered portion, together with the serrations, being soon worn away, and the tooth increasing in size with the growth of the rest of the jaw. It is, however, uncertain whether these teeth ever had any milk predecessors; if they had, these must have been shed very early, since in this specimen all the milk-molars are still in use. It is also possible that the incisors themselves may be regarded as permanently growing milk teeth, as it is most improbable that they could ever have been replaced. As has already been remarked above, these serrated incisors are similar to those found in the mandible which was made the type of *Phiomia serridens*, but which, it is now clear, really belonged to a very young individual of one of the smaller specimens of *Palæomastodon*. At the time when *Phiomia* was described, no specimen of the mandible of *Palæomastodon* in which the symphysis and the incisors were preserved had ever been seen, or the mistake would probably never have occurred.

The anterior milk-molar (m.m. 2) is wanting in the present specimen, but is preserved in that which has just been referred to as the type of *Phiomia serridens*. In this the tooth is laterally compressed and its crown consists of a large median cusp, to the anterior face of which is united a smaller and less prominent tubercle. The posterior end is occupied by a small compressed cusp, which may belong to the cingulum. In this case this tooth is supported by two roots, while in the specimen now under discussion, there is only a single alveolus, which, however, on one side shows some traces of division into two. The penultimate milk-molar (m.m. 3, Plate 32, figs. 2–4) is an elongated tooth supported on two roots, which are anterior and posterior, and of about equal size. The crown consists essentially of two pairs of transversely arranged cusps, the external one of each pair being the larger. In front of the anterior pair is an anterior lobe, consisting of a large cusp connected with the antero-external main cusp, and bearing on its anterior face a narrow accessory column. Behind the antero-external main cusp is a small accessory tubercle, which almost entirely blocks the valley between the anterior and posterior pairs of main cusps. Behind the posterior ridge there are two cusps arranged transversely, and forming a sort of talon; the outer is the larger, and is connected with the postero-external main cusp.

The last milk-molar (m.m. 4, Plate 32, figs. 2–4) is an extraordinarily elongated tooth, having the appearance of being almost divided into two halves, each supported by a separate root. The anterior half consists of a transverse crest, composed of two sub-equal tubercles; of these, the outer is connected antero-internally with a cusp which forms the anterior end of the tooth and is united with a smaller tubercle to form a sort of rudimentary transverse ridge. On the postero-internal side of the main cusp there is likewise a small secondary tubercle, almost filling the valley between the anterior and posterior halves of the tooth. The posterior portion of the tooth is considerably larger than the anterior; it consists of two transverse ridges, each originally composed of a larger outer and a smaller inner tubercle, which in wear become united. The outer cusp shows a tendency to give rise to accessory tubercles on its inner side, so that in wear the main cusp tends to become continuous with the anterior and posterior accessory tubercles, giving rise to a V-shaped surface, exactly as in the true molars. Behind the last ridge is a small talon, consisting of a larger outer and a smaller inner tubercle. This last milk-molar is therefore trilophodont, and is like the molars behind in its general structure, but is, as it were, long drawn out, so that the ridges and cusps are less closely and compactly arranged; moreover, the anterior accessory cusp is larger and more distinct than in the molars.

The first true molar has just come into wear: it is a trilophodont tooth similar to those described and figured elsewhere.*

This tooth is of relatively small size when compared to the molars behind it. These are represented in the present specimen by the germ of the crown of the second true molar only, which is bedded in the jaw behind m. 1 and not yet ready to be cut: it is likewise trilophodont.

The crowns of pm. 3 and pm. 4 were found in the jaw beneath the corresponding milk-molars: pm. 1 seems almost ready to erupt and displace m.m. 3; its crown consists of a main central cusp, somewhat compressed laterally and with small cingular prominences on both its anterior and posterior ends, as has already been described in the adult. The last premolar is a bilophodont tooth, the anterior crest being the higher. In both these premolars the enamel is raised into slight rugosities, particularly in the neighbourhood of the cingulum; this sculpture of the enamel is not as a rule developed to the same extent in the specimens examined in which the premolars are already in wear, but probably this is partly due to the completely unworn condition of these teeth in the present specimen, or it may be an individual peculiarity.

The upper milk-teeth of *Palæomastodon* (text-fig. 2) have already been described elsewhere,† but in order to complete the account of this dentition in the genus, it will be well to refer briefly to these teeth here also. As in the lower jaw, three milk-molars are present. The anterior one (m.m. 2) consists of a large main cusp strongly compressed laterally and having a small accessory tubercle on its posterior edge.

* See Catalogue, p. 143.

† *Op. cit.*, p. 140, Plate 13.

The cingulum is well developed in the front of the tooth where it bears a small cusp; it is also present on the inner side and forms the border of the prominent postero-angle of the tooth. M.m. 3 is somewhat elongated and is rather wider behind than in front: its anterior angle is formed by a small cusp of the cingulum. The rest of the tooth is bilophodont, each ridge consisting of a high outer cusp, scarcely at all

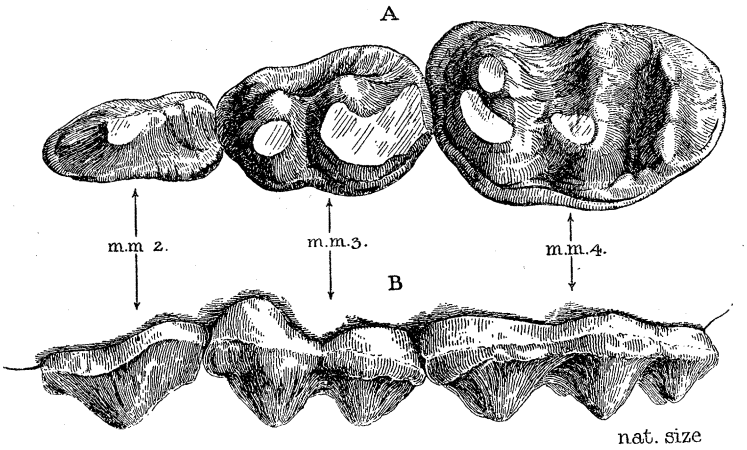


FIG. 2.—Left Upper Milk-molars of *Palæomastodon*.

A, crown view; B, outer view; m.m. 2–m.m. 4, second to fourth milk-molars.

worn in the specimen described, and a low rounded and much worn inner cusp. There seems to have been a posterior tubercle forming a sort of talon and in wear becoming continuous with the postero-internal main cusp. M.m. 4 is an elongated trilophodont tooth: each ridge is composed of a sharper outer and a blunter inner cusp. The antero-external angle of the tooth is formed by a cusp of the cingulum, which also appears opposite the openings of the transverse valleys and on the posterior border of the tooth.

In the upper jaw, all the milk-molars are replaced by premolars, instead of only the posterior two, as in the mandible, and, so far, the upper dentition retains a more primitive character than the lower. It will be noticed that in both upper and lower jaws the milk-teeth, at least so far as concerns the cheek-teeth, are, as it were, an epitome of the permanent dentition. Thus in the upper jaw the anterior milk-molar and the anterior half of the next (m.m. 3) are equivalent to the more secant premolar series of the adult dentition, and in the lower jaw the two anterior milk-molars seem likewise to represent the premolar series. As the posterior permanent molars are cut, the molariform milk-molars are replaced by more secant premolars, so that the balance between the two types of teeth is maintained. This peculiarity is, however, less clearly shown than in such a type as the pig, in which the difference in form of the molars and premolars is more distinctly marked.*

* See STEHLIN, "Ueber die Geschichte des Suiden-Gebisses," 'Abh. d. Schweiz. palæont. Ges.,' vol. 26 (1899), p. 204.

The dimensions (in centimetres) of the upper and lower milk-teeth, and of the mandible just described, are :—

	Length. cm.	Width. cm.
Upper milk-molars—		
M.m. 2	2·4	1·1
M.m. 3	2·9	2·0
M.m. 4	4·0	2·3

Lower milk-teeth—

	cm.
Incisors—	
Length along inner border	6·8
Width at base	1·8
Combined width at base	6·2

	Length. cm.	Width. cm.
Milk-molars—		
M.m. 3	19·5	14·5
M.m. 4	4·3	2·1
Molars—		
M. 1	4·7	2·8
M. 2 (germ)	5·8	—
Premolars—		
Pm. 3	3·6	—
Pm. 4	4·1	—

Mandible—	cm.
Width of symphysis (approx.)	5·5
Length of symphysis	14·0
Length from hind end of condyles to tip of symphysis	47·0
Length from hinder end of symphysis to tip of incisors	52·0
Width of ascending ramus	11·8
Width of condyle	5·3
Width between the alveolar borders of symphysis at the narrowest point	3·6

We can now give a short summary of the changes which the dentition of the Elephantidæ have undergone in passing from *Mœritherium*, in which three permanently functional premolars are present in both jaws; to the recent elephants in which these teeth have been completely lost. In *Mœritherium*, the most primitive form yet found, unfortunately the milk dentition is very imperfectly known, the only specimen showing it being an imperfect mandibular ramus, in which the molariform last milk-molar is about to be replaced by a simpler premolar; the first molar in this case is in wear, while the crowns of the second and third were already developed as

germs in the jaw. Nevertheless, although all the milk-teeth have not been directly observed, the presence of three premolars in each jaw in the permanent dentition makes it fairly certain that at least as many milk-molars were present in the young. In this genus, even the last premolar is not molariform, although the last milk-molar is already bilophodont, with a well-developed rudiment of a third ridge. In *Palæomastodon*, the presence of three milk-molars in each jaw has already been referred to, but here one of the premolars present in *Mœritherium*, viz., the second in the lower jaw, has been lost, and the posterior premolars have become bilophodont, but they still remain simpler than the molars in which a third ridge has been acquired. The posterior milk-molars have likewise become trilophodont, and it is the rule that the posterior milk-teeth in this group increase in complexity of crown structure in the same way as the true molars, although, in the genus *Elephas* even the last milk-molar in almost every case has fewer ridges than the molar behind it. In the latest types, like *E. primigenius*, in which the molars attain the maximum degree of complication, the milk-molars likewise reach their highest development; thus, in *E. primigenius*, the last milk-molar may have as many as 12 transverse crests.

In *Palæomastodon*, all the premolars and molars remain in use simultaneously till the end of the animal's life, and the most significant character noticeable in the molars, seen in the light of the subsequent history of the dentition, is the sudden enlargement of m. 2 and m. 3 compared to m. 1, for it is mainly in consequence of the increase in the size of the posterior molars that the peculiar characters of the dentition of the later Proboscidea arise. It is also interesting to note that, behind the last molar, large sinuses are present in the maxilla, almost as if in preparation for the further enlargement of that tooth; probably in part, at least, it is due to the presence of these sinuses that this further increase in size is possible.

In the next stage of which anything is known, that is to say, in *Tetrabelodon angustidens*, a considerable advance is observable. In this species also there are three milk-molars in each jaw, all being replaced by premolars in the upper jaw, the posterior two only in the lower, but although these premolars are cut and remain functional for a longer or shorter time, nevertheless the increase in size of the second and especially of the third molar is so great that, not being accompanied by any corresponding increase in the length of the portion of the jaws in which the cheek-teeth are situated, there is not sufficient room for the whole series to be in position at the same time. As the posterior molars come into use they move forwards in the jaw, so that the anterior teeth are, one after another, thrust out and shed till, in the adult, only the two posterior molars remain in use on each side of the upper and lower jaws, and even in this early type, probably the second molar also is shed in advanced age, so that finally only the enlarged third molars continue functional. The further history of the premolars is one of gradual suppression. Thus in *Tetrabelodon longirostris*, according to Röse, only one of the milk-teeth on each side is ever replaced by a premolar, and this is not the last, but the last but one, which

is cut when the first molar germ still lies in the jaw, and the crown of the second is not yet calcified.

In this case, however, it seems probable that the last premolar has escaped notice, since it is known to be present in later forms. For instance, premolars have been observed in *Elephas* (*Stegodon*) *clifti* and *Elephas* (*Loxodon*) *planifrons*, both of which species are very probably on the direct line of descent of the modern elephants. It is noteworthy that in the otherwise more primitive mastodons, such as *M. arvernensis* and *M. americanus*, the premolars were soon lost, and that it is these forms that have died out without leaving any descendants, so that here, as is usually the case, a more conservative type (at least so far as the replacement of the milk-molars is concerned) has given rise to the modern elephants, while the other forms which, in this respect at least, became early specialised, have been swept away probably on account of a loss of power of adjustment to a further change of circumstances.

EXPLANATION OF PLATES.

Plate 31.—Associated Skull and Mandible of *Palæomastodon wintoni*, Andrews.

Fig. 1.—From right side. The upper part of the skull is restored in outline. ($\frac{1}{5}$ nat. size.)

Fig. 2.—Mandible from above. ($\frac{1}{5}$ nat. size.)

Fig. 3.—Skull from below. ($\frac{1}{5}$ nat. size.)

Fig. 4.—Section across tusk close to the alveolus. (Nat. size.)

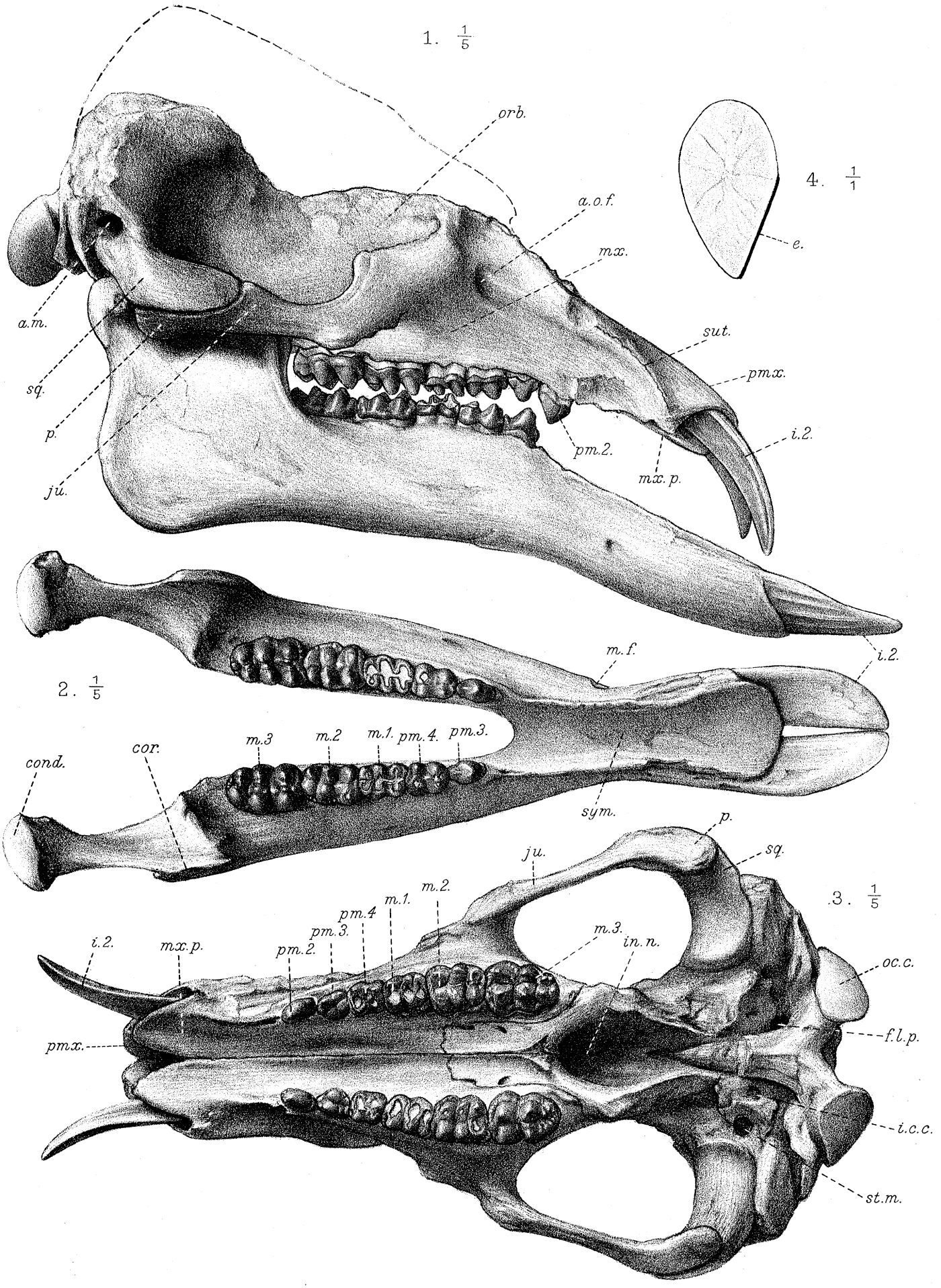
a. m., external auditory meatus.
a. o. f., antorbital foramen.
cond., condyle of mandible.
cor., coronoid process.
e., enamel of tusk.
f. l. p., foramen lacerum posterius.
foss., fossa between the premaxillæ and the anterior prolongations of the maxillæ.
i. 2, incisor tusks.
i. c. c., foramen of the internal common carotid artery.
in. n., opening of internal nares.
ju., jugal.
m. 1–3, molar teeth.
m. f., mental foramen.
mx., maxilla.
mx. p., anterior prolongations of the palatine plates of the maxillæ.
oc. c., occipital condyle.

orb., orbit.
p., process formed by under end of jugal.
pal., palatine.
p. mx., premaxilla.
pm. 2–4, premolar teeth.
sq., squamosal.
sym., symphysis of mandible.
st. f., stylomastoid foramen.
sut., maxillo-premaxillary suture.

PLATE 32.—MANDIBLE OF A YOUNG INDIVIDUAL OF *Palæomastodon wintoni*, ANDREWS, SHOWING THE MILK DENTITION AND THE SUCCESSIONAL TEETH.

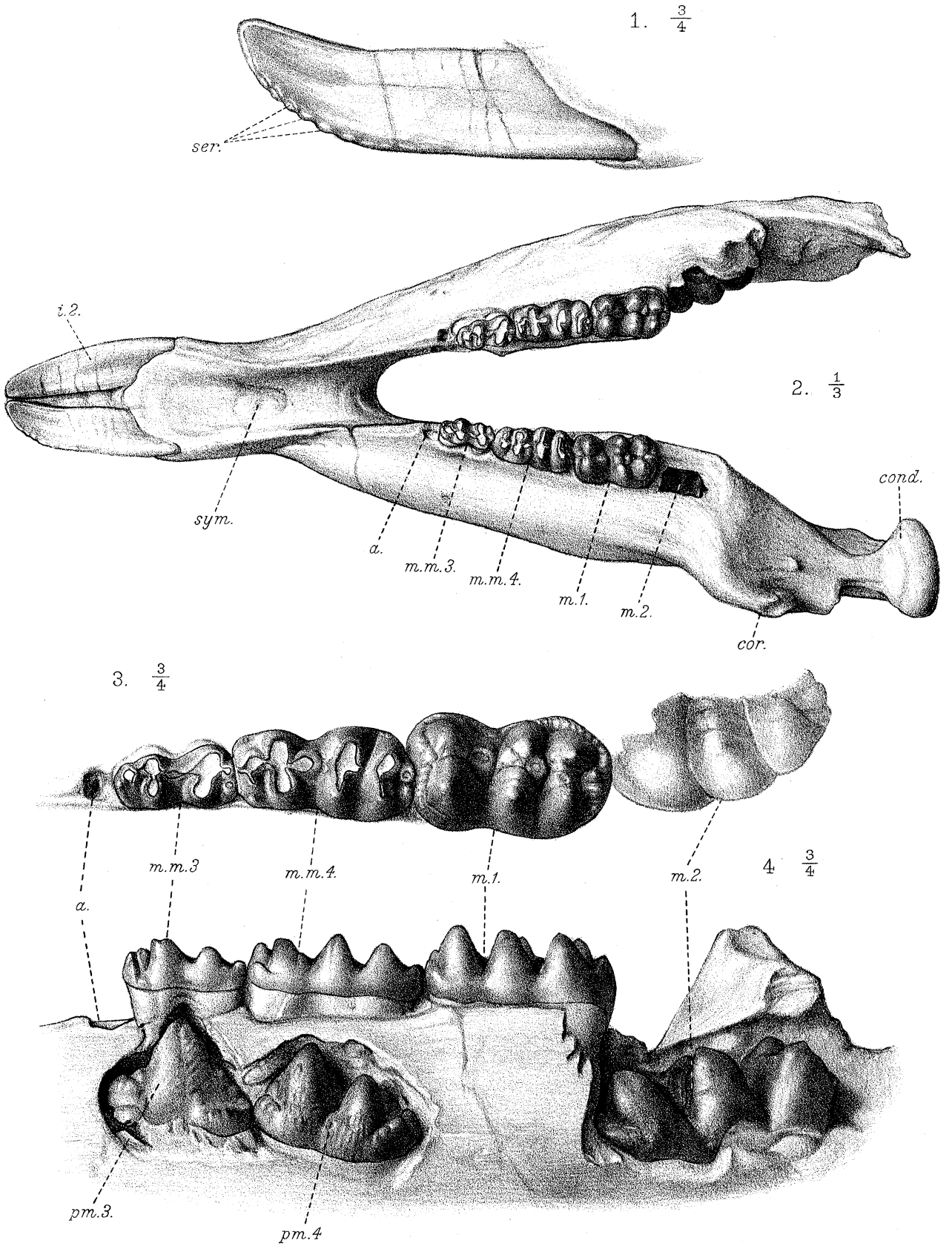
Fig. 1.—Upper view of left incisor. ($\frac{3}{4}$ nat. size.)
Fig. 2.—Upper view of the whole mandible, with the teeth. ($\frac{1}{3}$ nat. size.)
Fig. 3.—Crown view of the right milk-molars (*m.m.* 3, *m.m.* 4) and of *m.* 1 and *m.* 2. ($\frac{3}{4}$ nat. size.)
Fig. 4.—Side view of the cheek teeth of the right side, showing *m.m.* 3 and 4, with the replacing premolars *pm.* 3, *pm.* 4 beneath them; also the first true molar and the germ of the second. ($\frac{3}{4}$ nat. size.)

a., empty alveolus of *m.m.* 2.
cond., condyle of mandible.
cor., coronoid process of mandible.
i. 2, incisors.
m. 1, 2, first and second permanent molars.
m.m., 3, 4, third and fourth milk-molars.
pm. 3, 4, third and fourth premolars.
ser., serrations on edge of incisors.
sym., symphysis of mandible.



G.M.Woodward del.et lith. West, Newman imp.

PALÆOMASTODON.



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West, Newman imp.

PALÆOMASTODON.

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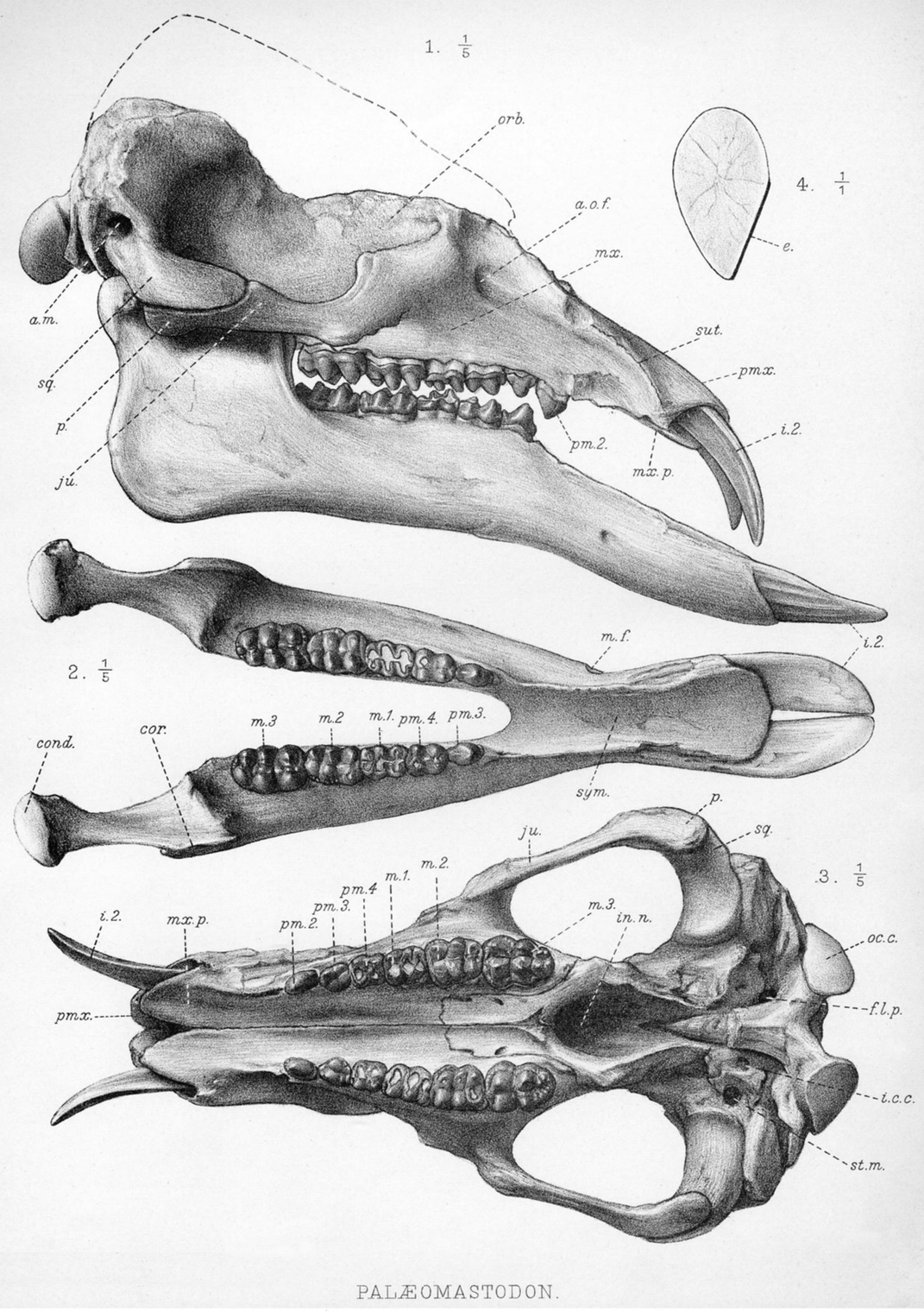

PLATE 31.—ASSOCIATED SKULL AND MANDIBLE OF *Palæomastodon wintoni*, ANDREWS.

Fig. 1.—From right side. The upper part of the skull is restored in outline. ($\frac{1}{5}$ nat. size.)

Fig. 2.—Mandible from above. ($\frac{1}{5}$ nat. size.)

Fig. 3.—Skull from below. ($\frac{1}{5}$ nat. size.)

Fig. 4.—Section across tusk close to the alveolus. (Nat. size.)

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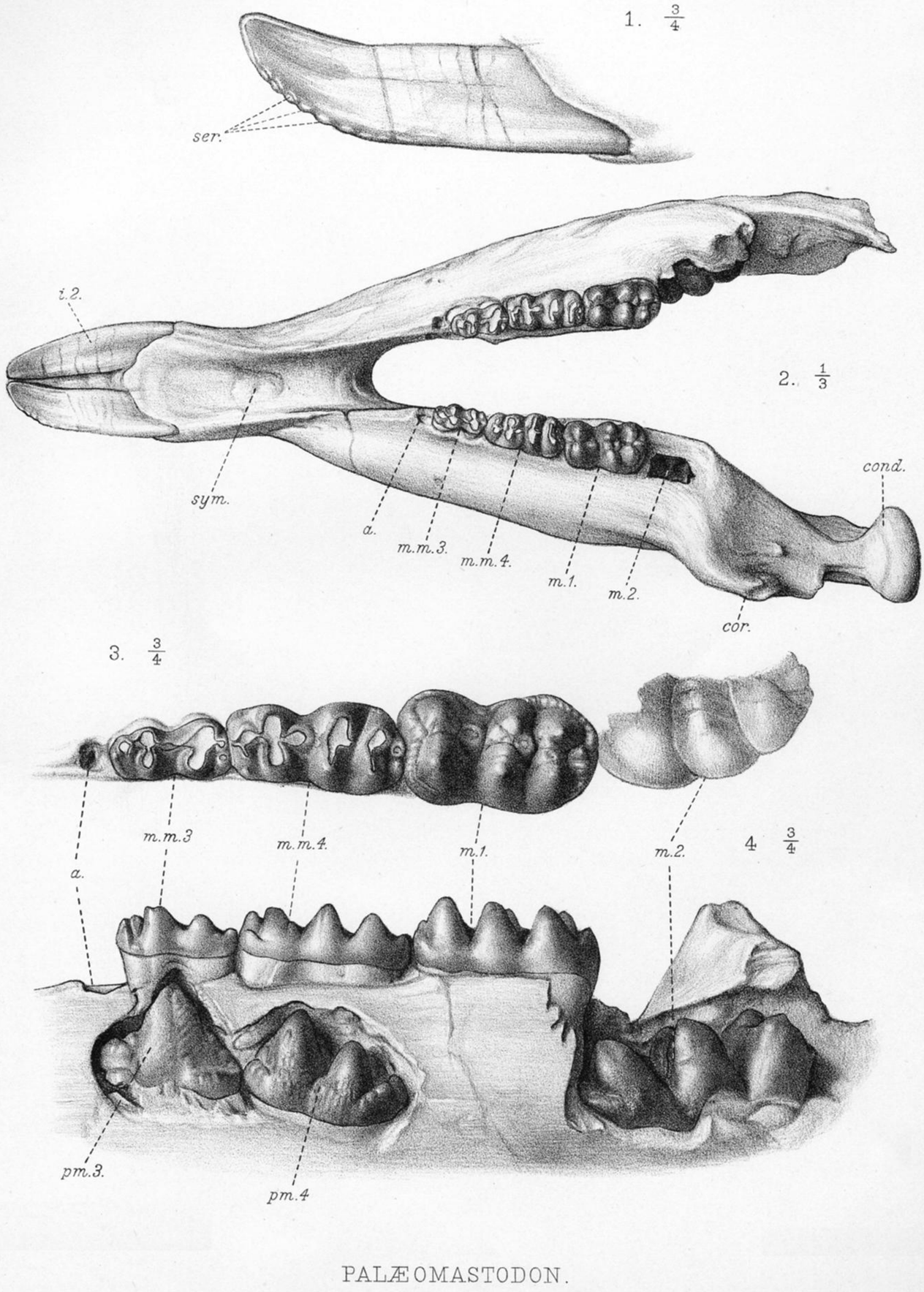
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



PALÆOMASTODON.

PLATE 32.—MANDIBLE OF A YOUNG INDIVIDUAL OF *Palæomastodon wintoni*, ANDREWS, SHOWING THE MILK DENTITION AND THE SUCCESSIONAL TEETH.

Fig. 1.—Upper view of left incisor. ($\frac{3}{4}$ nat. size.)

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