XV. *On the Affinities of* Thylacoleo.

By Professor Owen, *C.B., F.R.S., &c., Superintendent of the Natural History Department, British Museum.*

Received January 25,—Read February 1, 1883.

[Plates 39–41.]

In a former Paper on *Thylacoleo** was summed up what I then inferred from the fossil remains of the species "*carnifex*" which had reached me at that date, but acquiescence in those conclusions seemed, in the opinion of some contemporary Palæontologists, to require further evidence. I have, accordingly, omitted no opportunity of obtaining such, and the fossils so acquired form the subject of the present communication.

The locality which promised success in this quest was the limestone district of Wellington Valley, New South Wales, from one of the caves of which the first evidence of *Thylacoleo* had been obtained.†

And, here, I have to express my deep obligations to the Legislature of New South Wales for the Grants liberally voted for the further exploration of the caves and brecciated fissures of that district, and my acknowledgments of the friendly support given to my representations by the Premier, Sir Henry Parkes. The direction and supervision of these explorations were confided to the accomplished and able Curator of the Australian Museum, Sydney, Ed. V. Ramsay, F.L.S., to whom I am indebted for prompt transmission of the subjects of the present Paper, included in the results of his mission.

Dentition of the upper jaw of Thylacoleo carnifex.—Of the first or laniariform incisor the base only of the crown was the subject of fig. 1, 2, 3, Plate 11, p. 217, of the Paper above cited (1871). A detached crown of what I then inferred to have formed part of the homologous tooth is the subject of fig. 7 and 8 of Plate 11 (Paper, 1871). I have now the upper jaw with the entire dentition (Plate 39, fig. 1),

* "On the Fossil Mammals of Australia": Part IV., Phil. Trans., 1871, p. 213.

† By the then Surveyor General of Australia, Colonel Sir Thomas Mitchell, C.B., discoverer of the fertile region which he named after his great Commander. See Appendix to his 'Three Expeditions into Eastern Australia,' 8vo., vol. ii., 1838.

of which it seems necessary to add to former figures the palatal view only for comparison with fig. 3 of Plate 11 (Paper of 1871).

The foremost tooth (Plate 39, fig. 1, *i* 1) shows an exserted crown, 1 inch 3 lines in length, curved with the convexity forward, subcompressed, conical, pointed, obtuse anteriorly, trenchant behind where the enamel forms a finely serrate ridge; it is in shape and size a tooth suggestive of powers of penetration and prehension. It is deeply inserted by a stout cement-clad fang, indicative of limited growth. The entire length of the tooth, following the curve, is $2\frac{1}{2}$ inches.

The second tooth, (ib., ib., *i* 2) projects behind and partly mesiad of the base of the first, its crown is but 5 lines in length; other dimensions are shown in the figure. The working surface is bevelled off, before and behind, to a low ridge.

Next to this tooth and partially overlapping the hind and outer part of its crown is that of a larger trenchant tooth, *i* 3, 7 lines in longitudinal, 5 lines in transverse diameters, but barely exceeding the second tooth in height.

This is followed by a fourth, *p* 1, about the size of the second, *i* 2. Its crown is partly overlapped by the larger tooth, *i* 3; it is also subtrenchant lengthwise.

External to the hinder part of *p* 1, and about half the size, projects the crown of a tubercular tooth, *p* 2; it is immediately followed by a sixth tooth, *p* 3, of similar shape and size. This tooth is partly overlapped externally by the fore end of the great carnassial tooth, *p* 4.

The homologies indicated by the symbols of the five teeth crowded between *i* 1 and *p* 4 may be questioned, but that of the latter with the trenchant premolar in existing phytophagous Diprotodonts is plain. In plate 100, pp. 381–394 of the undercited work,* the eight chief modifications of the comparable Diprotodont dentition in existing Marsupials are described and figured. Of these the genera *Hypsiprymnus* and *Phascolarctos* offer the nearest approach to *Thylacoleo* in the proportions of antero-posterior to vertical extent of the crown of *p* 4. But the size of this tooth in those existing genera is much less relatively to the other teeth, especially to the bruising molars, four on each side of the upper, as of the lower jaw, which in them follow the trenchant premolar. In those genera, as in *Macropus*, *Petaurus* and *Phalangista*, three close-set incisors are lodged in the premaxillary; and, in *Macropus*, the third incisor is as much larger than the second, as is the third tooth (Plate 39, fig. 1, *i* 3) in the series of upper teeth in *Thylacoleo*.

In *Phascolarctos* and *Hypsiprymnus* a minute canine projects from the maxillo-premaxillary suture with a well-marked interval between the incisors in front and the trenchant premolar behind. In *Petaurus* and *Phalangista Cookii* two small premolars, *p* 3, *p* 2, precede the tooth *p* 4, which is in contact with the foremost of the four crushing molars.

With the five teeth, therefore, preceding the trenchant premolar, in the above-cited existing Diprotodonts may be homologized, in the aggregate, the five teeth between

* 'Odontography,' 8vo., 1840.

the foremost tooth, *i* 1, and the carnassial, *p* 4, in *Thylacoleo*. But to which of them the term canine may be assigned is doubtful. Relative size might weigh with the largest of these intermediate teeth, *i* 3, but its trenchant character is repeated in the third incisor of the existing Kangaroos; it is not a cuspidate tooth as restored in outline at *c*, in Plate 14 of the Paper of 1871. I have nothing to alter or add to former descriptions of *p* 4 and *m* 1 (ib., ib.). In existing Diprotodonts the latter tooth has a broad tuberculate or ridged masticatory crown, and is followed by three similar molars, absent in *Thylacoleo*.

Of the extreme modification of the Diprotodont type for carnivorous work I hold the opinion expressed in the former Paper (1871), and have only to add that the retention of the seemingly functionless teeth, *i* 2–*p* 3, crowded together in the upper jaw, is significant of a principle underlying the adaptive explanation.

Dentition of the lower jaw of Thylacoleo.—In the portions of mandible of *Thyl. carnifex*, figured in Plates 12 and 13 of the Paper of 1871, the dental formula was inferred, as in that of the upper jaw, from sockets of teeth. I am now able to submit three views of the entire dentition of a fossil mandible (Plate 39, fig. 2; Plate 41, figs. 1 and 2) discovered in contiguity with the subject of fig. 1, Plate 39.

The foremost laniariform tooth, *i* 1, repeats the shape and size described (pp. 226, 227) and figured (Plate 13, figs. 4–7, Paper of 1871) from a cast transmitted to me in 1870, of a tooth in the Museum of Natural History, Sydney, which was obtained by Mr. KREFFT from "a breccia cavern, Wellington Valley"; and its characters might well condone the conjecture that it was a feline canine tooth.

Two small teeth (Plate 39, fig. 2, *p* 2, *p* 3) are wedged in between the foremost tooth, *i* 1, and the carnassial, *p* 4.

In *Phalangista vulpina* one such tooth follows the front incisor; in *Phal. Cookii* there are two; in *Petaurus* there are three denticles between the incisor, *i* 1, and the premolar, *p* 4. To two of such seemingly functionless teeth those marked *p* 2 and *p* 3, in Plate 39, fig. 2, and Plate 41, figs. 1 and 2, may be homologous. Their interest lies, as in their homotypes in the upper jaw, in the manifestation of a diprotodont dentition under its extreme functional modification in the great extinct Marsupial Carnivore.

Two sockets, indicated by *p* 2 and *p* 3, in the fossil figured in Plate 12, figs. 2 and 3, (1871), but which might have lodged the two roots of a single tooth, are now demonstrated to have held two small close-set teeth, of which the hindmost is hidden from outer view by the forepart of the carnassial, *p* 4. The foremost, *p* 2, immediately following *i* 1, is more than twice the size of *p* 3, and has a cuspidate crown (Plate 39, fig. 2); but it is a dwarf by the side of the laniariform tooth, *i* 1. To former descriptions of this tooth there seems nothing to add to the present demonstration of its place in the dental series.

The tooth, *m* 1, succeeding the carnassial, repeats in general character that described (p. 224) and figured (Plate 13, fig. 2, *m* 1, 1871) from a photograph. The difference

in wear and the slight one in size may indicate the present fossil to have come from an older and somewhat (sexually ?) larger *Thylacoleo*. The apex of the anterior lobe has been worn off, and the lower hind lobe shows abrasion; but there is as little approach in relative size and conformation of crown in the present thylacolean m 1 to that tooth in the phytophagous Diprotodonts (Plate 41, figs. 3 and 4) as was indicated by the thylacolean subject which first came to my hands.

The tooth, m 2, as indicated by its socket in Plate 14 (1871), is of the same relative size, but with a more acuminate crown than is indicated by the conjectural outline there given.

The maxillary and mandibular fossils here described and figured add the entire dentition of *Thylacoleo carnifex* to the series of mammalian modifications of the dental system with which Comparative Anatomy is now enriched; and they afford sure grounds for physiological deductions as to the nature and habits of the extinct Marsupial.

Antibrachial bones of Thylacoleo.—Of the bones and portions of bone referable by size to this genus and discovered in the same cave with the jaws and teeth last described are those of the fore-arm (Plate 40), of which the ulna (fig. 4) lacks only two inches of its distal end, according to the proportions of that bone in the larger Felines: this comparison is made from its being associated with an entire radius (ib., fig. 1) of the same length as that of the Lion: both fossils form part of the same limb of the leonine Marsupial.

The articular surfaces in these fossils are as closely adapted to the divers movements of a fore-arm required for the application of the paw of a carnivore as in the Felines.

The proximal end of the radius is occupied by an articular surface (ib., fig. 2) in two continuous portions, the larger and terminal one (fig. 3, *a*) being moderately concave for adaption to the radial condyle of the humerus, the smaller convex surface (ib., *b*), bending down on the inner or ulnar border for articulation with the outer or radial concavity (fig. 5, *b*), continued from the larger and deeper trochlear surface (ib., *a*), near the humeral end of the ulna.

The proximal or humeral cavity of the radius is not circular as in herbivorous Marsupials, but is less oblong than in *Leo*; it is similarly continued upon a thick convex border, extended to form the surface *b*, fig. 3.

The shaft of the radius describes the same slight curve "radiad," or on the outer side, and maintains the same nearly uniform breadth to the distal expansion, as in the Lion. The radial, or free, border is similarly obtuse; the opposite border (*d*) is for the most part roughly trenchant. The process (fig. 1, *c*) for implantation of the *brachialis externus* muscle holds the same relative position to the proximal end as in *Leo*. At the expanded distal end the elongate tuberosity (*e*) above the produced radial or outer angle for the carpal joint shows the same oblique groove for the tendon of the *extensor carpi radialis*. The tuberosity (*f*) answering to that giving insertion to the tendon of the *supinator longus* in the Lion, is nearer the ulnar angle of the distal expansion,

instead of rising midway between the terminal angles: and here I may remark that the Felines agree with the Marsupials in the presence of this muscle. In all minor modifications the leonine characters are closely repeated in the present fossil radius.

The same general correspondence of structure prevails in the ulna (fig. 4). The olecranon (*c*) offers the same development, with tuberous and ridged indications for adequate implantation of the powerful extensors of the fore-arm: it is relatively longer, but with rather less breadth than in *Leo*. The proximal articular surface has the same trochlear character (*a*) and passes uninterruptedly, but with a similar defining line, into the concave surface (fig. 5, *b*) for the corresponding side of the head of the radius. The adaption of these joints for free pronation and supination, as well as flexion and extension of the fore-paw, is as strongly marked in *Thylacoleo* as in the similarly-sized placental Felines. The few noticeable modifications indicate the derivative relation to the inplacental group.

In the existing Diprotodont Marsupials, whether climbers, flyers, burrowers or leapers, the bones of the fore-arm are freely articulated for both rotatory and flexile movements, a power which has been suggested to relate to manipulations of the nursing pouch; therefore, to be needed by the Kangaroo group as well as the rest. But in none, save the Wombat, does the proportion of the olecranon come near to that in *Thylacoleo*. The modifications of the radius and ulna for burrowing actions present differences, in number and kind, from those in *Thylacoleo* which need only a glance at the skeleton of *Phascolomys* to be appreciated.

In other Diprotodonts, especially the species *Macropus major*, for example, nearest in size to *Thylacoleo*, the olecranon is not continued beyond the trochlear cavity to the extent of that joint longitudinally: the shaft of the ulna is relatively longer and much more slender. The radius, with a circular proximal end, gives a smaller and less definite lateral articular surface to a concomitantly smaller external ('radial') offset from the trochlear articulation: the shaft of the radius is also relatively longer and more slender, and is proportionally less expanded at the distal end than in *Thylacoleo*.

Claw-phalanx of Thylacoleo.—Passing over evidences of carpal and metacarpal fossils, my remarks will, here, be limited to the characters of the terminal or ungual phalanges.

Fossil claw-bones are not few from the Thylacolean cavern, and these in shape and structure add instructive evidence of the nature of the quadruped to which, by their size, they may be attributed. By these characters a phalanx of a fore-paw may be selected: the talon which such bone supported and wielded was fully as large as that of the Lion, and indicates that it was sub-compressed, decurved and pointed.

The basal articular surface (fig. 7, *a*) shows a pair of vertical concavities divided by a mid-ridge: it occupies the breadth and greater part of the height of the base, leaving about an equal but small extent of non-articular tuberous insertional portion above and below the trochlear joint.

But the most instructive part of the phalanx is the extension from the upper and

lateral borders of the base of a bony sheath (fig. 6, *b*), which overarches the proximal three-fourths of the claw-bearing part (*c*): this sheath is also continued from the sides of the broad, somewhat flattened under portion of the articular division of the phalanx, which terminates (fig. 8, *d*) where the compressed claw extends freely forward. The under surface (fig. 7) of the sheath-supporting division of the phalanx is perforated by a pair of canals, which transmitted the blood-vessels and nerves to the formative and reproductive organ of the talon.

I have not found any instance of such sheath claw-phalanx in the existing or extinct kinds of diprotodont Marsupials, other than *Thylacoleo.*

The placental Mammals which possess such claw-sheath are amongst the carnivorous, and, most conspicuously, the Feline species; also certain Edentates, more especially the great extinct Megatherioids.

The chief difference, in these placentals, is that the articular surface, in Felines, ends nearer the lower or palmar surface of the joint, which is overtopped by the prominence for insertion of the retractor tendon of the claw; while in Edentates the articular surface leaves a larger proportion of the under part of the base of the phalanx free and tuberous for insertion of the powerful muscles which deflect the claw.* In all Edentates the claw-bearing part of the sheathed-phalanx is relatively longer, thicker, and commonly less acute than in Felines.

In this comparison the ungual phalanx of *Thylacoleo* much more closely resembles that of *Felis Leo* or *Felis Tigris.*†

Mandible of Thylacoleo.—I finally submit a description and figures (Plate 41) of the fossil mandible with the Thylacoleon dentition, as the osseous evidence testifying most directly to the matter at issue.

Plate 41, fig. 1, gives the outside view of a mandible of *Thylacoleo carnifex*, in which a carnivorous modification of the dentition has been engrafted, as in the older extinct form *Plagiaulax* (ib., fig. 5), on a Marsupial and Diprotodont type.

In comparison with the mandible of the Koala (*Phascolarctos*, Plate 41, fig. 3) and Potoroo (*Hypsiprymnus*), which are selected by Professor FLOWER, F.R.S.,‡ as most nearly resembling that of *Thylacoleo*, may, first, be noted in *Thylacoleo*, fig. 1, the relative shortness of the dentigerous part of the mandible to its depth, especially at the fore end, and the outswelling wall of the socket of the great carnassial premolar (ib.,

* 'Memoir on the Megatherium,' 4to., 1860, plate 25, fig. 1, iii.; and 'Memoir on the Mylodon,' 4to., 1840, plates 15 and 17.

† The following is CUVIER'S description of this phalanx in the Feline family:—"La figure de cette phalange est celle d'un crochet fait des deux parties: l'une dirigée en avant, courbée, tranchante et pointue, reçoit l'ongle, dont la forme est à peu près la même: la base de cette première portion fait une espèce de capuchon osseux, dans lequel est reçue la base de l'ongle comme dans une gaîne." 'Leçons d'Anatomie comparée,' 8vo., ed. 1835, tome i, p. 434: "*Les dernières phalanges dans la famille des Chats.*" It is equally applicable to the subjects of figures 6 and 8 in Plate 40.

‡ "On the Affinities and probable Habits of the extinct Australian Marsupial, *Thylacoleo carnifex*, OWEN," Quarterly Journal of the Geological Society of London, March, 1868, vol. xxiv., p. 307.

fig. 1, *p* 4) : next, the relative extent and depth of the depression (*d*) for the insertion of the temporal, or great biting, muscle. The outline of the termination of the coronoid process (*b*) is given on the authority of Mr. RAMSAY, from other and fragmentary portions of Thylacolean mandibles. The upper border of the process extends backward at a more open angle than in the Potoroo or Koala (ib., fig. 3), and to an extent beyond the articular condyle. The inflected angle of the jaw, *a*, characteristic of the *Marsupialia*, is so abrupt in *Thylacoleo* that only the tip is visible in an outer view (fig. 1, *a*), and this, with the angle, hardly rises above the level of the lower border of the ramus. In the Potoroo and Koala (ib., fig. 3) the angle (*a*) is relatively larger, rises higher, is less directly inflected, and the whole comes into the outer view of the ramus, as in other Marsupial Phytophagans (see fig. 4, *Phalangista;* also the Paper of 1871, p. 260, fig. 16, *Dendrolagus*, and fig. 18, *Bettongia*).

In the vegetarian Diprotodonts the ascending ramus of the jaw supporting the articular condyle, *c*, and coronoid process, *b*, is relatively narrower and loftier than in the sarcophagous kinds. (Compare fig. 3 (*Phascolarctos*) and fig. 4 (*Phalangista Cookii*) with figs. 1 and 2, Plate 41.) The latter, indeed, comes nearer than *Phascolarctos*, in retaining the small, seemingly, functionless denticles between *p* 4 and *i* 1.

But the crucial test is the shape and relative position of the articular condyle, *c*. In all existing Phytophagans it rises above the level of the molar series, in most considerably, as in the figures cited: in the existing carnivorous Marsupials, as *Thylacinus* (*loc. cit.*, p. 235, fig. 11) and *Dasyurus* (ib. ib., fig. 12) it does not rise above that level. In the shape of the condyle, the transverse much exceeding the antero-posterior diameter of its convex articular surface, and in its sessile attachment forbidding predication of a neck, carnivorous characters are seen in *Thylacoleo* which are wanting in all Marsupial Phytophagans. In all the characters in which the mandible of the Marsupial Lion agrees with that of the smaller pouched Carnivores, the resemblance is still closer to that bone in the type Carnivores of the placental series.

In the Paper of 1871 I was unable to oppose Professor FLOWER'S conjectural restoration of the mandible of *Thylacoleo* (*loc. cit.*, p. 307), according to the type of that bone in the Koala and Potoroo by other than a conjectural restoration (ib. ib., fig. 8; and Plate 12, fig. 1) in which the inferred relative position of the mandibular condyle is indicated by the curved line, *b*, in the text. The two restorations may now be tested by the figures from nature in Plate 41.

Description of the Plates.

PLATE 39.

Fig. 1. Palatal or working surface of the teeth of the upper jaw, *Thylacoleo carnifex.*

Fig. 2. Corresponding surface of the teeth of the lower jaw, ibid.

Both figures are of the natural size.

PLATE 40.

Fig. 1. Radius, *Thylacoleo carnifex.*

Fig. 2. Proximal articular surface of the same bone.

Fig. 3. Proximal end of ditto.

Fig. 4. Ulna, *Thylacoleo carnifex.*

Fig. 5. Front view of proximal articular surface.

Fig. 6. Ungual phalanx, *Thylacoleo carnifex.*

Fig. 7. Under view of ditto.

Fig. 8. Claw-bearing portion, with one-half of the sheath removed.

(In ungual phalanges, probably of the hind jaw, the sheath is little, if at all, developed.)

PLATE 41.

Fig. 1. Outside view of mandible and teeth, *Thylacoleo carnifex.*

Fig. 2. Inside view of mandible and teeth, *Thylacoleo carnifex.*

Fig. 3. Outside view of mandible and teeth, with grinding surface of the molars, *Phascolarctos fuscus.*

Fig. 4. Inside view of mandibular ramus and teeth, *Phylangista Cookii.*

Fig. 5. Outside view of mandible and teeth, *Plagiaulax Becclesii.*

All the figures are of the natural size.

Fig. 1.

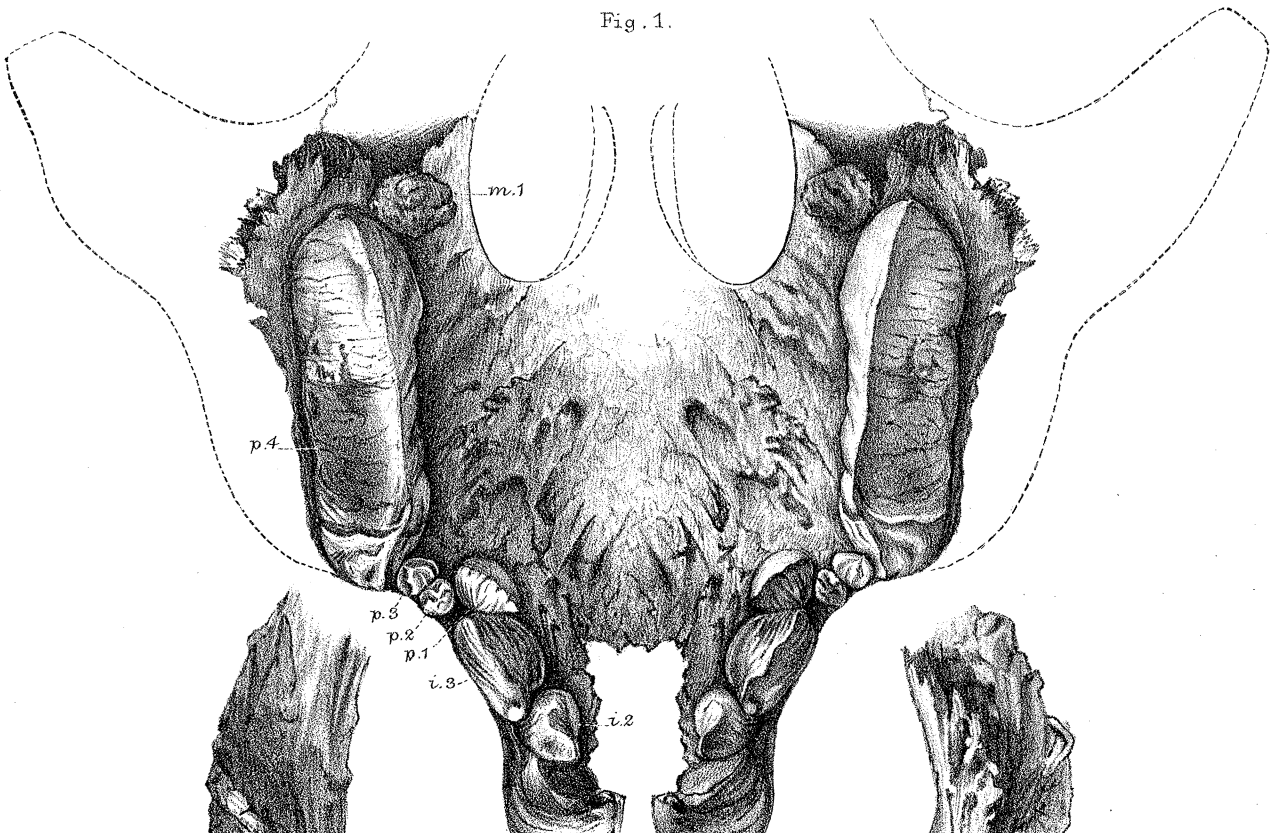
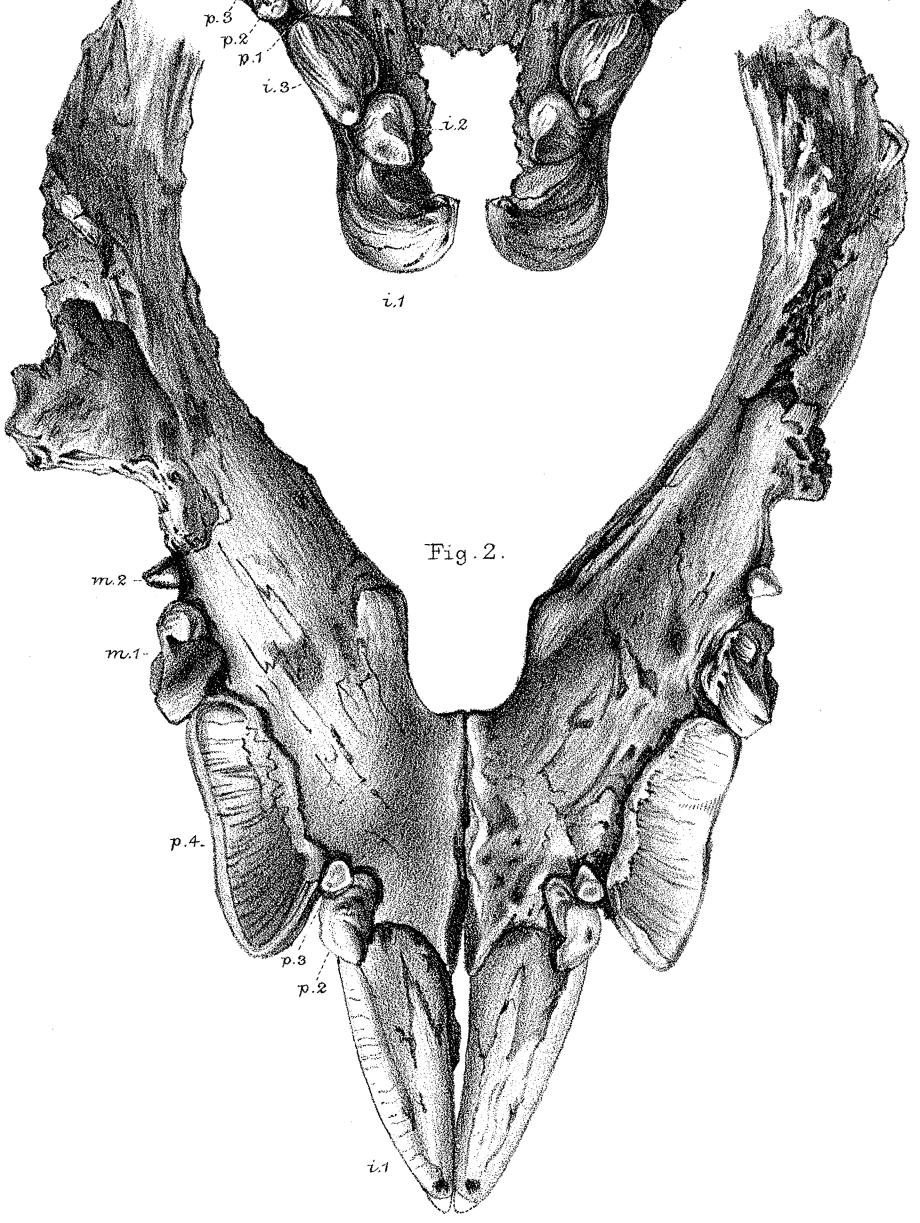


Fig. 2.



THYLOCOLEO CARNIFEX

West, Newman & Co. lith

Fig. 1.

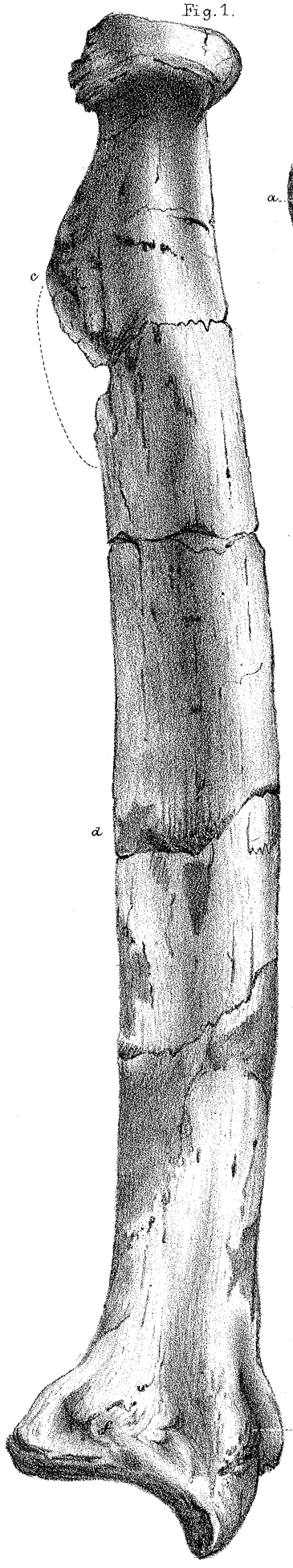


Fig. 2

Fig. 3.

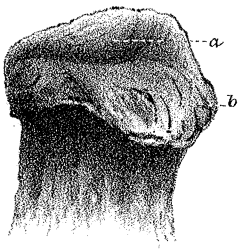


Fig. 4

Fig. 5.

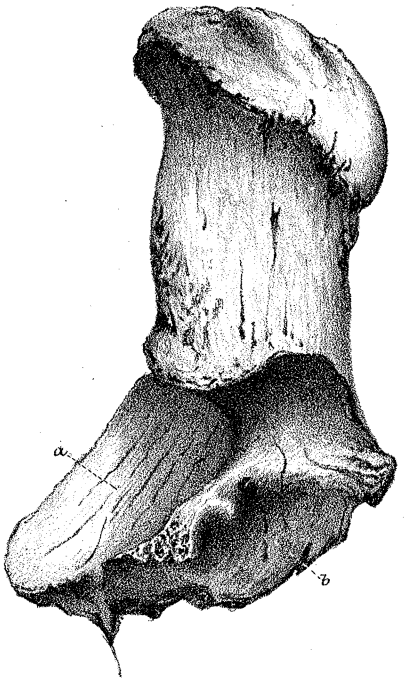


Fig. 6.

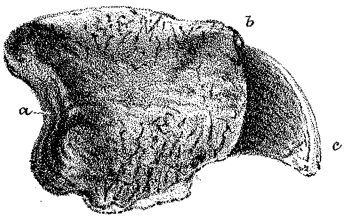


Fig. 7.

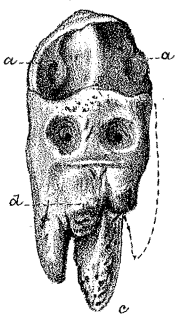
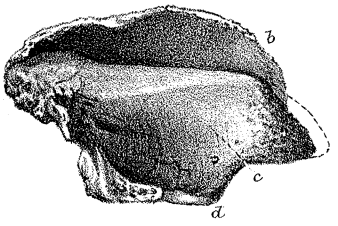
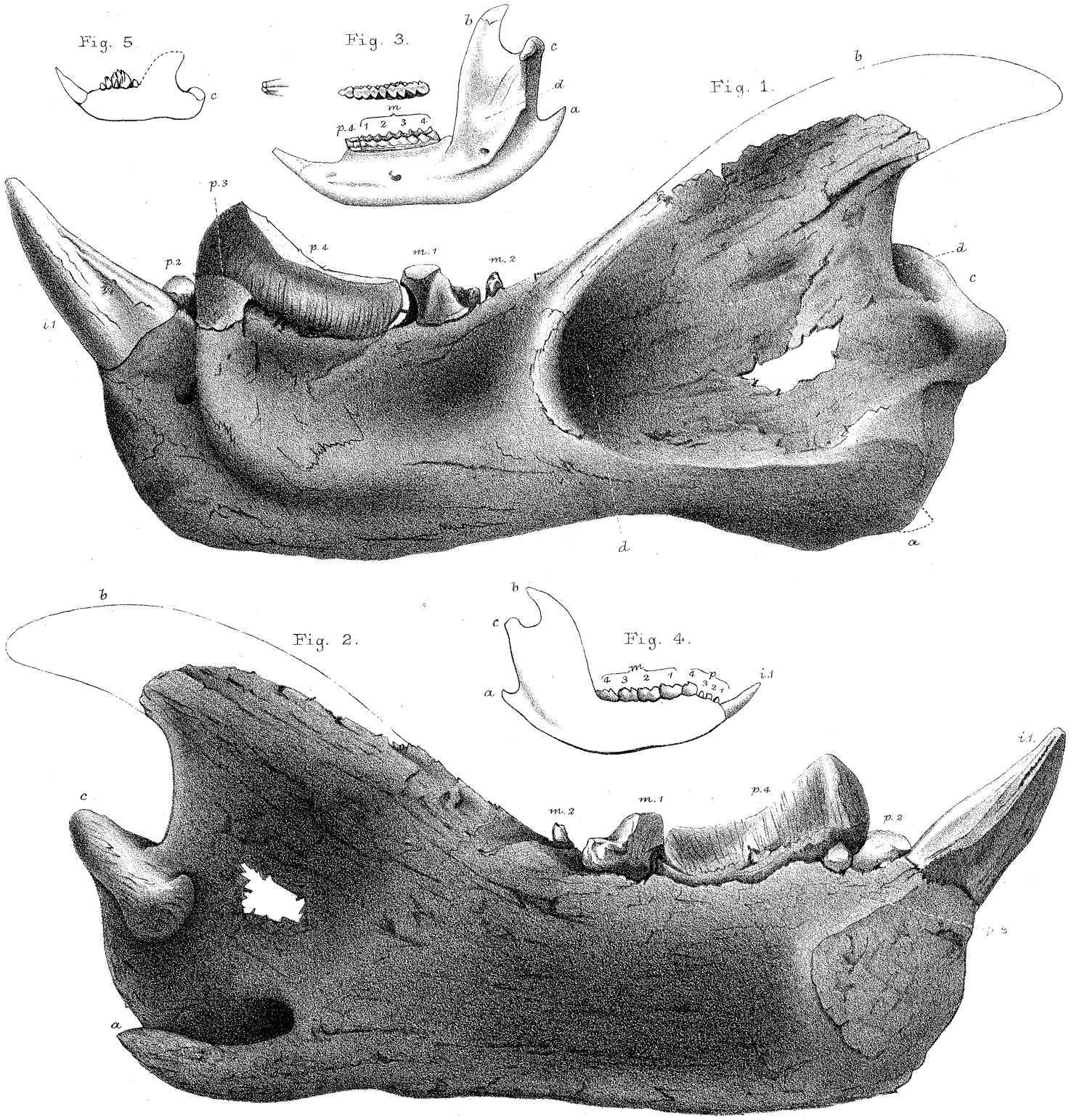


Fig. 8.



THYLOCOLEO CARNIFEX.

West, Newman & Co. lith.



West Newman & Co. lith.

THYLOCOLEO CARNIFEX.