IX. *On the Fossil Mammals of Australia.*—Part IV. *Dentition and Mandible of* Thylacoleo carnifex, *with remarks on the arguments for its Herbivority. By Professor* Owen, *F.R.S. &c.*

Received September 27,—Read November 17, 1870.

Contents.

§ 1. In former Papers on the Fossil Mammals of Australia (*Thylacoleo*, Parts I. & II.) I inferred, from the size and position of the socket of the anterior tooth, from the structure of the root of the tooth therein implanted, and, above all, from the characters of the associated and completely preserved teeth, that such front tooth must have been laniariform, *i. e.* subcompressed and pointed, adapted for piercing, holding, and lacerating, like the canine of a Carnivore*.

To this the late laborious and experienced palæontologist, Dr. Falconer, has objected that, in referring to my paper, he finds "that the body of the tooth, of which the shape and direction are adduced as terms of comparison, together with the fore part of the symphysis, is wanting"†.

* Philosophical Transactions, 1859, p. 318; ib. 1866, pp. 79, 80.

† Quarterly Journal of the Geological Society, June 1862, vol. xviii. p. 353; also 'Palæontological Memoirs

To my statement, "that there is a socket close to the symphysis of the lower jaw of *Thylacoleo*, which indicates that the canine may have terminated the dental series there, and afforded an additional feature of resemblance to the *Plagiaulax*"*, Dr. FALCONER remarks:—"In all this, it will be seen, the argument is within the domain of conjecture; the tooth oscillates between canine and incisor; and not merely so, but the principles which are followed as guides in this walk of investigation are set aside, to give place to the illusory indications of mutilated external form..... If palæontological investigations were conducted in this manner there would be no limit to conjecture; the landmarks we profess to follow would be disregarded, and disorder would face us everywhere. But, happily, science furnishes unerring principles, which provide the corrective. I need hardly add that the argument drawn from *Thylacoleo* has, in my view, no bearing on the incisors of *Plagiaulax*, and gives no support to the carnivorous inference"†.

This rebuke, being doubtless kindly meant and penned in the interests of palæontology, I have hitherto borne in silence, hoping that less fragmentary fossils of *Thylacoleo* would ultimately reach me; and sustained, I must own, by a confident belief that they would confirm the inferences drawn from the position of the alveolus, suggesting the alleged feature of resemblance of *Thylacoleo* to *Plagiaulax*.

Nevertheless, the portion of mandible figured in Plates XI. & XIII. of the Phil. Trans. for 1859 being represented by a plaster cast, and the figures 5 & 6 in Plate IV. of the Phil. Trans. for 1866 being from photographs, I could not feel surprised that arguments in favour of the herbivorous nature and affinities of both *Thylacoleo* and *Plagiaulax* should have met with acceptance and support from some Anatomists, Naturalists, and Palæontologists‡.

I have again been favoured, through the kind offices of Sir DANIEL COOPER, Bart., with a collection of fossils obtained by his friend, Mr. ST. JEAN, of Gowrie, from the freshwater deposits of that locality, in Darling Downs, Queensland, Australia, which collection included the alveolar portion and certain teeth of the right upper jaw (Plate XI. figs. 1–5), and the major part of the left ramus of the lower jaw with certain teeth (Plate XII. figs. 1–5) of a full-grown *Thylacoleo carnifex*.

The teeth in the upper jaw are:—the anterior incisor with the terminal half of the crown broken away (i_1), the carnassial (p_4), and three antecedent small and simple obtusely conical teeth ($p_{1, 2, 3}$).

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and Notes,' by the late HUGH FALCONER, F.R.S. &c., 8vo, 1868, vol. ii. p. 437. [In future references I shall use the numbers X. and XI. to signify the above volumes.]

* OWEN'S 'Palæontology,' 8vo, 2nd ed. (1861) p. 432.

† X. p. 354; XI. p. 438.

‡ *E. g.* Mr. BOYD DAWKINS, F.R.S., in Quarterly Journal of the Geological Society of London, vol. xx. 1864, p. 412; Mr. GERARD KREFFT, "On the Dentition of *Thylacoleo carnifex*, OWEN," Annals and Magazine of Natural History, 3rd series, vol. xviii. 1866, p. 148; Professor W. H. FLOWER, F.R.S., "On the Affinities and probable Habits of the extinct Australian Marsupial, *Thylacoleo carnifex*, OWEN," in Quarterly Journal of the Geological Society of London, March 1868, vol. xxiv. p. 307. [This volume and paper I shall refer to as No. XII.]

The teeth in the lower jaw are the root and base of the crown of the incisor ($\ddot{i}$), and the entire carnassial (p_4).

I was thus still driven, as far as these specimens went, to an inferential conclusion as to the form of the crown of the anterior incisor, both above and below. But, since preparing for the Royal Society a description of the specimens, I have been favoured by photographs and fossils of both these teeth nearly complete, and also with a plaster cast of the entire lower incisor, now in the Museum of Natural History at Sydney, New South Wales, through the kindness of the Trustees of that Museum and of their able Curator, Mr. GERARD KREFFT, Corr. M.Z.S.

The teeth transmitted and the subjects of the photographs were obtained from the Breccia-cave in Wellington Valley *, in the course of recent assiduous researches conducted by ALEX. M. THOMSON, D.Sc., Reader on Geology, Sydney University, and by Mr. KREFFT, in 1869, aided by the liberal grant of £200 voted by the Local Parliament of New South Wales in favourable response to the Memorial which I addressed to the Colonial Secretary, February 23rd, 1867 †.

Whatever interpretation may ultimately be accepted in palæontology of the habits and affinities of *Thylacoleo*, additional and valuable materials for such interpretation have thus been added to the subjects of former descriptions: an account of these additions, with their bearing on the arguments that have been opposed to my conclusions, I have now the honour to submit to the Royal Society.

§ 2. *Upper Jaw and Maxillary Teeth.*—The specimen of this part of the skull (Plate XI.) includes almost the entire premaxillary (figs. 1–5, $_{22}$), with its alveolar (a, a'), nasal (n), and palatal (p) portions.

The alveolar portion contains the socket (a) of the anterior large laniariform incisor (i_1), that of a much smaller incisor (i_2) opening close to the first, and, after an interval of two lines, the front half of the socket (c) of a small canine (fig. 9), the division of which socket is made, or rather indicated, by the premaxillo-maxillary suture (s, s'): this third socket is rather larger than the second, and is more outwardly placed.

The nasal portion of the premaxillary forms anteriorly, above the deep socket of the first incisor, a thick obtuse margin (fig. 4, $_{22}$), convex transversely, concave vertically and also laterally toward the nasal cavity (ib. n); it becomes much thinner above the socket, then regains thickness at its upper part, where the plate arches inward to join the nasal bone. A ridge (r) for the attachment of the inferior "turbinal" divides the fore part of the nasal chamber into an upper (n) and a lower (n') passage.

The palatal process (figs. 2 & 3, $p_{22'}$) is thick and short; it projects forward about four lines in advance of the first large alveolus (fig. 1, p‡), is grooved above, lengthwise, where it forms that part of the floor of the nostril, n'; and it is also grooved or chan-

* Discovered by Colonel Sir THOMAS MITCHELL, C.B., F.G.S., and described in his work, 'Three Expeditions into the Interior of Eastern Australia,' 8vo, vol. ii. 1838.

† "On the Fossil Mammals of Australia.—Part III.," Philosophical Transactions, 1870, p. 569.

‡ As shown in the subject of the Memoir, Philosophical Transactions, 1866, Plate II.

nelled longitudinally at its under part, which channel (figs. 2 & 3, 22′) gains breadth and depth as it passes backward; but it is broken away after contributing an inch to the median palatal suture (ib. *p*).

The facial plate of the premaxillary repeats the characters of that figured in Plate II. Philosophical Transactions, 1866, and the suture (*s*, *s′*) with the maxillary has the same crenate character and course.

The outlet of the socket of the first incisor is 9½ lines in fore-and-aft diameter, 6 lines in transverse diameter; the outer wall is outwardly convex, the inner one straight. The depth of the socket is 1½ inch; it contracts to the closed end. The outlet of the second socket (fig. 3, i_2) is circular and small, 4½ lines in diameter; it is also shallow, rapidly contracting to the closed end.

The outlet of the third socket (figs. 2, 3, *c*) is larger, deeper, and elliptical, 4½ lines in long (fore-and-aft) diameter, 4 lines in transverse diameter; it is separated by a diastema of two lines and more from the second, and its hind wall is formed by the maxillary (21), the proportion being the same as that which the maxillary contributes to the premaxillary for the lodgment of the canine in *Thylacinus*. Besides this contribution to the third socket, the portion of maxillary of *Thylacoleo* here preserved shows three sockets of small tubercular premolars (ib. $p_{1, 2, 3}$) and the major part of that of the great carnassial tooth (ib. p_4).

A portion of the outer alveolar plate (figs. 1 & 5, 21) is preserved, and also a portion of the palatal plate (figs. 2 & 3, 21), showing its concavity near the carnassial.

The socket succeeding the third (*c*) is on the inner side of the hind or maxillary part of that socket, showing that the tooth it contained (figs. 2 & 3, p_1) held the same relative position to the third tooth (ib. *c*) as does the anterior premolar to the canine in *Lutra*; thus adding another to the extremely few instances simulating, in *Mammalia*, the double row seen in certain lower Reptiles and Fishes. The outlet of this socket is subcircular, 4 lines by 3½ lines, and is 3 lines distant from the outer surface of the maxillary.

The next (fifth) socket (p_2) is nearer the outer border of the alveolar process, one line and a half behind the back part of the third socket; it is circular, three lines in diameter. It is immediately succeeded by a sixth socket (p_3) of similar size and shape, situated more outwardly as well as posteriorly, the alveolar wall curving from the premaxillo-maxillary suture outward and backward to the prominent fore part of the socket of the great carnassial (p_4).

This socket extends backward almost at a right angle with those of the three small antecedent teeth (fig. 3); its length from before backward is 2 inches 1 line; its greatest breadth near the fore part is 7 lines.

No part of the socket of the small tubercular molar shown in Plates XI. & XIV. fig. 1 of the Philosophical Transactions, 1859, is preserved in the present portion of the upper jaw; but this satisfactorily demonstrates the rest of the dentition of its side of that jaw, as respects size, kind, and number of teeth, and thus supplies what was less perfectly shown in the subject of Plate III., Philosophical Transactions, 1866. (I may add that photographs, and specimens of this tooth (m_1) from the breccia-cave, illustrate the constancy of character in the solitary spelæan example of the true or tubercular molar series from the upper jaw of *Thylacoleo*.)

Of the first incisor (i_1), nearly one inch projects from the outer wall of the socket in the subject of fig. 1, Plate XI.; the inner wall (fig. 2, ib.) extends two lines lower down the tooth. The dimensions of the outlet of the socket give those of the corresponding part of the tooth, which very closely fits and adheres to the socket. The anterior border of the exposed part of the incisor shows a moderate curve convex forward; the posterior border, three lines below the socket, shows, after a slight basal convexity, the beginning of a curve concave backward. The exposed base of the tooth retains for four or five lines below the socket a coating of cement beneath which the enamel emerges. This is thicker toward the back than at the fore part of the crown, but nowhere exceeds half a line. Much of it is broken away from the base of the crown here preserved; and at the outer and back part of the base of the crown the enamel presents a free rounded edge, for two lines vertically, as if it were there interrupted. The dentine is extremely dense; the diameters of the broken part of the crown, which I take to be about halfway from the pointed end of the crown, are 7 lines by $5\frac{1}{2}$ lines; the dentine here presents, in transverse section, a narrow oval form, broader before than behind, and more convex outwardly than on the inner side.

Of the second incisor (i_2) one can infer from its socket that it had a root about 5 lines in length, tapering to an obtuse point, and a crown measuring 4 lines in diameter at its base.

The third tooth which has been displaced from the somewhat larger socket opening upon the premaxillo-maxillary suture, and which makes a slight prominence on the outside of the alveolar tract, at a short distance from the second, I conclude to have been a canine (c); the fang, or implanted part, has been 9 lines in length, slightly curved, tapering to the end.

The tooth remaining in the socket (Plate XI. figs. 2 & 3, p_1) on the inner side of the hind part of the canine (c) has the summit of the enamelled crown broken away; the diameters of the base of the crown are 4 lines and 3 lines. The root is firmly fixed in the socket: I regard this as the first premolar (p_1). Its internal position, its implantation in the maxillary at some distance from the suture with the premaxillary, and its continuation of the oblique line of the succeeding premolars, weigh with me against regarding it as a canine, according to the hypothesis of the tooth (c, Plate XI. figs. 1–3) being a third incisor, as in some hypothetical restorations referred to in the sequel.

The second premolar (p_2) *in situ* in the specimen (Plate XI. figs. 1, 2, 3) is somewhat smaller than p_1, with a very short enamelled crown, forming a low ridge extending from the outer side to nearly the inner side, and there meeting and blending with a second low ridge at right angles, close to the inner border of the crown. The enamel is limited to forming the low-ridged cap or summit of the tooth; the rest of the tooth projecting from the socket is covered by cement. The length of the cement-clad root is given in the figure of, I believe, the homologous tooth in Plate XI. fig. 14.

The third premolar (p_3), also preserved in the specimen (Plate XI. figs. 1–3), is rather larger in size, has a similar extremely low and slightly prominent crown, with the same ridge running from the outer to the inner side, crossed by the shorter ridge at right angles near the inner side of the crown, to which the longer ridge extends, leaving the shorter ridge chiefly conspicuous behind it. The vertical extent of the cement-covered and enamelled part of the second and third premolars projecting beyond their sockets does not exceed 3 lines. This specimen resolves the doubt expressed with regard to their empty sockets in the specimen figured in Plate III. of the 'Philosophical Transactions' for 1866, p. 78*, and demonstrates that each socket contains its own small simply implanted tooth, and was not a division of a socket lodging a larger two-fanged premolar.

Beyond the third premolar the fore part of the crown of the maximized carnassial † (Plate XI. figs. 1 & 2, p_4) extends downward 10 lines. The shape, structure, vertical grooving, and dimensions of this tooth agree with those in the specimens described in the previous Memoirs.

The trenchant margin of the upper carnassial is worn, as usual, obliquely from without upward and inward, the cutting-edge of the enamel being external (Plate XI. fig. 2, p_4). This edge does not run straight, but sinks to form a low angle at the end of a well-marked external vertical groove (ib. *o*), marking off rather more than one-third of the hind part of the crown, which answers to the similarly but better defined hind lobe of the feline upper carnassial. The smoothly worn surface is thus divided into two parts, the anterior one being broadest anteriorly at the thickest part of the tooth, while the posterior gains breadth as it recedes toward the hind end of the crown. But the indications of resemblance to the feline carnassial, especially to that of *Machairodus* (Plate XI. figs. 15, 16), do not end here. The inner surface of the crown, about one-fourth of the way from the fore to the hind margin, projects and terminates in a ridge (*v*, figs. 2 & 3, Plate XI.), which expands to the base of the crown, representing the more developed ridge or vertical swelling of that part of the carnassial in *Machairodus* (fig. 15, *v*), from the broadening base (*v'*) of which the tubercle of the upper carnassial, wanting in *Machairodus* as in *Thylacoleo*, is developed in *Felis*. An opposite vertical ridge on the outer side of the crown in *Thylacoleo* (fig. 1, p_4, *u*) represents the most prominent part of the middle lobe of the carnassial in Felines (fig. 16, *u*), whence the outer surface bends inward to the angle or groove dividing that lobe from the hind one. The outer surface in *Thylacoleo* bends in the same direction to the corresponding angle or groove (*o*, figs. 1 & 3), then curves outward to the hind end of the crown. This is very low and subobtuse, as is the corresponding end of the carnassial in Felines. But the fore part of the crown, in

* "At the fore part of the carnassial socket the alveolar border is excavated by either a similar socket for a two-rooted tooth, or by two contiguous sockets for two small single-rooted teeth."

† No evidence has yet been had that this or the antecedent permanent teeth had displaced deciduous predecessors; the adopted symbol *p* is to be taken with this reservation.

Thylacoleo, rises with a backward inclination to the highest, or vertically longest, part of the crown, from which a well-marked ridge traverses or forms the anterior margin of the crown (figs. 2 & 3, *z*). The anterior root is longer but narrower, antero-posteriorly, than the posterior one, as in the upper carnassial of Felines.

In *Hypsiprymnus minor* (Plate XI. figs. 17, 18) the premolar has a straighter edge, not bilobed; the outer side of the crown is indented with the four or more parallel grooves and ridges, at the apical half; the inner side is uniformly and obliquely worn, in degree according to age.

§ 3. *Mandible and Mandibular Teeth.*—The portion of lower jaw (Plate XII. figs. 1–5) from the deposit at Gowrie includes 6 inches in longitudinal extent of the left ramus, viz. from the fore part of the symphysis (*s*) to the fore part of the strongly inflected angle (*a*). This latter character is acceptable as confirmatory of the marsupial nature of *Thylacoleo*, in a way more intelligible or convincing to some than the cranial and maxillary characters adduced in support of that induction in the original Memoir (Philosophical Transactions, 1859); although I am not aware that the marsupiality of *Thylacoleo* has been, by any objector, called in question.

The fossil is massive, heavy, much petrified; it retains the fang and base of the crown of the anterior and sole incisor (*ï*), the entire carnassial (p_4), and the two fangs of the anterior molar (fig. 3, m_1).

The small and simple socket of the second molar is indicated (m_2); and two or three small and very shallow alveoli (Plate XII. figs. 2 & 3, p_3, p_2) intervene between the incisor-socket and the inner side of the anterior fourth part of the carnassial. From the condition of the upper small premolars it may be inferred that there were two or three similarly small functionless and speedily lost teeth between the carnassial and the laniariform incisor of the lower jaw, occupying the sockets (p_3, p_2, figs. 2 & 3).

Assuming these to be three in number, the first and second are on nearly the same transverse line, so close together that the broken thin partition (?) gives the appearance of a single socket.

The entire length of the alveolar tract is 3 inches; from the back part of the last socket to the hind fractured end of the present fossil is 3 inches. As the extent from the fore part of the upper carnassial to that of the glenoid cavity in the skull figured in Plate II. & III., Philosophical Transactions, 1866, measures 5 inches 10 lines, it may be inferred that such must have been nearly, if not quite, the extent of the mandible from the fore part of the lower carnassial to the fore part of the condyle; consequently the entire length of the mandible would not be less than 7 inches. We may reckon that 1 inch, at least, is wanting from the broken hind part of the specimen figured (Plate XII.); and we may certainly infer that a greater proportion of the mandible was allotted to the joint and to the muscular forces working that instrument than to the dental weapons with which it was armed; concentrated as they here are, as in the fellest *Carnivora*, for fatal efficiency.

The symphysial contour (ib. figs. 1 & 2, *s*, *r*) rises from the lower border of the horizontal ramus at an angle of 120°. The vertical diameter of the ramus anterior to the carnassial tooth is 1 inch 10 lines; it is the same anterior to the origin of the coronoid plate; and, save that the upper border is undulated by the alveolar opening, it runs parallel with the lower one. The outer wall swells out to lodge the anterior root of the carnassial, the vertical swelling subsiding at the lower fourth of the jaw. The dental canal has two small outlets anterior to the swelling. The outer wall becomes slightly concave lengthwise between the socket of the carnassial and the origin of the coronoid, which is broad and thick anteriorly (*c*), where it divides that concavity from the deeper one behind for the insertion of the large crotaphyte muscle (*f*, figs. 1 & 3, Plate XII.).

The specimen shows only the fractured base of the coronoid plate, the length of which in a straight line is 2 inches 6 lines; its direction is curved with the convexity inwards (fig. 3, *c*, *c'*): the fore part, formed by the buttress-like development of the outer wall of the ramus (*c*), is 7 lines in thickness; it rapidly decreases to $1\frac{1}{2}$ line, and returns to $2\frac{1}{2}$ lines in thickness at the hinder part (*c'*). The osseous tissue at the fore part of the coronoid is compact and dense. Toward the hind part is exposed the dental canal (fig. 2, *d*), broken across where it was traversing the base of the coronoid; the canal here is narrow tranversely. A narrow longitudinal groove between the base of the inflected part of the "ascending ramus" and the part of the dental canal (*d*) exposed by the fracture is continued as a shallow impression with a slight curve downward and forward, and then straight for a little way, becoming obliterated below the vertical parallel of the last molar (m_2). This is the only indication interpretable as a "mylohyoid groove."

The course of the fracture at the base of the coronoid from its thick fore part is backward and downward. The lower border of the ramus forms a thick ridge at the lower end of the symphysis, and subsides into a rounded or convex tract, gaining breadth as it recedes, and becoming flattened as it expands by the increased production of the angle of the jaw (Plate XII. fig. 4, *a*, *a'*). The crotaphyte fossa (ib. fig. 1, *f*) is not continued forward into the substance of the horizontal ramus, as in Potoroos and Kangaroos.

The symphysis (ib. fig. 2, *r*, *s*) is subtriangular, the lower and longer side being rather convex, the upper side almost straight; the base, which is turned backward and downward, is bilobed, the upper lobe, with the convex contour, being the longest. The length of the symphysis is 2 inches; the basal depth is 1 inch 5 lines. The upper part of the symphysis forms a slightly concave tract or platform, 9 lines in breadth at the fore and inner part of the carnassial, which increases as it recedes, sloping downward and backward (ib. fig. 3, *s*). It is bounded externally by the sockets of the incisor (*ï*) and of the premolar teeth (p_{1-4}) in continuous series. There is no true diastema between the laniary and the carnassial; the three closely aggregated empty sockets of probably as many single-rooted, small, soon shed, functionless premolars occupy the intervening tract and something more, viz. by encroaching on the inner side of the fore part of the socket of the carnassial (Plate XII. figs. 2 & 3, p_2, p_3). Behind the symphysis the inner wall of the ramus (fig. 2) is moderately convex vertically, concave in a less degree lengthwise at the lower part, where the curve becomes deepened posteriorly by the inbending of the angle (*a*). This part gains in thickness as it extends inward; the inner surface of the part preserved in the specimen described is vertical, and in that direction measures 6 lines (fig. 2, *a*). The fractured end (fig. 5, *a*) shows the three-sided character of this part of the angle, the upper and under surfaces converging to the thin horizontal plate (ib. *b*) connecting the angle with the part supporting the coronoid and condyle (ib. *c'*). The fore part or beginning of the neck of the condyle may be indicated by the smooth tract (fig. 3, *e*), which would then define the hind border of the coronoid process; or this narrow tract may indicate a minute transverse perforation of the ascending ramus. On the first notion the preserved fore-and-aft extent of the part relating to the support of the condyle (*e*, *c'*) is 10 lines.

One may hope ere long to receive a specimen with the whole of the rising branch of the mandible complete, showing both the shape and position of the condyle. Seeing that in *Bettongia* (p. 250, fig. 18), *Hypsiprymnus* (p. 250, fig. 17), *Phascolarctos* (p. 233, fig. 6), and all the marsupial vegetable feeders with a high-placed condyle there is a corresponding course of the base of the coronoid from before upward and backward, whilst in *Thylacinus* (p. 235, fig. 11) and *Sarcophilus* (p. 235, fig. 12), with a low-placed condyle, the base of the coronoid runs straight backward, I take ground for inferring a similar or relatively lower position of condyle from the slope of the base of the coronoid from before downward and backward, as indicated in the present jaw of *Thylacoleo*, and deem it not improbable that it may have resembled in both respects the *Plagiaulax*; thus exemplifying in the form of the mandible, correlatively with the dentition, the higher degree of carnivority in these extinct marsupial and diprotodont genera.

§ 4. *Photographs and Cave-specimens of Maxillary Teeth.*—Since finishing the description and figures of the foregoing specimens of maxillary and mandibular structure and teeth of the *Thylacoleo*, I have been favoured by receiving (May 20th, 1870) from the Colonial Secretary's Office, Sydney, New South Wales, a series of Photographs of Fossil Remains, and some duplicate specimens, obtained by Dr. A. M. THOMSON and GERARD KREFFT, Esq., from Limestone Caves in Wellington Valley, under the circumstances detailed in my paper on *Diprotodon*, p. 569, Philosophical Transactions, 1870.

I have subsequently been favoured by the Trustees of the Museum of Natural History, Sydney, and the able Curator, Mr. GERARD KREFFT, with Photographs, some of them duplicates of the above, others of fossils since acquired from the same breccia-caves. The Trustees of the Sydney Museum have also transmitted to the British Museum duplicate specimens of these cave-fossils.

From this rich series of photographic illustrations and specimens I select for description and figures the following, which supplement and almost complete our knowledge of the permanent or fully developed dentition of *Thylacoleo carnifex*.

The tooth in "Photograph No. 28" (Plate XI. figs. 6, 7) is the anterior incisor, left side, upper jaw. It has its crown a little worn at the point; it is plainly "canine" in function as in shape. The enamelled part of the crown which projects beyond the cement measures 1 inch 2 lines along the anterior curve. This is convex lengthwise, angular transversely, being traversed at the fore part by a low ridge (*r*, fig. 7, Plate XI.); the posterior border beyond a slight basal convexity is feebly concave lengthwise, rather flattened across, but chiefly bounded by a longitudinal ridge of enamel near the outer side: this ridge is feebly notched; the thinner enamel is continued from it, obliquely to the inner side of the crown, where the thicker enamel, of less longitudinal extent than the outer enamel, also developes a trenchant posterior ridge. The entire length of the tooth following the curve is 2 inches 3 lines: the fore-and-aft breadth of the base of the crown is 8 lines; the transverse breadth 5 lines: it accords, therefore, closely with the anterior incisor preserved in the portion of jaw above described (Plate XI. figs. 1, 2, 3, i_1). The photograph (No. 28 *b*) of the outer side of the answerable tooth shows a greater extent of preserved fang, though not quite entire at the end; the serration or notching of the long outer hind trenchant ridge or edge of the enamel is better marked than in the specimen. Together they concur in demonstrating the effective laniary character of the foremost tooth of the upper jaw of *Thylacoleo*.

A tooth in the photograph No. 28 *c* of upper teeth of *Thylacoleo* accords with the indications, as to form of fang and basal breadth of crown, afforded by the alveolus symbolized in figs. 2 & 3, Plate XI., as of the second incisor (i_2). I have therefore added a copy of it, fig. 9, in that Plate. It shows a root tapering to an obtuse point, 5 lines in length, and a crown 4 lines in diameter at its base, short, subconical, and obtuse, and may well be i_2 with a rather longer root from a less aged individual *Thylacoleo*: the crown of this tooth must project close behind the base of the crown of the front incisor.

The tooth (Plate XI. fig. 10) from the photograph No. 28 *d*, with a fang 10 lines in length, fitting by its fore-and-aft breadth such a socket as that marked *c* in figs. 1, 2, 3, Plate XI., answers to the indications there given. Another subject of the same photograph (fig. 11) is a more perfect canine of the opposite side, its bend of fang being contrary to that indicated by the right upper socket (*c*) in Plate XI.

Accordingly, I conclude the canine, *c* (Plate XI. figs. 9 & 10), to have a small subobtuse subcompressed crown, with a convex front outline from before backward, where it meets the hind shorter border of the crown at an angle which seems to form the rather blunt point of the tooth. The length of the enamelled crown is 4 lines, taken in the tooth's axis along the middle of the crown; the fore-and-aft breadth of the crown is 6 lines; the fang is an inch in length and rather curved, contracting to an obtuse point.

Amongst the duplicate cave-teeth are the crowns with portions of the fang of two such canines; the best-preserved fang is similarly curved (Plate XI. fig. 12), with a subtrihedral transverse section; but this form is more strongly marked in the short enamelled crown, the outer and inner sides meeting, anteriorly, at a trenchant border, strongly curved to the apex, which bends beyond the hind side (ib. fig. 12, *b*); this is flattened transversely, and is feebly concave lengthwise. The enamel has much less vertical extent here than along the anterior trenchant convex side of the crown. The outer side is slightly convex, and marked in one specimen by a longitudinal linear groove (ib. fig. 10); in the other by two grooves (ib. fig. 11), recalling those in the upper canines of *Felis*; the inner side (fig. 12, *a*) in both teeth shows two longitudinal grooves, and a ridge of enamel behind the hindmost groove.

Of the three succeeding small teeth which I have assigned to the premolar series (*ante*, p. 214), I recognize, in the cave-specimens, by the similarity of their very short crown and straight root, those answering to p_2 and p_3 in the upper jaw (Plate XI. figs. 13 & 14); but there is a photograph of a larger tooth, though less than the canine, which in size at the base of the crown corresponds with the p_1 in place (id. ib.) on the inner and hinder side of the canine. This tooth has a low conical crown, 3 lines long by $4\frac{1}{2}$ in basal antero-posterior breadth. The premolar (fig. 14, p_2) has a root 10 lines in length, curved near the end to which it contracts.

The two smaller succeeding premolars in place in the unique jaw (Plate XI. figs. 1–3) I have not thought proper to displace; the photographs, which plainly show the same very short extent of enamelled crown, give to an example of p_2 a straight fang of 7 lines in length, and to one of p_3 a similar fang 8 lines in length; both taper to an obtuse point. Amongst the duplicate teeth transmitted is a p_2 with half an inch of the solid straight fang, and the crown of a p_3 corresponding with that in the upper jaw (Plate XI. fig. 3).

The photographs include three specimens of the great carnassial (p_4) with an enamelled crown 2 inches in fore-and-aft basal extent, 9 lines in greatest vertical extent. The subject of one figure shows the two roots; the foremost of which is 1 inch 6 lines long and 1 inch in fore-and-aft breadth, where it becomes free; the hind root or division is 1 inch in length and about the same in fore-and-aft extent; its greatest transverse thickness is 6 lines, and it contracts to an obtuse hinder border. Both roots are shown to be strongly marked, as in the tooth *in situ* (Plate XI. figs. 1 & 2), by fine subwavy longitudinal striæ near their extremities, adding to the closeness of attachment to the alveolar periosteum. The characters of this huge carnassial in the fossil specimen are so closely repeated as to render figures of these photographs unnecessary.

A side view and a view of the grinding-surface of the small tubercular molar are given in the photograph No. 7: a similar specimen I have worked out of the breccia (Plate XI. fig. 3, m_1). This tooth closely resembles that shown on the inner side of the hind end of the great carnassial in Plate XI. Phil. Trans. 1859, and in Plate III. ib. 1866.

It is evident that the five small teeth between the upper laniary (i_1) and the carnassial (p_4, figs. 1–3, Plate XI.) can have had but insignificant functional relations. They could not be opposed to mandibular teeth, if even their homotypes had been present or retained in the lower jaw. But of these there seem to have been but two, or at most three, developed, of very small size, on the inner side of the fore part of the lower carnassial; and I have seen no specimens of mandible in which they are retained.

§ 5. *Photographs and Cave-specimens of the Mandible and Mandibular Teeth.*—The following are the most instructive photographs of portions of the mandible with teeth of *Thylacoleo* from the Breccia-cave of Wellington Valley, in the series above referred to.

No. 10 gives two views of a portion of the right ramus (the outside view is given in Plate XIII. fig. 1). It is similar to the fossil from Queensland above described (Plate XII.), but more mutilated at the back part. The chief value of the specimen photographed is the retained incisor (*ï*), from which only the apex of the crown is wanting, by an oblique fracture from above and behind downward and forward. In a photograph of a more mutilated mandible (ib. fig. 2), the inner wall of the alveolus of the incisor is broken away as far as the vertical line dropped from the fore part of the carnassial (p_4). The outer wall remains a few lines in advance of this in the subject of figure 1, but sufficient of the cement-covered root of the tooth is exposed to show a commencing contraction toward its implanted end. The incisor is directed upward at an angle of 130° with the long axis of the ramus, and the crown shows a curvature with the convexity forward and downward as in the lower laniaries of *Thylacinus*; the hind border is not straight or convex like the answerable upper border in the same tooth of *Bettongia* and *Hypsiprymnus*, but is serrato-trenchant and slightly concave lengthwise. A photographic view giving the transverse breadth or thickness of the incisor would have been instructive; but the portion of the tooth retained in the mandibular ramus figured in Plate XII. fig. 1, *ï*, *a*, shows the more essential distinction from the long procumbent lower incisors of the herbivorous Marsupials in the degree of lateral compression of the crown and its proportion to the antero-posterior breadth, which in the laniary of *Thylacoleo* is intermediate between that in *Machairodus* and *Felis*.

The two anterior outlets of the dental canal are present, and in the same position in the cave-fossil (Plate XIII. fig. 1, *o*) as in the Queensland specimen (Plate XII. fig. 1, *o*). The postero-inferior emargination of the symphysial surface is repeated on the inner surface of the ramus of the subject of fig. 1, Plate XIII., as in Plate XII. fig. 2, *r*.

All the characters of the carnassial tooth (p_4) in the Queensland specimen are closely repeated; the crown is abraded in the same direction and to the same extent.

The crown of the first molar (m_1) is preserved in both the cave-specimens photographed, showing its raised, anterior, subtrenchant lobe, and its small low hind tubercular talon. On the outer side of this tooth is shown the subvertical surface formed by attrition against the hind part of the upper carnassial. The proportions of the anterior and posterior roots of m_1 are indicated in the photograph of the inner side of the subject of fig. 1, Plate XIII. The socket of the minute p_3 (ib.) plainly appears on the inner side of that for the anterior root of p_4 in the same photograph; but the shallower and larger ones of p_2 and p_1 have left no impression—were probably obliterated in the fossil. There can be no doubt as to the specific identity of the Wellington Valley cave-fossils with those of *Thylacoleo carnifex* from Melbourne (Lake Colungoolac) and from Queensland (Gowrie Creek).

The second fossil of *Thylacoleo* from the breccia-cave, the subject of the photograph

No. 29 of the series, is a smaller portion of the fore part of a right ramus, with the entire incisor, the carnassial, and first molar *in situ*. The whole length of the base of the incisor is exposed, and the obtuse termination of the closed and contracted end of the root (Plate XIII. fig. 2). The fractured state of the bone also shows portions of the fore and hind roots of the carnassial (p_4), the latter apparently the larger, contrary to that in the lower carnassial of Felines, which is not the homologous tooth, although with a similar adaptive modification of crown. The length of the incisor is 3 inches 3 lines, that of the enamelled crown appears to be about 1 inch 8 lines; the antero-posterior breadth of its base is 9 lines. The position, direction, and curvature of the incisor in this specimen accord with those in the photograph copied in fig. 1, Plate XIII., and with the restoration based on the direction of the empty socket in the subject of Plate IV. fig. 6, Philosophical Transactions, 1866. The vertical extent of the fore part of the carnassial (p_4) is 1 inch 9 lines, that of the enamelled crown being $7\frac{1}{2}$ lines.

All the evidences yielded by the specimen (figs. 1–3, Plate XII.), by the casts (Plate XI. fig. 3, Phil. Trans. 1859), and by the photographs (Plate XIII. figs. 1 & 2, p_4) concur in showing the closer resemblance of this sectorial tooth to the carnassial of the large placental *Carnivores* (Plate XII. figs. 9 & 12) than to the sectorial premolar in Rat-Kangaroos (ib. figs. 8 & 10). The crown of the tooth (fig. 11) is bent lengthwise, with the convexity outward, the concavity inward; and this is chiefly at the hinder half of the tooth (fig. 3, p_4). The fore part of the crown is the thickest, and that by the prominence of the inner surface at the anterior fourth, which makes a low obtuse ridge (*r*, fig. 11, Plate XII.) divided by a depression or channel from the anterior ridge (*a*) or border of the crown, which represents the prebasal ridge (*a*) in the carnassial of the *Hyæna* (fig. 12). The broader part of the trenchant surface (*b*, fig. 11) is anterior, as in *Hyæna* (*b*, fig. 12). The trenchant margin does not extend in a straight line, but is subconcave, though less so and more continuously than in *Hyæna*. The effect of these curves of the cutting part of the blades in *Thylacoleo*, as in *Felis* and *Hyæna*, is to make them meet at successive parts in the act of cutting, not by simultaneous opposition of the entire cutting-edges of the opposed blades. The vertical undulation of the enamel is finer, less marked, in the lower than in the upper carnassials, and is confined to the basal part of the inner surface, not to the apical half of the crown as in *Hypsiprymnus* (fig. 10).

In the cast of a specimen of a right mandibular ramus with the carnassial less worn than in the specimen Plate XII. figs. 1–3, the abraded surface is interrupted midway, indicating a bilobed character of the unworn margin, as in the lower carnassial of Felines; the abraded surface in the cast expands from the unworn part of the dividing notch forward toward the anterior end of the tooth and backward to the posterior end (Plate XII. fig. 11). The subject of figure 6, Plate XII., is a specimen worked out of the breccia transmitted by the Trustees of the Australian Museum, and shows the proportions of the two roots of p_4, lower jaw.

The Photograph No. 7 includes views of five examples of the large laniariform lower incisors, both outer and inner surfaces of the most entire specimen being given.

No. 1 shows the outer side of a left lower incisor wanting only the tip of the crown. The closed contracted end of the root is truncate. The length is 3 inches 4 lines, the greatest breadth from before backward 9 lines.

No. 3 in the photograph is of the inner side of a similarly entire right incisor (Plate XIII. fig. 4). The ridge (*d*) defining the inner side from the narrow posterior facet of the crown is clearly given in this photograph, which appears to be the incisor removed from the socket of the subject of fig. 1, Plate XIII., the same mutilation of the summit of the crown being shown. The implanted end of the root contracts in the same degree, and shows the same truncation, as in the subject of figs. 5 & 6, Plate XIII.

Photograph No. 43 gives, somewhat reduced, the inner side of the fore part of the right ramus, showing the symphysial surface, the carnassial, and the first molar. The extent and shape of the symphysis, as in Plate XII. fig. 2, are here repeated with the same vertical extent and lower contour of the fore part of the mandible. Photograph No. 37 is of the outer side of the same specimen, on the same scale, showing the trenchant part of the crown of the first molar (m_1) as in *Plagiaulax*. A view of the carnassial *in situ*, in a small fragment of the left ramus, showing the oblique external smooth wear of the trenchant tooth, is also given in photograph No. 43.

These evidences are acceptable as testifying to the constancy of the characters of the lower jaw and dentition in *Thylacoleo carnifex*.

§ 6. *Cave-specimens and Cast of Inferior Incisor.*—I have been favoured by Mr. KREFFT with a cast of the entire inferior incisor of *Thylacoleo*, from the breccia-cave in Wellington Valley; and since penning my notes on this cast and the photographs, an entire lower incisor and portions of others have come to hand in the series of cave-specimens worked out of the masses of breccia transmitted from the Wellington caves.

The incisor (Plate XIII. figs. 5, 6, 7) is long, subcompressed, subrecurved; the crown is pointed, trenchant anteriorly. The entire tooth is about equally divided into crown (fig. 5, *a'*, *b*) and fang (ib. *f*); but the enamelled part (*e*), when the root-cement is scraped away, is longer than at first appears; for the cement encroaches upon the enamelled crown in angular prolongations from the root, and further on the inner (fig. 6, *c*) than on the outer (ib. fig. 5) or hinder part (fig. 7) of the tooth. The crown becomes three-sided a little below the apex (*e*); the outer side (fig. 5, *a*) is broadest, and is transversely convex, the posterior border forming that of the crown. The inner side (fig. 6, *a*, *d*), of less breadth, is flat, but is divided by a longitudinal ridge (*d*) into two facets, the hinder one being the narrowest and inclining transversely to the hinder border (*n*). Toward the base of the crown the hind surface (*h*) becomes feebly concave between these marginal posterior ridges.

Thus the perforating part of this tooth is strengthened by four longitudinal enamel ridges, in which the serrate or finely undulated or wrinkled character is more or less manifest, especially on the trenchant anterior border, defining the outer (fig. 5) from the inner (figs. 4 & 6, *i*) surfaces of the crown, also on the supplementary ridge (*d*) on the inner facet (*i*).

As the fore-and-aft breadth of the crown increases from the apex downward, the stronger convexity of the antero-external part is limited to the fore part of that facet, the hinder part of the facet becoming less convex or almost flattened, and at the base of the crown even feebly concave, where the cement (fig. 5, *c*) encroaches on the enamel. A similar concavity marks the outer part of the base of the laniariform incisor of *Plagiaulax*, FALCONER, X. fig. 1, p. 366; XI. pl. 33. fig. 1, *a*. The anterior subserrate ridge is the longest, the postexternal ridge subsides a little sooner in approaching the base, the postinternal ridge is next in length, and the supplementary inner ridge is the shortest. The enamel-case of the crown is entire, but is thickest upon the more convex anterior part of the antero-external facet, and where it forms the ridges (see the section, Plate XIII. fig. 8).

The posterior facet at the apical part of the crown meets at a right angle the inner side, but lower down it slopes from the postinternal ridge, backward as well as outward, to meet the outer facet at *b*. This gives a more trenchant character to the subserrate ridge or border (*d*) between these surfaces.

The effective cutting power of the postinternal ridge, where the angle between the posterior and internal surfaces of this three-sided bayonet-like tooth becomes a little open, is enhanced by the prominence of the ridge, supplemental strength being given to the piercer by the added postinternal ridge. The cement-clad root (Plate XIII. figs. 5, 6 & 7, *c*, *f*) gradually contracts to its subtruncate closed extremity.

In the specimens of lower laniary above described, as in the cast and photographs of that formidable tooth of *Thylacoleo*, evidence is given of its conforming in its limited or temporary growth, as in its shape, proportions, and structure, with the canine of the Felines, but with superadded modifications strengthening and perfecting it for its work as a piercer, holder, and lacerator.

§ 7. *Guide to inferring function from form of Teeth.*—Thus, through the cooperation of a liberal and enlightened Legislature and Administration, and of esteemed friends and fellow-labourers in Sydney, New South Wales, ample evidence has been got of both upper and lower laniary incisors, as well as of the rest of the dentition of *Thylacoleo carnifex*.

It is with pleasure, though without surprise, that I have been enabled to confirm the inferences expressed in my former papers, on such elements of that dentition as I then only knew "in part."

Whether the "principles which are followed as guides in this walk of investigation were" therein "set aside, to give place to the illusory indications of mutilated external form"*, I cannot determine, because Dr. FALCONER does not define the principles to which

* X. p. 354; XI. p. 437.

he refers. It is certain that the indications of the mutilated parts of my original specimens have not proved "illusory."

But such indications were not the sole grounds of my conclusions; I was also guided by a principle. It is that laid down by CUVIER in the van of his immortal work of Restoration of the extinct Mammals of the Paris Basin.

The aberrations of some contemporary labourers in this field show that it will bear repetition:—"La première chose à faire dans l'étude d'un animal fossile est de reconnoître la forme de ses dents molaires; on détermine par-là s'il est carnivore ou herbivore"*.

These test-teeth were fortunately entire in the upper jaw of the skull of *Thylacoleo*†, and in the cast of the lower jaw originally described‡.

The major part of the molar series was represented by one large and most efficient carnassial, followed by a single small tubercular above, which was opposed to a semi-tubercular molar and a second more minute tubercular tooth below.

Here was no molar machinery for the mastication of vegetable food, but a maximized modification of the teeth for the division of fleshy fibre, and so much of the tubercular form added for the final crush or squeeze of gristle or other tough part escaping the shears, as exists in the most carnivorous of the placental mammals.

§ 8. *Location of Laniaries.*—From these facts, with faith in the Cuvierian principle, I inferred a concomitancy of laniary teeth at the fore part of the jaw "to pierce, retain, and kill"§ the prey, whether such laniaries held the relative position to a suture technically determining them to be "incisors" or "canines." It is now determined that these laniaries are, as was inferred in my Second Paper||, incisors. A co-adapted pair at the fore part of the lower jaw were opposed to a slightly separated pair in the upper jaw.

To this demonstration applies the following objection against the inference as to function:—

"Throughout the *Mammalia*, where teeth perform the functions of canines to 'pierce, retain, and kill,' they are held well apart through the interposition of a line of incisors—the end being obvious: the points of penetration are doubled, the grasp is strengthened by widening the base, and the dilacerating and killing powers are multiplied"¶.

To this I reply that, were a pair of bayonets cemented side by side and the forces of two brawny arms concentrated on the thrust, their perforating and lethal power would be increased. I fail to see how such "collateral arrangement in the axis" of the piercing force "would place them at a disadvantage to the end to be attained"**.

Dr. FALCONER admits that "a Rat when seized can inflict a smart wound on the hand"††. I can add experience of loss of young poultry showing by the wounds on their legs how they had been brought down from the perch, and by wounds on the neck how they had

* Recherches sur les Ossemens Fossiles, 4to, tom. iii. (1822) p. 1.

† Philosophical Transactions, 1859, Plate XI. figs. 1 & 2.

‡ Id. ib. fig. 3.

§ OWEN's 'Palæontology,' 8vo, 1860, p. 320.

|| Philosophical Transactions, 1866, p. 80.

¶ X. p. 352; XI. p. 435.

** Id. ib.

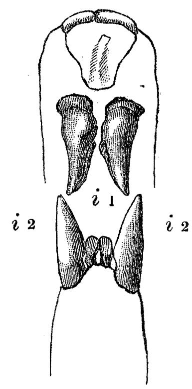
†† Id. ib.

been killed, and then more or less devoured by the nocturnal murine omnivorous Rodent, thus demonstrated to have acted in this carnivorous fashion by virtue of the pair of scalpriform incisors "arranged collaterally in the axis," &c.

But there are several genera and species of CUVIER'S "Carnassiers" in which incisors having the size, form, and office of laniaries* are not "held well apart through the interposition of a line of 'other' incisors"†.

The European Otter (*Lutra*) shows, indeed, this divaricate arrangement, but an African Otter (*Potamogale*, Cut, fig. 1) does not; a co-adapted pair of laniaries (i_1) at the fore part of the upper jaw were opposed to a slightly separated pair in the under jaw (i_2).

Fig. 1.



Laniary incisors, front view, *Potamogale velox*: twice nat. size‡.

In the *Insectivora*, as in the *Marsupialia*, there are two types of the teeth which are developed and shaped "to pierce, retain, and kill," in other words, two local conditions of "laniaries." In some, *Gymnura* §, *Centetes* ||, *e. g.*, the laniaries answer to the 'canines' of *Carnivora*, and are separated by interposed 'incisors' in both upper and lower jaws, as they are in *Sarcophilus* and *Thylacinus*; in other *Insectivora* the laniaries are approximated, and are formed by 'incisors'; as, *e. g.* in *Solenodon*¶, *Erinaceus***, *Scalops*, *Urotrichus*, and other *Soricidæ* generally, in which a juxtaposed pair at the fore part of the mandible†† oppose a corresponding pair at the fore part of the upper jaw. These incisors usurp the functions of the canines in *Gymnura*, *Talpa*, &c. The transference of the laniary form and function from the canines to the incisors, the development of these latter into the dental instruments "modified to pierce, retain, and kill," is the rule, or is found in the majority of *Insectivora*. In the Japanese Mole-shrew (*Urotrichus talpoïdes*)‡‡ "the incisor is long, conical, and pointed;" it is grooved on the inner side: "the lower canine is small, its office being transferred to the incisor"§§. This large laniary tooth may be

* "Technical canines vary as much in shape, proportion, and function as do technical 'incisors;' are sometimes, indeed, implanted by two roots instead of one." See 'Odontography,' pl. 110. fig. 3 (Mole).

† X. p. 352; XI. p. 435.

‡ For the subject of this Cut I am indebted to the author of the instructive Memoir on *Potamogale*, Zool. Trans. vol. vi. p. 1, Professor ALLMAN, F.R.S., of the University of Edinburgh, where the unique skeleton of the *Potamogale* is preserved.

§ OWEN'S 'Odontography,' pl. 111. fig. 4, *a*, *b*.

|| Ib. pl. 110. fig. 6.

¶ 'Odontography,' pl. 111. fig. 1 (the front view (*b*) may be compared with that of *Thylacoleo* in XII. p. 312, fig. 2).

** Ib. pl. 110. fig. 5.

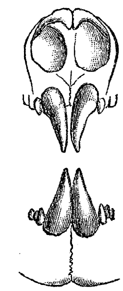
†† *Sorex*.—"In the lower jaw there is, as is known, one very elongated pointed incisor on each side." "The canine is a small conical tooth, the smallest of the lower jaw."—MIVART, "On the Osteology of Insectivora," Journal of Anatomy and Physiology, vol. ii. p. 11.

‡‡ Catalogue of Bones in the British Museum, 8vo, p. 109.

§§ MIVART, *ut suprà*.

the homologue of the laniariform i_2 in *Potamogale*; but the pair of developed incisors in *Urotrichus* are what Dr. FALCONER would have described as "approximated and placed collaterally, as in the placental Rodents"[*]; *i. e.* they are in contact, side by side (Cut, fig. 2). In the large African Ferine (Carnassier, CUV.), with the habits and food of the Otter, discovered and called *Potamogale* by DU CHAILLU, the first incisor of the upper jaw (fig. 3, i_1) "closely resembles a large projecting canine"[†]. In the lower jaw "the first is very small. The second incisor is high, conical, curved; it is sharp-pointed, and resembles a canine"[‡]. "The condyle is borne on a distinct neck"[§]. The low position of the condyle (*b*), associated with these laniariform incisors in *Potamogale* (fig. 3), is not alluded to either by ALLMAN (*l. c.* p. 11) or by MIVART (*l. c.* p. 127).

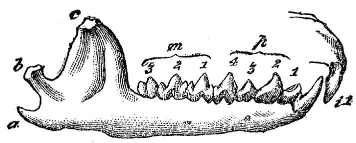
Fig. 2.



Front view of laniary incisors, magn., *Urotrichus talpoïdes*, TEMMINCK.

It is important in association with the position and juxtaposition of the laniaries in this large fish-hunting Ferine, with regard to the moot question of the carnivority of *Thylacoleo* and *Plagiaulax*.

Fig. 3.



Side view of upper laniary and mandibular dentition, *Potamogale velox*, nat. size (*ex* ALLMAN, *loc. cit.*).

In *Myogale*, as in *Solenodon*, the first upper incisor "is much larger and more vertically extended than in any other tooth in the skull. Its crown is triangular, it is in contact with its fellow of the opposite side, and predominates more than does any other form yet reviewed, except, perhaps, that of *Sorex*. It is opposed mainly to the second incisor of the lower jaw, the first being much smaller......This second incisor is exceedingly large, pointed and conical"[||]. "The canine is a small obtusely pointed tooth[¶]," as in *Thylacoleo*. In *Solenodon*, *Potamogale*, and *Myogale* the laniariform incisors of the lower jaw, to which those in *Urotrichus* and *Sorex* may be homologous, are divided from each other, at their base, by a very small pair of anterior incisors; but the extent of separation is slight, and cannot affect in any appreciable degree their piercing power.

Indeed, to concentrate is to give force, to divide is to weaken. If it be not carried too far, divarication may aid in the secondary work of holding the pierced prey: but for the primary lethal operation, the base for the grasp of the biting muscles is as broad in *Thylacoleo* as in *Felis*. An estimate of the concentrated force of these enormous muscles

* X. p. 352; XI. p. 435.

† ALLMAN, "On the Characters and Affinities of *Potamogale*," Trans. Zool. Soc. vol. vi. (1866) p. 6. I am indebted to the accomplished author of the above-cited interesting Monograph for the drawing which is the subject of the Cut, figure 1.

‡ Ib. p. 7.

§ Ib. p. 11. (Compare this "pedunculate" character with that in *Plagiaulax*, figure 10.)

|| MIVART, *op. cit.* Journal of Anatomy and Physiology, vol. ii. p. 124.

¶ Id. ib. p. 125. "*Scalops*. The first incisor is very large, and is opposed to one nearly as long in the lower jaw, where the canine is wanting, or represented by a most minute and rudimentary tooth."—Ib.

upon the pair of lower laniaries approximated as one piercing, lacerating organ, with the superlative degree of carnassiality of the premolar, suggested the expression of the pouched Lion having been "one of the fellest and most destructive of predatory beasts"*.

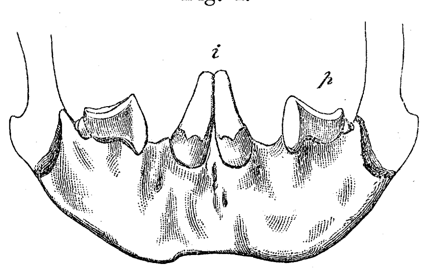
The Curator of the Museum of the Royal College of Surgeons, and now Hunterian Professor, adopts the argument from divarication of the laniaries in the *Carnivora* known to Dr. FALCONER, and salves the exceptions by affirming "the *modus operandi* of the Hedgehog in snapping up and devouring a beetle is totally different from that of a Cat in seizing and killing a Rat or a Rabbit"†. And one may conclude that the *Thylacoleo*, from the nearer resemblance of its laniaries and of the jaw working them to those of the Cat, would show, also, some difference from the Hedgehog in the snapping or seizing of its prey. But Professor FLOWER, in a question of such importance to Physiology as the reconstruction of *Thylacoleo*, should have defined the 'total difference' between the mode of application by the Hedgehog of its 'approximate' laniaries and that of the application of the Cat or Stoat of their 'divaricate' ones in the killing of a young Rabbit; for the Hedgehog invades the burrows of the prolific rodent to devour the offspring; it is by no means exclusively insectivorous.

Was the well-armed mandible, with its low and advantageous joint for a strong grip, applied by *Potamogale* in piercing, holding, and killing its fish in so different a fashion from that of the like mandible in *Lutra*, as to lend any countenance to the assumption that the juxtaposed long terminal incisors of the lissencephalous Otter were put to the service of an herbivore—to the same service as they are in the Koala, *e. g.*? Yet, if Professor FLOWER'S argument and diagrams‡ mean any thing, they mean this!

The *Thylacoleo's* approximate incisors§ are relatively as long, as sharp, as laniariform as are those of *Potamogale*; and if we turn to the teeth (Plate XIV. p_{2-4}, $m_{1, 2}$), which tell us truly the use to which such incisors were put, they speak directly and plainly that it was for capturing and killing a higher prey than fishes.

§ 9. *Comparison of the Teeth of Thylacoleo with those of Phascolarctos.*—The light thrown by the large carnassial and small tubercular teeth on the application and function of the laniaries of *Thylacoleo* is sought to be obscured by conjectural figures of the structure of those laniaries and of the jaw that works them.

Fig. 4.



Front view of mandible and teeth (*Thylacoleo*), as restored, one-third nat. size, by Professor FLOWER (XII. p. 312, fig. 2).

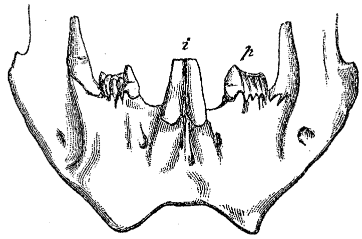
In fig. 2 (XII. p. 312), entitled "*Thylacoleo carnifex* restored," Professor FLOWER represents the incisors with truncate summits, like those of an herbivorous marsupial. This restoration is reproduced in Cut, fig. 4. The carnassial of *Thylacoleo* (ib. p) has features too broad and pronounced to be misunderstood. The herbivorous Marsupial selected

* Philosophical Transactions, 1859, p. 319. † XII. p. 318. ‡ XII. p. 317, & pp. 312, 313, figs. 2, 4, 5.

§ These teeth are represented too broad in proportion to their length, or too short in proportion to their breadth, in XII. fig. 2.

by Professor FLOWER for comparison (in XII. p. 313, fig. 4), copied in Cut, fig. 5, appears to have a similar carnassial (*p*); but this appearance is due to the foreshortening of the series of the grinding-teeth of the Koala.

Fig. 5.



Front view of mandible and teeth (*Phascolarctos*), three-fourths nat. size (after Professor FLOWER, XII. p. 313, fig. 4).

My business here is simply to set forth the facts which guide to a right conclusion, and to put them as correctly as I am able. The incisors of *Thylacoleo* are neither truncate nor flattened by attrition at their ends; their character, from nature, is given, of the natural size, in the front view of the mandible (Plate XIII. fig. 3). They may be blunted by use, or the point may be broken off, as in figures 1, 4, Plate XIII., from the photograph No. 10. The laniaries of an old Lion usually show the same effects of usage. Professor FLOWER gives a front view of the incisors of *Phascolarctos*, and a side view of the incisors of *Hypsiprymnus*; but a view of the working surface, from which the best idea can be formed of the use to which such incisors, in the two Marsupial herbivores, are put, is not given. I have supplied this omission in the upper figure of Cut 6, *i*, where the working surface of the lower incisor of the phytophagous diprotodont Marsupial may be compared with that of the zoophagous one (Plate XIII. fig. 7).

Returning to CUVIER'S test of the diet of an extinct animal, which test gives the use of the long anterior teeth, whether canines or incisors, of such animal, I may recall attention to the single, small,—one may truly say, viewing the enormous carnassial against which it abuts—minute tubercular in the upper jaw of *Thylacoleo* (Plate XI. fig. 3, m_1). Then, as regards the lower jaw (Plate XIII. fig. 1), the molar (m_1) following the carnassial (p_4) has the anterior half of the crown compressed transversely, the sides converging to a trenchant margin: this approximation to the form of its homologue in Felines, from the close and extensive abutment of the tooth against the upper carnassial, forms a continuation of the shear-blade structure, and gives the lower blade an extent equal to that of the larger carnassial above. The tubercular part of m_1 below forms a mere basal talon to the carnassial part of that tooth, whilst m_2 is a truly minute tubercular, and, seemingly, soon lost.

The demonstrated structure of the laniaries of *Thylacoleo* is in harmony with the zoophagous work which the molar teeth are plainly designed to transact.

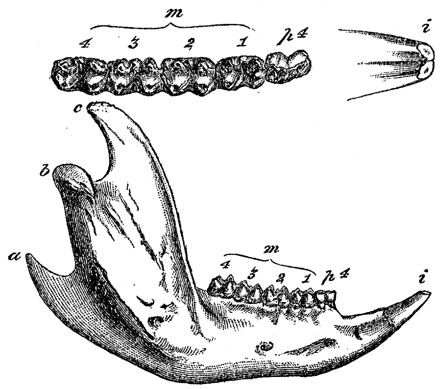
Now, being solely desirous to test CUVIER'S principle in reference to the approximate pair of long incisors of *Phascolarctos*, I subjoin what is essential to such test, and what Professor FLOWER omits, viz. a side view of the dentition of the Koala, reduced one-half, together with a view of the grinding-surface of the molar teeth, natural size (Cut, fig. 6), corresponding with those of the *Thylacoleo* shown in Plate XI. fig. 3, Plate XII. fig. 3.

The tooth (p_4), probably homologous with the carnassial of *Thylacoleo*, and that which most resembles, or rather least differs from, it in the shape of the crown, occupies less than one-eighth of the dental series in *Phascolarctos*, in *Thylacoleo* it occupies nearly one-half; in *Phascolarctos* it forms one-fifth of the molar series, in *Thylacoleo* it forms two-thirds of that series; these proportions are masked in the foreshortened view, fig. 5.

The premolar in the upper jaw of the Koala (p_4, fig. 6) presents a flat surface, with a breadth of crown two-thirds of the length, the surface being slightly raised by a border of thick enamel at the periphery, and by a plicate island of enamel in the middle. It is a true pounder of vegetable substances, with the structure of a type-grinder of an herbivore. Such contrast in proportions, structure, form, and function with p_4 in *Thylacoleo* *, as is presented by the tooth (p_4) of *Phascolarctos*, would not be surmised by an uninstructed comparer of the restored *Thylacoleo* (fig. 4, copied from XII. fig. 2) with the corresponding view of its alleged herbivorous analogue and ally (fig. 5, copied from ib. fig. 4).

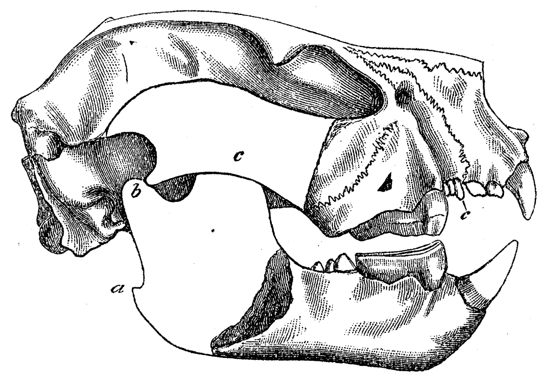
§ 10. *Mandibular Characters of Carnivorous and Herbivorous Marsupials.*—A high-placed condyle is associated with the rotatory movements of the jaw in herbivorous Marsupials (XII. fig. 3) as in herbivorous Placentals. Professor FLOWER's restoration

Fig. 6.



Mandible of Koala (*Phascolarctos fuscus*), one-half the natural size, and grinding-surface of teeth, natural size, from nature.

Fig. 7.

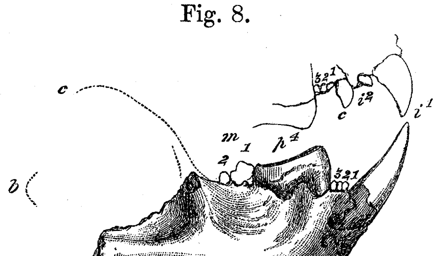


Skull of "*Thylacoleo carnifex*, restored," one-fourth natural size (after FLOWER, XII. p. 312, fig. 1).

(fig. 7, copied from XII. p. 312, fig. 1) gives a similar position to the mandibular condyle (b) in *Thylacoleo*, and the angle (a) is there indicated after the pattern of the lower jaw of the Koala (fig. 6, a).

The first fossil mandible of *Thylacoleo* which permits a deduction to be made of the relative position of the parts in question (Plate XII. figs. 1 & 2, and Cut, fig. 8), demonstrates the fallacy of the restoration in fig. 7, and shows a structure harmonizing with powerful vertical movements of the mandible, not with the horizontal grinding required for the comminution, and mixing with abundant saliva, of vegetable matters.

Fig. 8.



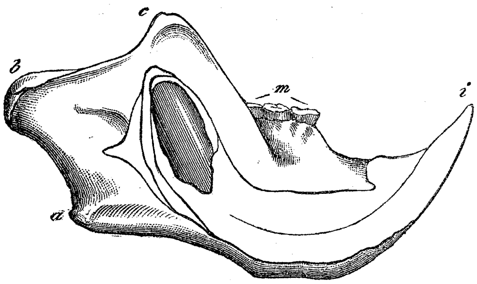
Right mandibular ramus, mutilated behind, from nature, one-fourth natural size (*Thylacoleo*).

* Figured in Plate XI. figs. 1 & 2, Philosophical Transactions, 1859.

The fact is patent; but the inference has been called in question.

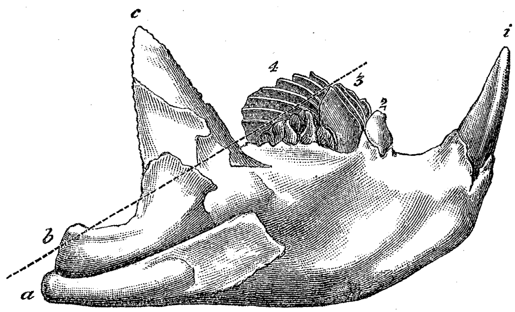
Dr. FALCONER writes, in June 1862, "Next, as regards the depressed position of the condyle—below the level of the grinding-teeth. The author of 'Palæontology' states that it is 'a character unknown among any herbivorous or mixed-feeding animal.' I again refer my reader to the figure (pl. 34. fig. 13) of the lower jaw of the Aye-aye"*. This figure is essentially the same as that in my Memoir read before the Zoological Society, January 14th, 1862 (fig. 9). Prior to that date the depressed position of the condyle *to* the level of the grinding-teeth (fig. 9, *b*) was a character unknown in any herbivorous or mixed-feeding animal; it is still so unknown as depressed *below* that level, such as we see it in *Plagiaulax* (fig. 10). Dr. FALCONER, proceeding with his evidence of the herbivority of the gnawing Lemur and his comparison of its mandible with that of *Plagiaulax*, admits that "the condyle looks still more depressed in *Plagiaulax Becklesii*; but this is, in part, owing to the inflected margin of the angle being broken off in the fossil, while it is entire and salient in the recent form, thus elevating the condyle above the lower plane of the ramus, and leading to an appearance of a greater amount of difference than exists in nature"†.

Fig. 9.



Mandible of *Chiromys Madagascariensis*, natural size (Zool. Trans. vol. v. pl. 20. fig. 9, Memoir of January 14, 1862).

Fig. 10.



Mandible of "*Plagiaulax Becklesii*, magnified four diameters" (after FALCONER, XI. pl. 34. fig. 1).

Here we are at issue on a matter of fact. I affirm that the condyle (*b*, fig. 10) in *Plagiaulax* would not be so elevated above the lower plane of the ramus if the angle (*a*, fig. 10) were entire and salient, because the saliency has an inward, not a downward, direction. The correspondence in this respect, as well as in the low position of condyle, of *Plagiaulax* with the carnivorous Thylacoleo, Dasyures, and Thylacines, and its difference from the herbivorous marsupials (fig. 6) and larvivorous Lemur (fig. 9) is as clearly demonstrated in the Purbeck fossils, as if the inflected angle had received no fracture whatever.

For other differences of mandibular structure and configuration between *Plagiaulax* and *Chiromys*, invalidating Dr. FALCONER'S argument in favour of a common herbivorous or rodent nature associated with a common depressed position of condyle, I refer to figs. 9 & 10.

In reference to the subject of the latter illustration, Dr. FALCONER has remarked, "Pro-

* X. p. 361; XI. p. 445.

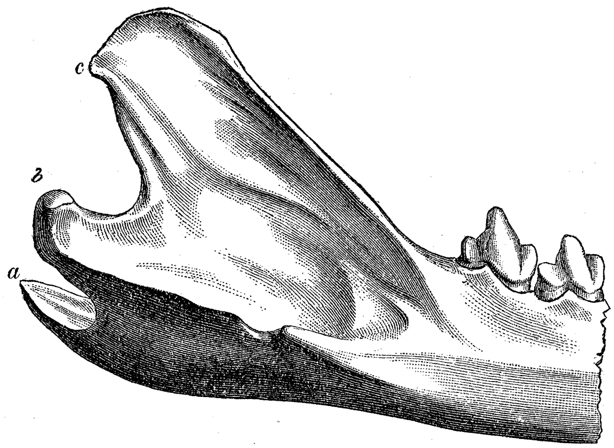
† X. p. 361; XI. p. 446.

fessor OWEN meets the argument in my paper by the assertion that the condyle of *Plagiaulax* is 'pedunculate, as in the predaceous marsupials.' If so, I invite him to adduce the instance, bearing in mind that the question here is one of degree*".

The virtual acceptance of this "invitation" had been given years before in the instance of the Phascolothere†, which, like *Plagiaulax*, is an extinct marsupial carnivore from an oolitic deposit.

The required structure is shown in the Cut (fig. 11, *b*) of the articular extremity of

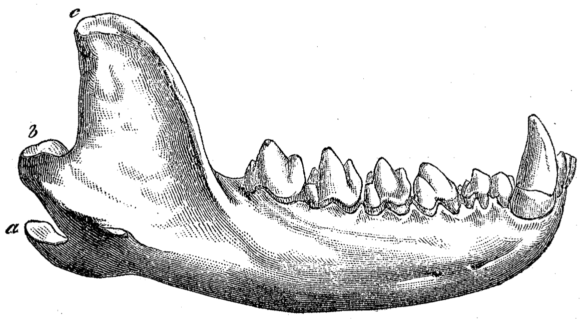
Fig. 11.



Articular end of mandible, *Thylacinus cynocephalus*: two-thirds nat. size.

the mandible in *Thylacinus cynocephalus*‡. In nearly the same degree is the condyle pedunculate in *Potamogale* (fig. 3), and in a somewhat less degree in *Sarcophilus* (fig. 12, *b*).

Fig. 12.



Mandible of *Sarcophilus ursinus* (after nature).

I may assume that the extent of condylar prominence and position in the instances cited will be admitted to have justified, as, indeed, they formed the basis of, the assertion of the community of the "pedunculated condyle," such as it is shown in figs. 10 & 11 at *b*.

* X. p. 362; XI. p. 447.

† Transactions of the Geological Society of London, 2nd series, vol. vi. (1839) p. 58, pl. 6.

‡ See 'Descriptive Catalogue of the Osteological Series contained in the Museum of the Royal College of Surgeons of England,' 4to, 1853, p. 347. nos. 1903–1908.

It will be observed that, in the Thylacine—the most carnivorous of modern Marsupials—the depth of the notch between the condyle (*b*) and coronoid (*c*), or what Dr. FALCONER indicates by the term "pedunculate," is relatively greater than in *Sarcophilus*. The two recede in this respect progressively further from the Koala and the Aye-aye. If *Plagiaulax* had shown less degree of "pedunculation" and a higher position of the condyle than in *Thylacinus* or *Sarcophilus*, and had, in these respects, approached nearer to *Chiromys* or *Phascolarctos* in mandibular modifications, an inference of corresponding approximation in diet, or herbivorous application of jaw, would have been legitimate. I claim the same quality for my conclusion, that as the carnivorous characters of the lower jaw are maximized in *Plagiaulax* (fig. 10) with strong indications of the same structure in *Thylacoleo* (fig. 8), so the carnivority of both genera is the more plainly demonstrated.

It is not, however, a solitary character, but an association of characters, which establishes this conclusion.

Position of condyle relates to the force with which the mandible is worked, shape and pedunculation of the condyle to the direction of the working force.

The flattened or less convex articular surface favours the rotatory movements; the more convex, especially transversely extended and pedunculate or subpedunculate, condyle indicates the ginglymoid articulation with greater extent of divarication or wider gape, and more habitual movements of the jaw in one plane, or limited more or less thereto. The rotatory grinding movements of the mandible are commonly associated with a high position of the condyle and vegetable diet; the vertical biting movements are commonly associated with a low position of the condyle and animal diet. But the advantage of a long lever afforded by a lofty coronoid process (figs. 10, 11, 12, *c*) and low-placed condyle (ib. *b*) may correlate with powerful biting and gnawing actions, as in the working of the maximized scalpriform teeth of *Chiromys* (fig. 9, *i*).

Here, however, the coronoid (*c*) is comparatively low: the condyle (ib. *b*) is narrow; its convex curve is chiefly longitudinal, or from above downward; there is no constriction or neck; the supporting part of the articular surface is continued directly upward and forward to the coronoid (*c*), and almost as directly downward and forward to the angle (*a*)*.

In similarly placed condyles for biting, piercing, lacerating, and killing actions of the mandible, and where such condyles are associated, as is the rule, with laniariform not with scalpriform anterior teeth, the condyle is more prominent; the part of the ascending ramus supporting the condyle curves toward the coronoid process, in a course at first more or less deeply concave, then vertical or recurved; and a similar well-marked concavity divides the condyle from the angle of the jaw, save in the most decidedly zoophagous of the *Marsupialia* (*Sarcophilus*, *Thylacinus*, *Plagiaulax*), in the latter of which the convex condyle forms, as it were, the upper and back part of the angle itself.

The condyle in *Plagiaulax* (fig. 10, *b*) projects a little below the horizontal level

* OWEN, 'Monograph on the Aye-aye,' 4to, 1863, p. 20. pl. 8. figs. 7, 9 (also 'Transactions of the Zoological Society,' vol. v. pt. 2. pl. 20. figs. 7, 9).

of the alveolar series; in *Chiromys* and *Carnivora* it is on that level. But if the mandibular condyle in *Plagiaulax* agreed in all characters with that of the rodent Lemur, this would not show *Plagiaulax* to be a vegetable feeder. The direct testimony of the insectivorous or rather larvivorous habits of the Aye-aye is too strong and too sure to be done away with by the enforced food on which a captive individual may have been compelled artificially to subsist.

However, for the instruction of any physiologist or palæontologist who may still deem the position of the condyle in *Chiromys* to throw light upon the food and nature of *Plagiaulax* and *Thylacoleo*, it may be stated that in every secondary mandibular character *Plagiaulax* differs from *Chiromys*, and resembles *Sarcophilus*, *Thylacinus*, and *Phascolotherium**. The supporting part of the condyle sinks below the transversely extended upper part of the convex articular surface, before curving forward and upward to the coronoid, leaving an entering notch between that process and the coronoid which, in the type specimen of *Plagiaulax Becklesii* (fig. 20 F, p. 258), closely corresponds in form with that in *Thylacinus* and *Phascolotherium*.

The fractured line of the angle of the jaw is not beneath the neck of the condyle, but on the inner side of the inferior border of the rising ramus passing to the lower end of the condyle. That part of the angle which has been broken off did not extend, as Dr. FALCONER states, below the condyle as in the Aye-aye, but to the inner side thereof, as in *Sarcophilus*, *Thylacinus*, and *Phascolotherium*†.

Whoever may have watched a living Thylacine or Ursine Dasyure must have been struck with the width of its gape. The extent of such motion of the mandible is due to the freedom of the joint (figs. 11, 12, *b*) and its distance from the moving lever (*c*). The like or even greater relative backward position of the condyle must have equally or more favoured "the power of separating the jaws in front essential to a predaceous animal having laniary teeth," like those of the *Thylacoleo* and *Plagiaulax* (fig. 10), "constructed to pierce, retain, and kill"‡. And we have direct proof in the sessile condition of the condyle in the Aye-aye that the power of separating the jaws was more restricted in that carnivorous and rodent Lemur.

§ 11. *Testimony as to the native food of the Aye-aye.*—The advantage to the forcible action of the jaw by the backward position of the condyle is recognizable, whether the fore teeth of the jaw be fashioned for "biting," *i. e.* piercing as a dagger and becoming infixed in a prey, or for "eroding" hard wood, as a gouge or chisel.

Modifications of the mandible might be expected to be associated with the different actions and applications of the fore teeth, aided or advantaged by the carrying back the condyle and lengthening the lever of the biting powers.

Prior to 1861 such backwardly placed as well as low-placed condyle was not known

* British Fossil Mammals, 8vo, 1846, p. 65.

† It is this "broad" part of the condyle which gives it the "ovate or pyriform outline" (XI. p. 445). In *Thylacinus* and *Sarcophilus* a part of the articular surface also extends down from the back of the condyle.

‡ XI. p. 447.

in any real or alleged herbivorous or mixed-feeding animal. The anatomy of *Chiromys* added, in that year, the interesting and instructive exception (admitting the Aye-aye to be a mixed feeder). If it had been contended that the lower-placed condyle shown in *Plagiaulax*, and deducible in *Thylacoleo*, was absolute, independently of other characters and considerations, in demonstrating the carnivorous nature of these marsupials, the discovery of the structure of the mandible of the Aye-aye would have placed a seeming objection and a feasible argument in the hands of an advocate of the non-carnivorous character of *Thylacoleo* and *Plagiaulax*. If it were proved that the Aye-aye is a vegetable feeder, not to say herbivorous, the same advantage would be his who had interpreted the fossil remains of *Thylacoleo* and *Plagiaulax*, notwithstanding the low-placed condyle, as those of vegetarians, having their nearest affinities "to the marsupial herbivores, such as *Halmaturus*, *Hypsiprymnus*, and *Phascolarctus*"*.

But the only testimony we have at present of the natural food of *Chiromys* shows it to be "carnivorous" in the sense of subsisting on the flesh or insect-tissues of wood-boring larvæ; all the peculiarities of its structure are physiologically or teleologically intelligible only on this basis. HUNTER, it is true, made his captive Sea-gull subsist wholly on grain†, and induced a Kite to eat and thrive on bread alone‡.

Save for loyalty to truth in the abstract one might be willing to accept the evidence adduced by Dr. FALCONER § of the food given to captive Aye-ayes as proof of its being naturally a vegetable feeder; but I believe the position of the mandibular condyles to be related to the powerful working of the pair of incisors. Such work is not needed for dividing the stems of rice or the stalks of dates or bananas. Nor are the Aye-aye's conditions of condyle present in *Hypsiprymnus* or in any other vegetable feeder. No one can admit the Aye-aye to be a strict vegetarian who gives credit to the subjoined testimony:—

"It so happened that the thick sticks I now put into his cage were bored in all directions by a large and destructive grub, called here the *Moutouk*. Just at sunset the Aye-aye crept from under his blanket, yawned, stretched, and betook himself to his tree, where his movements are lively and graceful, though by no means so quick as those of a Squirrel. Presently he came to one of the worm-eaten branches, which he began to examine most attentively; and bending forward his ears, and applying his nose close to the bark, he rapidly tapped the surface with the curious second digit, as a Woodpecker taps a tree, though with much less noise, from time to time inserting the end of the slender finger into the worm-holes as a surgeon would a probe. At length he came to a part of the branch which evidently gave out an interesting sound, for he began to tear it with his strong teeth. He rapidly stripped off the bark, cut into the wood, and

* X. p. 352; XI. p. 435.

† HOME, 'Lectures on Comparative Anatomy,' 4to, vol. i. p. 271. OWEN, 'Catalogue of the Physiological Series, Museum of the Royal College of Surgeons,' 2nd ed. 8vo, p. 151, prep. no. 523.

‡ HUNTER, 'Animal Economy,' OWEN's Ed. 8vo, 1837, p. 112.

§ X. p. 364; XI. p. 449.

exposed the nest of a grub, which he daintily picked out of its bed with the slender tapping finger, and conveyed the luscious morsel to his mouth. I watched these proceedings with intense interest, and was much struck with the marvellous adaptation of the creature to its habits, shown by his acute hearing, which enables him aptly to distinguish the different tones emitted from the wood by his gentle tapping; his evidently acute sense of smell, aiding him in his search; his secure footsteps on the slender branches, to which he firmly clung by his quadrumanous members; his strong rodent teeth, enabling him to tear through the wood; and lastly, by the curious slender finger, unlike that of any other animal, and which he used alternately as a pleximeter, a probe, and a scoop"*.

SONNERAT, besides specifying the compulsory food on which his captive Aye-aye perished in two short months, not being able longer to sustain life thereon, describes the long slender naked middle digit:—"il s'en sert pour tirer des trous des arbres les vers qui sont sa nourriture"†. I understand this to mean that larvæ—"vers"—are its natural or staple food. The affirmation may have been made from SONNERAT'S observations on *Chiromys* in a state of nature, or on the reports of natives of Madagascar, or on both authorities. It is a better testimony of its natural "nourriture" than the compulsory diet of confinement, and ought to be quoted in a consideration of the present important question.

For to what condition is Comparative Anatomy reduced if we reject the testimony which Dr. FALCONER does not cite, and admit, upon the testimony he does cite, that *Chiromys* is a vegetable feeder! Were the scalpriform teeth enabled, through the low position of a terminal condyle, to gouge out the hard woody fibre for food in order that the animal might masticate such fibre? Only upon this hypothesis could *Chiromys* be cited as an exception to the correlation of such position of mandibular joint with animal diet. But xylophagous habits involve complex ever-growing molars, like those of the Voles, the Beavers, and Capybaras. A reference to the molar teeth of the Aye-aye at once indicates its true diet, and the part played by the lower jaw and its chisels in obtaining it. Observation of the living animal in its native woods vindicates the Cuvierian principle, and gives the rational explanation of both dental and maxillary machinery. Instead of being an exception, the low condyle enters into the rule of its association with the getting of food of an animal nature.

Now let us return to the application of the Aye-aye's mandibular structure to the explanation of that in *Thylacoleo* and *Plagiaulax*. "The large front teeth in *Chiromys* are curved in segments of circles, the working surface is elongate, in breadth equalling that of the base of the tooth, with a front convex enamelled border, forming the obtuse apex of the gouging surface"‡.

* Letter from Dr. SANDWITH, quoted in "OWEN on the Aye-aye," Trans. Zool. Soc. vol. v. pt. 2. 1863, p. 37.

† Voyage aux Indes Orientales, &c., Paris, 4to, 1782, p. 122.

‡ OWEN, 'On the Aye-aye,' 4to, 1863, p. 25.

With what molars are these scalpriform teeth associated? Few, small, tubercular. Adapted for squeezing the soft animal nutriment out of the tegumentary covering of a caterpillar, not adapted for trituratory mastication of such vegetable food as calls for the more complex and massive molars of the Kangaroos, Potoroos, and Koalas. With what kind of teeth is the low-placed and backwardly placed condyle of *Thylacoleo* and *Plagiaulax* associated? and what may be the diet indicated by such association? For the response to these questions the palæontologist, guided by the Cuvierian principle, refers to the great carnassial and the small tubercular molar teeth.

§ 12. *Comparison of the Mandibular Condyle in Thylacoleo, Plagiaulax,* and *Rodentia.*—In placental Rodents the mandibular condyle is longitudinally horizontal, transversely convex; its long diameter is from before backward; it represents the section of a cylinder. The glenoid cavity of *Thylacoleo* shows that its condyle has been convex from before backward or longitudinally, and with its long diameter transverse; not limiting the jaw, as in Rodents, to horizontal movements chiefly to and fro, but adapting the jaw to hinge-like vertical motion, needed for the due action of the terminal laniaries and the large carnassials.

The mandibular condyle in the more ancient and smaller Marsupials with a closely analogous dentition is demonstrably similar to that which is here inferentially ascribed to the condyle of *Thylacoleo*. It is in *Plagiaulax* convex longitudinally, or from before backward, and that in so great a degree that the most prominent part of the convexity looks backward. "Its long diameter is disposed subvertically, and the outline is ovate or pyriform, the broad end being uppermost"*. This broad end is the transversely extended part of the convex condyle†. Dr. FALCONER, nevertheless, affirms that the form of condyle presented by *Plagiaulax* is "common in the placental Rodents"‡; yet is constrained to add, "with the difference, however, that in the latter the condyle having to work backwards and forwards in a groove, its articular surface is disposed longitudinally"§.

But this difference precludes an ascription of community of form of condyle between *Plagiaulax* and *Rodentia*; and in so far as the difference is such as to enable the condyle in *Plagiaulax* to work the jaw upward and downward, or vertically, it lends itself to those actions which the jaw has to perform "among the *Carnivora*."

The kind and degree of difference which the mandibular condyle presents in *Chiromys* and in *Plagiaulax*, already pointed out, in like manner illustrates its application in the latter to predatory actions, and is consequently and concomitantly associated with a difference of form of the entire mandible: that part in *Plagiaulax* conforms with the lower jaw in *Sarcophilus* and *Thylacoleo* in as marked a degree as it differs from the mandible in *Chiromys*, in placental Rodents, in *Phascolarctos*, and in *Hypsyprimnus*.

* X. p. 360; XI. p. 445.

† OWEN, Monograph on British Mesozoic *Mammalia*, pl. 4. fig. 10, A, *c* & B.

‡ X. p. 360; XI. p. 445.

§ Id. ib.

§ 13. *Comparison of Incisors of Diprotodont Paucidentata with those of Chiromys and Rodentia.*—*Thylacoleo* and *Plagiaulax*, it is affirmed, "agree with *Chiromys* in the collateral position and upward direction of their strong incisors"*. Doubtless; but they differ in the character of the terminal surface indicative of the kind of work to which those incisors were respectively put in *Thylacoleo* and *Chiromys*. Admitting the Aye-aye to be "as rare and aberrant among existing Mammalia"† as are *Thylacoleo* and *Plagiaulax* among fossil Marsupials, yet the Aye-aye shows on its lower front teeth a long smooth sloping surface, the result of the scraping, cutting, chisel-like action of the opposed scalpriform incisors‡.

Thylacoleo and *Plagiaulax* preserve the pointed termination of the lower incisors, or if they be blunted or broken, they show no signs of habitual attrition. *Chiromys* combines a compressed form with peculiar fore-and-aft breadth of the incisor, which has its thick enamel limited to the front border and to a contiguous portion of the sides, but coextensive in length with the deeply implanted tooth. The lower incisors of *Thylacoleo* and *Plagiaulax* have the proportion of transverse to fore-and-aft breadth, and the continuous sheath of enamel (Plate XIII. fig. 8) limited to the exposed crown, which are characteristic of the laniaries in *Potamogale* and *Felis*: consequently the crown or exposed part of the long and large incisor of *Thylacoleo* and *Plagiaulax* is that alone which is curved, and the division into crown and root is recognizable. The entire scalpriform incisor of *Chiromys*, like that of true Rodents, is curved in the segment of a circle§ and the tooth (fig. 9, *i*) preserves its diameters of depth and breadth from the end of the worn, sloping, eroding surface of the crown (*i*) to the base of the implanted part, and this part is much longer, with a concomitantly longer socket, than in *Thylacoleo* and *Plagiaulax*. The above-defined broad and striking differences between the lower incisors of *Chiromys* and those of *Plagiaulax* and *Thylacoleo* militate strongly against the conclusion of *Plagiaulax* and *Thylacoleo* being Marsupial forms of Rodent, or "Rodent types of Marsupial"‖, and are decisive against the alleged "clear evidence of their phytophagous and rodent plan of construction"¶.

Dr. FALCONER pursues his argumentation as follows:—"Let us now consider OWEN'S inference as to the function of these teeth. It is expressed thus: 'The large front tooth is formed to pierce, retain, and kill; the succeeding teeth are like the blades of shears, adapted to cut and divide soft substances like flesh,' &c. Professor OWEN has elsewhere described the premolar of *Hypsiprymnus* as trenchant**, and I have shown above that the tooth is essentially alike in *Plagiaulax*," (as Professor FLOWER contends that

* X. p. 364; XI. p. 449.

† Id. ib.

‡ OWEN, 'On the Aye-aye,' &c., pl. 20. fig. 3.

§ "The incisors are long, large, much compressed, regularly curved in segments of equal circles, the upper pair describing one-fourth, the lower pair one-half of such circle."—OWEN, *op. cit.* p. 55.

‖ X. p. 349; XI. p. 431.

¶ X. p. 353; XI. p. 436.

** Odontography, vol. i. p. 389.

it likewise is in *Thylacoleo* *). "If, therefore," proceeds Dr. FALCONER, "the function is to be deduced with such facile certainty from the mere form, the premolar of *Hypsiprymnus* ought also to be carnivorous. But we know that the genus is so strictly herbivorous that the family to which it belongs has been regarded as representing in the *Marsupialia* the Ruminants of the placental Mammals. With this fact before us, is it likely that the premolars of *Plagiaulax* and *Thylacoleo* 'were applied to cut and divide flesh'?"†

To this I reply; consider the difference of the molar teeth following the trenchant one in *Plagiaulax* and *Hypsiprymnus* respectively, and the true solution will be given‡.

§ 14. *Interrupted and continuous applications of Teeth.*—The deduction of the carnivorous nature of the extinct Marsupials in question was drawn not from shape merely, but from correlation of teeth. The "arbitrariness," if such quality be predicable of the conclusion, is applicable to the guiding principle, not to the palæontologist confiding therein. If reference to confirmatory and collateral facts was omitted in the Papers of 1859 and 1869, it was under the belief of their being the common property of the interpreters of fossil remains.

In the adaptively modified dentition of the class *Mammalia* the differently shaped teeth are put, some to occasional and interrupted, others to continuous use. The incisors of the child biting a piece of bread and butter exemplify the first functional character; the molars which pound the piece bitten off, the second. These incisors are trenchant or sharp-edged like the premolar of a Bettong or the carnassial of a Cat; their action in the human subject leaves a clean semicircular border of the bitten slice. The teeth, of whatever kind, incisors, premolars, or molars, which have the continuous work show its effects by an abraded surface. Those which have the occasional and interrupted work show little or no indication of such. The laniaries of *Carnivora*, when they have pierced and lacerated the prey, have done their work; the gnawing off of the pieces of flesh adapted for the imperfect tubercular mastication and for deglutition is effected by continuous action of the sectorial blades, the mouth being turned sideways to the food, as may be seen in the Felines and other *Carnivora* which have the largest and best-shaped carnassial teeth. Such action and application of these teeth are exemplified by the clean-worn, smooth, oblique surface sloping in the opposed blades down their opposite and opposed sides.

The same functional character, relating, that is to say, to "time" or "prolongation of use," is indicated by the incisors. Those in *Thylacoleo* and *Plagiaulax* show no evidence

* XII. p. 310. "The great cutting premolar of *Thylacoleo* bears no real comparison with the carnassial tooth of the Carnivora, but with the compressed premolar of the *Hypsiprymni*."—Ib. p. 316.

† X. p. 356; XI. p. 440.

‡ Dr. FALCONER, indeed, does strengthen his attack by calling in the argument from correlation; but he selects a different tooth from that of the Cuvierian principle:—"When this conclusion as to the herbivority of *Plagiaulax*" and *Thylacoleo* "from similar trenchant characters of premolars with those of *Hypsiprymnus* is coupled with the obviously phytophagous type of the incisors, the conviction will be confirmed."—X. p. 357; XI. p. 440.

of mutual continuous attrition. In Rodents, whether placental or marsupial, the oblique surface of wear or use in both upper and lower pairs of the large front teeth has suggested the comparison with the chisel, and the term "scalpriform." Such incisors have a trenchant margin as the human incisor has; but the superadded sloping surface of attrition in the Rodent indicates the continuous as distinguished from the occasional application of such front teeth. The Lemurine Aye-aye presents the same character as a guide to the inference of function of incisors, and at once exemplifies the difference of such function and that of the homologous pairs of pointed unworn teeth in *Thylacoleo* and *Plagiaulax*.

It is proper, in pursuing comparisons for the purpose of arriving at truth, that, besides the front view of the incisors of the Koala*, we should contrast their working surface (fig. 6, *i*) with that in the corresponding teeth of *Thylacoleo*. A comparison of Cut, figure 5, *i* with figure 3, Plate XIII., will show that the one has the continuous or frequent action, the other the intermittent and occasional. It is evident that the six incisors of the upper jaw, as well as the lower pair, in the Koala, work much and continuously in cropping and gnawing off the vegetable food which the large, numerous and complex grinders (fig. 6, *m*) pound to pulp for the bolus of deglutition.

A minor but sufficiently conspicuous degree of attrition characterizes the narrower upper and the lower procumbent incisors of the Bettongs and Rat-Kangaroos.

In the *Bettongia penicillata*, with such worn incisors and with all the molars in place and showing habitual use, the trenchant premolar retains its vertical groovings to the cutting-edge of both the outer and inner sides. They have been used to divide the grass-blade or the leaf-stalk, or other tough part or fibre of the vegetable food; but the more important and continuous work of mastication has had grinders in number, size, massiveness, and complexity of horizontal area fitted to perform it. Old age is attended with seeming exceptions to this rule in both human incisors and hypsiprymnal premolars, which then show the wear or work of a life.

Independently of the correlative guide, the worn surfaces of the *Thylacoleo's* carnassials show, like those of the Lion's, and like the scalpriform incisors of the Rodents, that their work and office were of the continuous kind; which, with their shape and position in the jaw, was for flesh-cutting, not for wood-cutting, or leaf-cutting or grass-cutting; for the succeeding few and small tuberculars could do nothing to the purpose with slices of such vegetable substances.

How far this deduction of function from mere form may be "facile" or "arbitrary" it is not for me to say; but it by no means authorizes any one to infer, because the correlation of the premolars of *Thylacoleo* and *Plagiaulax* with few and small tuberculars and large laniaries favours their carnassiality, that "the premolars of *Hypsiprymnus* ought also to be carnivorous"†. All that the mere form of that tooth shows is, that it cuts. What manner of substances were so cut can be inferred from the asso-

* Exclusively given by Professor FLOWER in his advocacy of the herbivority of *Thylacoleo*, XII. p. 313, fig. 4.

† X. p. 357; XI. p. 440; also XII. p. 318.

ciated teeth, more especially those defined by CUVIER as the fittest to yield the required information.

§ 15. *Work of Molars in Herbivora.*—Vegetable substances need for their assimilation not only dividing but crushing and reduction to pulp by commingling of salivary secretions during the grinding process. Hence large salivary glands are associated with numerous broad-crowned grinders. Palæontology is not left in so helpless a condition as it is made to appear in the following passage:—"There is no reason to suppose that the large trenchant premolars [of *Thylacoleo*] were not as well adapted for chopping up succulent roots and vegetables as for 'dividing the nutritive fibres' of animal prey"*. But my task has been to show, not only for what they were adapted, but what they did "chop up." "It may have been," proceeds the writer, "some kind of root or bulb; it may have been fruit"*. And so it may, according to the conditions of life and organization imagined by Professor FLOWER, but not according to those of the Creation open to our observations and comparisons. No known herbivorous Mammal is limited to teeth for slicing or "chopping up" vegetable food.

There is no difference, indeed, between X. and XII. on the main question at issue between them and me; but they are at variance between themselves on one point. Dr. FALCONER was unable to resist the proofs of carnivority from the demonstrated molar dentition of *Thylacoleo*; but, having committed himself to a different interpretation of the like dentition in *Plagiaulax*, he defended his position with an ingenuity which excited in the author of XII. and others the sentiments expressed by the epithets "masterly," "amply demonstrated," &c.

Professor FLOWER, however, with the unmistakable evidences of essential conformity between the dentition of *Plagiaulax* and *Thylacoleo*, consistently applied himself to show that *Thylacoleo* was as good an herbivore as *Plagiaulax*. He says, "Dr. FALCONER, in his anxiety to show that *Plagiaulax* could not have been carnivorous, has endeavoured to separate it as much as possible from *Thylacoleo*, laying great emphasis on all the points of divergence that could be found between them. He was evidently under the impression that the latter had been proved to be a carnivorous Marsupial, without staying to inquire into the arguments on which the assumption rested"†.

§ 16. *Family relations of Thylacoleo and Plagiaulax in the Marsupial Order.*—Of the existing groups of pouched *Herbivora* Professor FLOWER, in his paper on the Affinities of the extinct Australian Marsupial, which is "branded with such a direful title as *Thylacoleo carnifex*"‡, inclines to select the *Macropodidæ* as the one to which that Marsupial belonged; and, therein, more especially the *Hypsiprymni* or Rat-Kangaroos, in which he "sees at once in the great cutting premolar a miniature of that of *Thylacoleo*"§.

In a "Postscript" he derives encouragement of his views from "some remarks 'On the Dentition of *Thylacoleo carnifex*, Ow.,' by Mr. GERARD KREFFT, the able Curator of the Australian Museum, Sydney, in the Ann. & Mag. Nat. Hist. vol. xviii. ser. 3, p. 148,

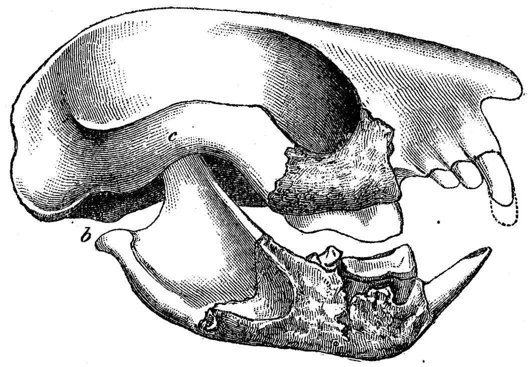
* XII. p. 318. † Ib. p. 308. ‡ Ib. p. 314. § Ib. p. 310.

1866;" accompanied by "a conjectural restoration of the then unknown anterior part of the skull and incisor teeth," which, Professor FLOWER proceeds to assert, "subsequent discoveries have in great measure confirmed"*.

I may here remark that, as my "Description of an almost entire Skull of the *Thylacoleo carnifex*," was "Received June 8,—Read June 15, 1865" (Phil. Trans. 1866, p. 73), the anterior part of the skull and incisor teeth were not unknown in September 1866, nor at the date of Mr. KREFFT's paper, May 24, 1866. The degree of confirmation which the restoration of the skull, according to the herbivorous hypothesis, has subsequently received, may be estimated by the comparison of fig. 7, p. 233 and fig. 13, with Plates XI., XII. & XIII., and more especially with Plate XIV. of the present paper.

Mr. KREFFT in this communication, and in its conjectural illustration (fig. 13), inclines to refer *Thylacoleo* to the *Carpophaga*†, deeming it "not much more carnivorous than the Phalangers of the present time‡".

Fig. 13.



Restoration of the skull and teeth of *Thylacoleo*, by Mr. KREFFT, on the herbivorous hypothesis. (Ann. & Mag. Nat. Hist. 1866, vol. xviii. pl. xi.)

But in the "List of the Fossils from the Caves of Wellington Valley," appended to the 'Report to the Trustees of the Australian Museum regarding the examination of those Caves,' Mr. KREFFT writes:—"5. Teeth and bones belonging to the gigantic Kangaroo-Rat named *Thylacoleo carnifex* by Professor OWEN."

Of the same opinion I infer to be Mr. BOYD DAWKINS, F.R.S., from the following passage in his instructive paper "On the Rhætic Beds and White Lias of Western and Central Somerset:"—"The presence of the *Macropoda* (Van der H.) (=*Poëphaga*, OWEN) is proved by the discovery of the Kangaroo-Rat allies,—viz. in the Purbeck beds, of the *Plagiaulax*, the true affinities of which have been so amply demonstrated by Dr. FALCONER§; in the Rhætic bone-bed, of the *Microlestes* of Frome and Diegerloch, closely allied, according to Professor OWEN, to *Plagiaulax* (Palæont. p. 303); and, lastly, in the strata below the bone-bed, by the discovery of the *Hypsiprymnopsis Rhæticus* of the Watchet shore"‖.

To the evidence and question of the affinity of *Thylacoleo* and *Plagiaulax* to existing groups or families of the Marsupialia I next address myself.

* XII. p. 319.

† OWEN, "Classification of the Marsupialia," Trans. Zool. Soc. ii. p. 322.

‡ Ann. & Mag. Nat. Hist. 1866, xviii. p. 149.

§ Quart. Journ. Geol. Soc. vol. xiii. p. 261, vol. xviii. p. 348.

‖ Id. ib. vol. xx. 1864, p. 412. But see the examination of the grounds of the determination of this rhætic fossil as the tooth of a Potoroo, in my "Monograph on Mesozoic Mammals," in the volume for 1870 of the Palæontographical Society, pp. 8–10.

The pouched *Mammalia* show two taxonomic modifications of the anterior mandibular teeth: in one, several pairs of incisors intervene between the canines; in the other, one pair of incisors of large size are present and no canines. The first condition characterizes the "polyprotodont section," the second the "diprotodont section"*. The existing representatives of the latter group of *Marsupialia* are confined to the Australasian area; some of the former group are American.

In both sections there are modifications of dentition, of digestive organs, and limb-structures, which in an interesting degree run parallel with each other,—the arboreal diprotodont Phalangers and Petaurists, *e. g.*, with the Opossums and Phascogales, and the saltatory *Bandicoots* and *Chœropus* with the Potoroos and Kangaroos; while the gradatory carnivorous Polyprotodonts have no known existing diprotodont correlatives.

But my knowledge of mammalian organization does not authorize me to assert that the diprotodont type of *Marsupialia* could not be so modified as to subserve carnivorous habits. I recognize no sufficient ground for the confidence that predatory dentition must be associated with three or more incisors antecedent to the canine, or "by the interposition of a line of incisors" between the two canines of either the upper or lower jaw.

Dr. FALCONER, in reference to the known Marsupial genera, asserts:—"In all the carnivorous genera and species, fossil or recent, of which the dentition has been accurately determined, there are three or more incisors, followed by a canine, on each side of the jaw, above and below; and the empirically observed result is consistent with a rational interpretation of the arrangement, in reference to their food and the means of procuring it. On the other hand, in all the existing strictly phytophagous genera, there is only a solitary incisor (being that next the axis) on either side of the lower jaw, and no canine"†. I shall presently inquire how far this alleged generalization applies to known existing species, premising that it can only be affirmed as bearing on the interpretation of the fossil remains of *Thylacoleo* and *Plagiaulax*, by demonstrating the inaccuracy of my determinations of the dentition of those extinct genera, and by resting on the foregone assumption that no Marsupial genus can or could be carnivorous unless it had the canine or caniniform tooth preceded by three or more incisors, and that "a solitary incisor," however shaped and associated with other teeth, must make a "strictly phytophagous Marsupial."

My endeavours, and whatever success may have attended them, in the interpretation of animal structures, have depended mainly on careful avoidance of antecedent assumptions of the extent of secondary modifications with which a dentition primarily fashioned for animal food might be associated. I leave my mind open, for example, to deduce consequences from observing the modifications of size, shape, and direction of the "solitary incisor on either side of the lower jaw," and the form, size, and number of the premolars, and more especially of the true molars associated therewith. To think or reason otherwise would be simply to argue in a circle, as thus:—"All carnassial Marsupial genera have incisors as well as a canine; *ergo*, no Marsupial genus with a laniari-

* OWEN's 'Anatomy of Vertebrates,' vol. iii. p. 293.

† X. p. 351; XI. p. 434.

form tooth not preceded by incisors can be carnivorous. All phytophagous Marsupial genera have a pair of developed incisors, approximated and placed collaterally in the lower jaw as in placental Rodents; *ergo*, a Marsupial fossil mandible with such incisors must be of an herbivore." But it is affirmed:—"the incisors of *Plagiaulax* are framed, in regard to number, order of suppression, collateral position, and relation to the premolars, in exact correspondence with the type of the Marsupial herbivores, such as *Halmaturus*, *Hypsiprymnus*, and *Phascolarctos*, and wholly at variance with the Carnivorous type"*. And if considerations of the shape of the incisor, modification of its working end, angle of its projection, degree of curvature of the tooth, evidence of its temporary growth or otherwise be set aside, the same may be affirmed of the lower incisors of *Thylacoleo*.

Any one enjoying a sense of confidence in the impossibility of a modification of the diprotodont type of Marsupial dentition for carnivorous habits may well dispense not only with a consideration of all those characters of the teeth in question which truly point to their function, but also of the modifications of size, shape, and number of the molar teeth associated with such pair of lower laniariform incisors.

I am not cognizant of any facts subversive of the Cuvierian principle as to the teeth which should first be observed in an unknown fossil by the palæontologist in quest of the nature of its food, and I cleave to the belief of their primary importance as throwing light on the problem to be solved.

I have qualified Dr. FALCONER'S generalizations even when restricted to existing Marsupials, as "alleged." Let me recall to the recollection of his followers some of the instances which invalidate the general averments adduced to show that *Thylacoleo* and *Plagiaulax* must be herbivorous because diprotodont.

The small insectivorous Marsupial *Tarsipes* combines with its two "well-developed, long, slender, and pointed lower incisors"†, minute molars unfitted, as in *Plagiaulax* and *Thylacoleo*, for mastication of vegetable food. Its simple alimentary canal, only exceeding the entire length of the animal by about one-half, is "destitute of cæcum"‡, as in the small Polyprotodont *Phascogale*§. "When intent upon catching flies it would sit quietly in one corner of the cage, eagerly watching their movements"||.

According to the "fundamental principles which comparative anatomy supplied" to Dr. FALCONER "for his guidance" (but which principles he nowhere defines), *Tarsipes*, like *Thylacoleo* and *Plagiaulax*, having "a pair of developed incisors approximated and placed in the lower jaw collaterally," should have been "phytophagous."

Let us test the contrasted conditions of the generalization as to incisors by another appeal to living Nature. "The Root-feeding Dalgyte"¶, or Australian "Native Rabbit" (*Peragalea lagotis*), is a miscellaneous eater. The specimen in the Zoological Gardens

* X. p. 352; XI. p. 435.

† WATERHOUSE, 'Natural History of Mammalia' (*Marsupialia*), p. 342.

‡ *Op. cit.* p. 343.

§ OWEN, Art. "*Marsupialia*," Cyclopædia of Anatomy, vol. iii. p. 300, fig. 122 (*Phascogale flavipes*).

|| GOULD, 'Mammals of Australia,' vol. i. (*Tarsipes rostratus*).

¶ GOULD, 'Mammals of Australia,' vol. i. Introduction, p. xvii.

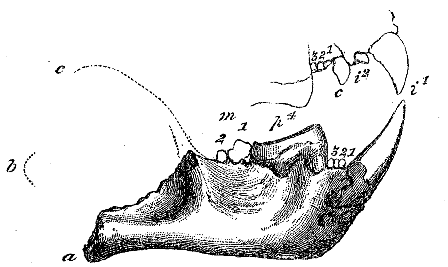
was dieted on bread and milk. "In its native grassy haunts its food consists of insects and their larvæ, and the roots of trees and plants"*, for the mastication of which its broad flat grinders† are well adapted. Nevertheless the canines proper are separated in the upper jaw by not fewer than ten incisors, and in the lower jaw by six incisors‡.

The cloven-footed *Chœropus*, equally polyprotodont, but with digital characters more closely resembling those of the Artiodactyle Ungulates than in any other marsupial genus, is not carnivorous. The condition of the molars associated with the "three or more incisors followed by a canine on each side of the jaw," clearly points to that fact. The accomplished naturalist and explorer of Australian haunts of animal life thus testifies of *Chœropus castanotis*:—"As its dentition would indicate, its food consists of insects and their larvæ, and of vegetable substances of some kind, probably the bark of trees and tuberous roots"§.

In fact the parallel and convergent modifications of all those structures which truly influence and indicate the food and habits of the animal have been noticed by all who have devoted the requisite attention to the Marsupial order. GOULD well remarks, "*Hypsiprymni* grub the ground for roots, and live somewhat after the manner of *Peramelides*, with which, however, they have no relationship" ‖; meaning within the ordinal limits—the one group being "diprotodont," the other "polyprotodont," with modifications of the two subordinal types bringing them to close similarity, if not identity, of locomotion, diet, and mode of obtaining food.

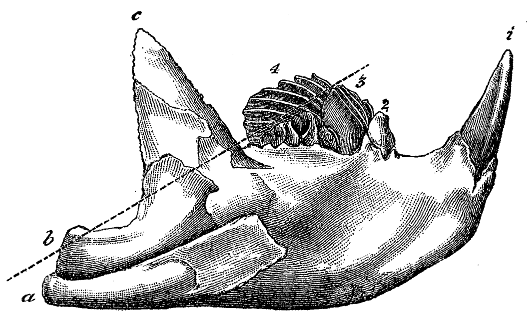
In the case of a fossil mandible of either genus the palæontologist, referring to the molar teeth, would be led to the like inference as to food and habits, although he would see in one a pair of large approximate incisors and no canines, in the other canines with small incisors interposed.

Fig. 14.



Mandible and teeth, *Thylacoleo*, reduced to one-fourth nat. size.

Fig. 15.



Mandible and teeth, *Plagiaulax*, magnified 4 diameters. (After FALCONER, Quarterly Journal of the Geological Society, vol. xiii. 1857, p. 280, fig. 14.)

Thylacoleo (fig. 14) and *Plagiaulax* (fig. 15) more closely resemble each other in

* GOULD, *tom. cit.* (*Peragalea lagotis*).

† Cyclopædia of Anatomy, vol. iii. (1841), Art. "*Marsupialia*," p. 274, fig. 96.

‡ Ib. Art. "*Marsupialia*," *ut suprà*.

§ GOULD, 'Mammals of Australia,' vol. i. (*Chœropus*).

‖ Id. ib. Introduction, p. xix.

their dentition and shape of mandible than they do any other family of diprotodont Marsupials*. From the characteristic reduction in size and number of the molar teeth I have associated them as members of a "paucidentate" family or section.

To which of the existing families of Diprotodonts is the paucidentate one most nearly allied? *Thylacoleo* best lends itself to the solution of this question, its maxillary as well as mandibular dentition being now, I may affirm, accurately determined. It is highly probable, from the close conformity of *Plagiaulax* to *Thylacoleo* in the peculiarly and extremely modified dentition of the lower jaw, that the maxillary teeth also resembled those of the larger diprotodont carnivore. Of this the dental formula is:—

$$i.\ \frac{2-2}{1-1},\ c.\ \frac{1-1}{0-0},\ p.\ \frac{4-4}{4-4},\ m.\ \frac{1-1}{2-2}:\ =30.$$

No existing Diprotodont offers a like formula. That of the *Poëphaga*† departs further than in most other diprotodont families, because there is no tooth interposed between the incisor and sectorial in the lower jaw, and in most Kangaroos not more than two are developed between the front incisor and sectorial in the upper jaw on each side, the two intervening teeth being both incisors—both anterior to the maxillo-premaxillary suture. *Hypsiprymnus* and *Bettongia* have a small canine in that suture, and two incisors between the larger front incisor and the sectorial in the upper jaw, but no teeth in that interspace in the lower jaw (figs. 17, 18). Of the more important true molar teeth (id. ib. m_{1-4}), the first three have "a quadrate form, presenting four equidistant blunt tubercles which are joined in pairs by transverse ridges, but with these ridges less elevated than the points of the tubercles; there is a slight trace of the band of the tooth" ('cingulum' of my 'Odontography') "on the front and back part of each molar as in *Macropus*. The hindermost" (fourth) "molar is generally small, almost round. Cases occur in which the last molar tooth is absent; and, what is more extraordinary, I have observed an extra tooth on each side of the upper jaw in a species of *Hypsiprymnus*"‡.

Thus in these mixed feeders, but with the vegetable diet predominating, the molar teeth adapted to such diet are never fewer and commonly more in number than in the most typical placental *Herbivora*. In relation, apparently, with the drier and tougher vegetable fibres of Australia, the premolar is trenchant and strengthened by vertical grooves and ridges. In one of the New Guinea Tree-Kangaroos (*Dendrolagus dorcocephalus*) this trenchant tooth (*p*, fig. 16) is proportionally larger than in the Australian Potoroos and Bettongs, but the light-giving teeth (the true molars) "are conformable with the *Macropus* type"§.

* Dr. FALCONER asserts, "*Thylacoleo* and *Plagiaulax* may be regarded as being as wide apart among the Marsupials as the two former (*Machairodus* and *Moschus*) are among placental Mammals."—X. p. 358; XI. p. 442.

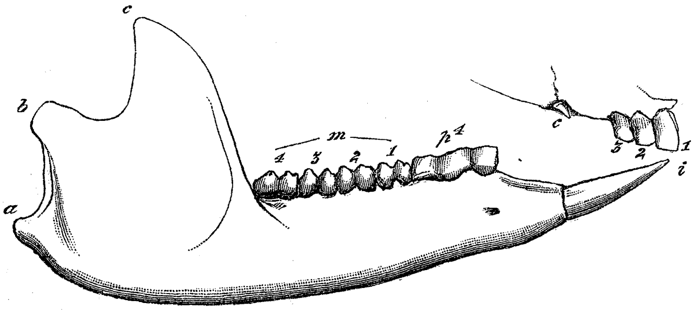
† I hold by this term, preferring it to the subsequently propounded one, *Macropoda*, of VAN DER HOEVEN, because the latter is equally applicable in its descriptive sense to the long-legged, saltatory Polyprotodonts.

‡ WATERHOUSE, 'A Natural History of the Mammalia' (*Marsupialia*), 8vo, 1845, p. 194.

§ Ibid. p. 182, pl. 10. fig. 3. In my 'Odontography' I showed that the "maximum of development of the trenchant premolar was attained in the arboreal Potoroos of New Guinea (*Hypsiprymnus ursinus* and *Hyps. dorcocephalus*), in the latter of which its antero-posterior extent nearly equals that of the three succeeding molar

There is no greater contrast in the Diprotodont series than that presented by the molars in the *Poëphaga* and the *Paucidentata*—the Kangaroos and Potoroos on the one hand, the *Thylacoleo* and *Plagiaulax* on the other. A trenchant tooth may exist for other purposes than that of cutting vegetable matter, notwithstanding the stress laid by Messrs. FALCONER, FLOWER, and BOYD DAWKINS on the degrees of resemblance subsisting between the sectorials in the *Paucidentata* and *Poëphaga*. The differences which are pointed out in the present paper outweigh the resemblances in number and importance, irrespective of the characters given by the rest of the dentition.

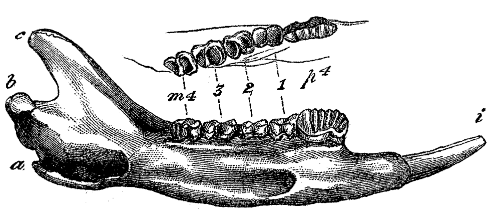
Fig. 16.



Macropus (*Dendrolagus*) *dorcocephalus*, mandible and teeth, nat. size.

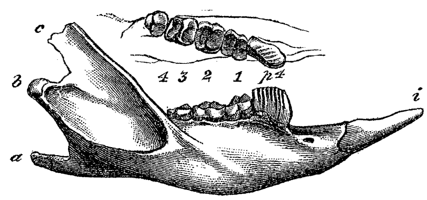
First, as to relative size. With all the additions of poëphagous species made to our Zoological Lists since 1840, I still find the *Macropus dorcocephalus** (fig. 16) to present the nearest approach to *Thylacoleo* in the relative magnitude of the trenchant premolar (ib. *p* 4). Including with that tooth the four succeeding molars, as the "molary series," the premolar constitutes nearly two fifths of that series: in *Thylacoleo* (fig. 14) the pre molar (p_4) constitutes seven-tenths of the molary series.

Fig. 17.



Hypsiprymnus minor, mandible and teeth, nat. size.

Fig. 18.



Bettongia penicillata, mandible and teeth, nat. size.

In some Potoroos, *Hypsiprymnus minor*, *H. Grayi*, e. g. (fig. 17), the premolar (p_4) a little exceeds in fore-and-aft extent the two succeeding molars (m_1 & $_2$), but in most it

teeth" (p. 389). Dr. FALCONER misquotes this as a "statement that in two Potoroos of New Guinea its antero-posterior extent nearly equals that of the three succeeding molars."—X. p. 358; XI. p. 442. But in *Dendrolagus ursinus*, *D. inustus*, and *D. Brunii* the proportion of the premolar does not exceed that of *Hypsiprymnus Grayi*.

* The many and small gradations which those additions have made known, in retained rudimental or functionless canines, in hairiness of muzzle, of tail and other parts, in shape of ears, in proportion of fore and hind

falls short; and in *Bettongia penicillata* (fig. 18) it is reduced to the extent of one and a half of the succeeding molars, or to one-fourth of the entire "molary series."

A comparison more closely bearing upon the use to which a sectorial premolar has been applied is that of the relation of its fore-and-aft length with the length of the "diastema" or interval between it and the incisor; for the jaws of marsupial *Herbivora* are commonly characterized by length, and those of *Carnivora* by shortness.

Long as the premolar is in *Dendrolagus dorcocephalus*, the slender jaw is prolonged to as great an extent before it gives exit to the procumbent incisor; this interval is never less, usually more, than the fore-and-aft length of the trenchant premolar in all *Poëphaga*. In *Thylacoleo* the interval between the fore border of the homologous lower premolar and the outlet of the incisor's alveolus is one-fourth the fore-and-aft extent of such premolar.

The contrast between *Thylacoleo* and herbivorous Diprotodonts, in the proportion of the trenchant premolar of the upper jaw to the succeeding molars (which in the great carnivore are reduced to one, Plate XI. fig. 3, m_1, as in *Felis*), is still more striking and decisive as to the use of such premolar than in the lower jaw. With the predominance of antero-posterior over vertical extent of crown in the trenchant border, and in the proportions of the two roots of the lower one, the resemblance of the premolar of *Thylacoleo* to that in any poëphagous or herbivorous Diprotodont ceases. It has not the parallel ridges and grooves which characterize the homologous tooth in the Potoroos (*Hypsiprymnus*, *Bettongia*, *Potorous*, &c.).

In the upper sectorial premolar of *Thylacoleo*, the two best marked ridges are the one defining the anterior border (Plate XI. figs. 1–3, *z*), and the one terminating the inner prominence of the swollen fore part of the tooth (ib. *v*) answering to the somewhat more developed ridge in the upper carnassial of *Machairodus* (ib. figs. 15, 16, *v*).

The slight outswelling of the base of this ridge (Plate XI. figs. 2, 15, v') I regard as a rudimental homologue of the internal tubercle of the upper carnassial in *Felis*. Thus the carnassial in *Machairodus* (*Drepanodon*) offers an instructive intermediate modification of that tooth between *Felis* and *Thylacoleo*. I am the more impressed by the degree of resemblance through adaptive modification of the sectorial premolar in the carnivorous marsupial, seeing the differences that might be expected, as, indeed, some do exist, in homologous teeth, developed for the same office, in two such different routes of derivative modification as are exemplified by the Marsupial and Placental series of mammalian structures.

One vertical ridge on the outer and broader fore part of the crown (Plate XI. fig. 1, p_4, *u*) feebly represents the second lobe of the feline carnassial; it is divided by a shallow vertical depression from the part (ib. *z*) representing the anterior lobe of that tooth*.

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limbs, in length or curvature of claws, &c., have afforded the "Gattungsmacherei" grounds for *Halmaturus*, *Lagorchestes*, *Heteropus*, *Petrogale*, *Osphranter*, *Dendrolagus*, *Hypsiprymnus*, *Bettongia*, *Potorous*, *Dorcopsis*, &c.

* This structure is better marked in an upper carnassial of *Thylacoleo* from the breccia-cave, of which photographs of the outer and inner sides were transmitted to me in the series above noted.

The rest of the outer surface is feebly undulated, and that more toward the base than the upper part of the crown. On the inner side, the basal undulation, through vertical risings and sinkings of the enamel, is more feebly marked*. The chief vertical indent on the outer side of the crown of the Thylacolean upper carnassial is near the posterior third (Plate XI. figs. 1, 3, *o*), and answers to the deeper vertical notch in *Machairodus* (ib. fig. 15, *o*) and *Felis* which defines the posterior lobe of their upper carnassial. It is interesting to note that this notch is less marked in *Machairodus* than in *Felis*, and also that the concavity of the outer side of the carnassial from before backward (*i. e.* from the outer ridge representing the second or middle lobe in *Machairodus* and the hind end of the crown) represents the more angular concavity due to the deeply vertical groove on the outer part of the carnassial in the above placental *Carnivora*.

Professor FLOWER (XII. p. 309) states that the resemblance of the great premolar of *Thylacoleo* to the carnassial of the true *Carnivora* is merely superficial; and he specifies among the differences, "especially the absence of any distinct inner lobe or tubercle" (in the upper molar) "supported by a third fang" (ib. p. 310). He was, probably, not cognizant of the example afforded by one of the extinct true *Carnivora* of the absence of the inner lobe or tubercle, or, rather, its reduction to a ridge, the lower swollen base of which (Plate XI. fig. 15, *v'*) may be compared to "a less developed homologue of the inner tubercle in the normal species of *Felis*"†.

Dr. FALCONER, indeed, repudiates this partial homology, and affirms "of the upper carnassial of his Sewalik *Machairodus*" that "neither the anterior lobe nor the middle one bears the slightest indication of bearing an internal tubercle" (XI. p. 456); and this further evidence of transitional structure between the Feline and Thylacoleonine carnassials will probably be acceptable to Professor FLOWER, though it is enunciated, as I think, in exaggerated terms.

The well-defined vertical ridges and intervening grooves on both outer and inner surfaces of the crown of the sectorial premolar of the Potoroos vary in number in different species, but are countable and pretty constant in such species, rising from four to eight or more; they are best marked on, and sometimes limited to, the apical half of the crown, the enamel at the base being smooth and even. The fore part of the Potoroo's sectorial is not broader (is usually narrower) than the hind part, and the cutting-edge runs straight or nearly so.

The transverse expansion of the fore part of the lower carnassial of *Thylacoleo*, representing the thicker anterior lobe of the carnassial of the Felines, the fore-and-aft convexity of the outer surface of the crown, and the concavity of the inner surface answering to that which defines the two lobes of the blade in Felines are better marked than

* Dr. FALCONER, quoting my original description of the carnassial in *Thylacoleo* as being "slightly grooved vertically on the inner side," correctly proceeds: "these indentations disappear about halfway up towards the edge, where the surface becomes reticulately rugose, being precisely the reverse of what occurs in the last premolar of *Hypsiprymnus*" (X. p. 356, XI. p. 440).

† OWEN, British Fossil Mammals, 4to, 1846, p. 178.

are those correspondences in the upper carnassial, and are unmistakable. A broader well-defined prominence on the fore part of the inner surface of the crown of the lower sectorial (Plate XII. fig. 11, *r*) leaves a part anterior to it (ib. *a*) representing the anterior basal talon, chiefly marked or extended upon the inner surface of the fore part of the crown in the lower carnassial of *Felis* and *Hyæna*. The indications of vertical elevations of enamel are more feeble in the lower than in the upper sectorial, and are chiefly seen at the basal part of the inner surface. The notch at the middle of the trenchant border in the less worn lower carnassial (Plate XII. fig. 11) clearly indicates divisions resembling, though more feebly marked, the anterior and posterior lobes of the homologous tooth in the placental *Carnivora* (ib. fig. 12).

The absence of the anterior transverse expansion, and the straight line described by the trenchant border of the lower sectorial of the Potoroos, is, at least, as strongly marked in the lower jaw (ib. figs. 8, 10, 13) as in the upper one (Plate XI. figs. 17, 18). In juxtaposing the specimens of the homologous teeth in *Thylacoleo* and any Potoroo for a true deduction of comparative similarity and difference, "one sees at once that the great cutting premolar of the *Hypsiprymni* or Rat-Kangaroos is" not "a miniature of that of *Thylacoleo*"*. And, if it were, the function of such sectorial could not be deduced from mere shape, but from the nature of the other teeth wherewith it is associated, and the modifications of the jaws by which such dentition was worked.

The student in reading of the "great cutting premolar of the Rat-Kangaroos" must bear in mind that the epithet is relative. Where such tooth is greatest in those vegetarians it is small in comparison with its homologue in *Thylacoleo*. The difference of shape, direction, term of growth, and of every character meaning function is still greater and more obvious in the incisors of the Diprotodonts compared than in the sectorials; and the degree and kind of difference shown by *Thylacoleo* testifies to the carnassiality of the main representative tooth of the molary series.

Against the association of that great carnivore with the *Poëphaga* "(= Macropoda, V. d. H.)," there are opposed not only the differences above demonstrated in the homologous sectorial teeth, but the absence of the third pair of upper incisors and the presence of premolars in advance of the sectorial one in both jaws of *Thylacoleo*. It will be admitted by candid readers of both my Papers on that genus that I have been reticent of conjecture or assumption; but I venture to say that when the limbs of *Thylacoleo* are restored they will not be "macropodal," not minimized at the fore part and maximized at the hind part of the body, for bipedal saltatory actions to bear it swiftly away from carnivorous pursuers, or to carry it far abroad from pasture to pasture and from scrub to scrub in quest of vegetable food, but that they will agree in the main with the limbs of *Leo*, *Thylacinus*, and *Sarcophilus*.

Pursuing the comparison of *Thylacoleo* with other *Diprotodonts*, we may at once dismiss the arboreal *Phascolarctidæ*, with a trenchant premolar (at least in the young Koalas), on the same grounds as those on which the *Poëphaga* are rejected from the association.

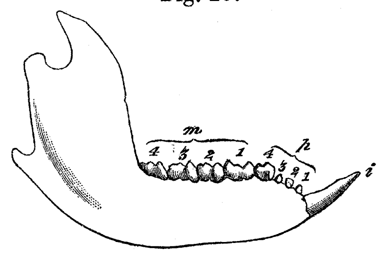
* XII. p. 310.

The superficial resemblance in the comparative views given in XII. pp. 312, 313, figs. 2 & 4, of the skulls of the Koala and of the *Thylacoleo* (as restored by Professor FLOWER), vanishes when they are turned from the front to the side view, as in figs. 6 & 8, p. 233.

The sectorial of *Phascolarctos* forms one fifth of the molary series, and mainly through "the greater relative size than in other vegetable-feeding Diprotodonts of the four following molar teeth"*. The incisor formula differs by excess, as the premolar formula does by defect, compared with the dentition of *Thylacoleo*, and this in the same way and degree as in Kangaroos and Potoroos.

We must pass to another family of Diprotodonts to find the two minute (I termed them "functionless") premolars† in advance of the last which retains its sectorial use and equality of length with the succeeding molar. In *Phalangista ursina*, *Ph. maculata*, and *Ph. chrysorrhoa* the functional premolar is preceded by two rudimental premolars as in *Thylacoleo*. In *Phalangista Cookii* (fig. 19), where the upper canine is minute and protrudes at the maxillo-premaxillary suture, two small premolars intervene between it and the homologue of the upper carnassial of *Thylacoleo*: the same degree of correspondence in numerical formula is represented by some Petaurists‡; but I have failed to find any species of "*Carpophaga*"§ in which three premolars appear between the functional one and the canine, or any species in which the upper incisors are reduced to two on each side. That a tendency to deviate by such reduction was amongst the inconstant characters of organization of diprotodont *Marsupialia* is exemplified by the Wombats, in which no incisors are developed behind the large upper anterior pair. *Thylacoleo* shows an interesting intermediate stage of the incisive formula, viz. $i. \frac{2-2}{1-1}$, between the $i. \frac{1-1}{1-1}$ of *Rhizophaga*|| and the $i. \frac{3-3}{1-1}$ of all other existing families of Diprotodonts.

Fig. 19.



Mandible and teeth, *Phalangista Cookii*, nat. size.

Of all known *Marsupialia*, recent or fossil, *Plagiaulax*, so far as its dentition is accurately determined, is most closely allied to *Thylacoleo*. In the lower jaw the true molars are similarly reduced to two of small size and tubercular form. One cannot suppose that they were opposed by more tuberculate molars above; the analogy of *Thylacoleo* (Plate XIV.) would point to fewer. A character, indeed, of the first of the inferior molars of *Plagiaulax*, overlooked by Dr. FALCONER, would indicate that it worked sectorial-wise, like the fore part of the anterior lower molar of *Thylacoleo*, upon the back part of the blade of a large upper carnassial; I allude to the smooth vertical wall-like surface of the inner side of the outer half of the crown of *m* 1, in *Plagiaulax*¶.

* OWEN, "Classification of *Marsupialia*," Trans. Zool. Soc. (1839) p. 326.

† *Loc. cit.* p. 323.

‡ E. g. *Petaurus* (*Belideus*) *flaviventer*, Cycl. of Anat. Art. *Marsupialia*, tom. cit. p. 264, f. 89.

§ OWEN, "Classification of *Marsupialia*," *ut suprà*, p. 322.

|| Ibid. p. 329.

¶ OWEN, Monograph on Mesozoic Mammals, *tom. cit.* t. iv. figs. 9, 12.

Taking the same range of the molary series for comparison as in *Thylacoleo* and existing Diprotodonts, in reference to the character of size of the last trenchant premolar, the tooth equals in antero-posterior extent one-half of that series in *Plagiaulax*. But in this more ancient Diprotodont the premolars anterior to the last large one have not undergone the extreme degradation which they show in the tertiary fossil (*Thylacoleo*) and in some existing Diprotodonts of Australia. They are modified, in *Plagiaulax*, for sectorial function, and are so combined with the last and largest sectorial as to work with it as one instrument, obliquely ridged and notched at the convex cutting-margin, like a section of a circular saw. I have elsewhere* pointed out the advantage of this modification of carnassial in dividing the integuments and other tissues, tougher and drier than those in Mammals, of the lacertian members of the cold-blooded class which so abounded with the small carnivorous Marsupials in the same Mesozoic period and place.

If it be admitted that, so far as the lower jaw and its dentition show, *Plagiaulax* (figs. 10 & 15), with its two or three reduced anterior premolars, its suddenly enlarged hind premolar, its disproportionately small and few (two) tubercular molars, and its large laniariform upcurved incisor, comes nearest to *Thylacoleo* (figs. 8 & 14), it is plain, from the antecedent comparisons with existing Diprotodonts, that there are no grounds for inferring the *Macropoda* to have been derived from the *Paucidentata*, or these from Rat-kangaroos.

What we do learn from consideration of the fossils in question is, the fact of an additional and most interesting modification of the Diprotodont section of the Marsupial order or subclass, unknown before the discovery of these fossils. We further learn that such modification, which, from the extreme reduction of the true molar series, I have been led to take as the character of a "paucidentate" family of Marsupials, was already established at the Purbeck period; yet with modifications interestingly exemplifying the tendency to the "more generalized condition of structure" as compared with the newer tertiary extinct form.

§ 17. *Tendency from the general to the particular in the Dentition of the Paucidentate Marsupials.*—But I am here met by another objection. Dr. FALCONER, attacking the principle of the tendency to transition in organisms from generalized to specialized structures as they approach in geological position the present time, writes: "Among other arguments, they insist that the earliest Eocene Mammalia, both carnivorous and herbivorous, possessed, in most cases, the full complement of teeth; while forms characteristic of later times, such as the Felidæ and Ruminantia, are remarkable for special suppression of these organs. If the generalization were really of as wide an application as has been claimed for it, we ought to find evidence of closer adherence to the general archetypic model the further back we recede in time. But so far is *Plagiaulax*, at present the oldest well-ascertained herbivorous mammal yet discovered, from giving any countenance to the doctrine, that it actually presents the most specialized exception, so to speak, from the rule to be met with in the whole range of the *Marsupialia*,

* OWEN, Monograph on Mesozoic Mammals, *tom. cit.* t. iv. figs. 9, 12.

fossil or recent. It had the smallest number of true molars of any known genus in that subclass, six at least of the normal number of incisors being also suppressed" *.

But *Plagiaulax*, viewed as a member of the same predaceous group of *Marsupialia* as *Thylacoleo*, affords an interesting instance of adherence to the law above disputed. The extinct pouched carnivore of the tertiary period shows a single carnassial tooth on each side of the lower jaw; the extinct pouched carnivore of the oolitic period retained in one species three premolars of the carnassial type, in another species four (the normal or type number) on each side of the lower jaw. The parallel runs very close with that which the placental *Carnivora* show within the limits of tertiary time; as when we compare the miocene *Hyænodon* and its three lower carnassials with the modern *Hyæna*, where they are reduced to one, or when we compare the miocene *Amphycyon* with its three upper true tubercular molars with the modern *Ursus*, where they are reduced to two, or the modern *Felis*, where they are reduced to one. If, also, the oolitic *Phascolothere*, although it is known (to me) only by half its lower jaw and the teeth of that moiety or "ramus," be compared with the modern Opossum, represented by the same part, the more generalized type is conspicuous in the absence of the degree of differentiation of the individual teeth in the oolitic fossil jaw which characterizes the homologous teeth in *Didelphys*. The canine is marked by only a slight superiority of size from the antecedent teeth, which are of similar shape, and divided from each other by similar intervals, in *Phascolotherium*. In *Didelphys* the canine is marked by greater relative size and difference of shape from the close-set group of small incisors anterior to it. The seven molars in *Phascolotherium* show gradational differences of size, but none of shape; save some simplification of the two smallest, which are the first and the last of the series of seven teeth. In *Didelphys* the last four molars are abruptly and markedly differentiated from the three preceding ones, so that zoologists distinguish the four as "true molars" from the three which are their "false molars." *Phascolotherium* does not lend itself to this distinction †.

A still more generalized type of dentition is shown by the multiplication of slightly differentiated teeth in the genera *Amphitherium*, *Amphilestes*, *Spalacotherium*, *Peralestes*, *Stylodon*, &c., of the lower and upper oolites. One solitary form (*Myrmecobius*) alone remains at the antipodes with minute and slightly differentiated teeth, in number exceeding the type one in most modern Mammals, and recalling that in lower and wider vertebrate groups.

The two or three smaller but functional premolars in advance of the large lower carnassial in the mesozoic *Plagiaulax* are reduced to two more minute functionless and speedily lost premolars in the neozoic *Thylacoleo*.

* Quart. Journ. Geol. Soc. vol. xiii. p. 276; XI. p. 427.

† This well-known fact in comparative odontology is here repeated in reply to the question addressed by Professor Huxley to the London Geological Society: "in what circumstance is the *Phascolotherium* more embryonic, or of a more generalized type, than the modern Opossum?"—Quarterly Journal of the Society, vol. xviii. (1862) p. li.

This fact invalidates the averment of "the contradictory bearing of the dental system of *Plagiaulax* upon the assumption that the earliest Mammals had the full complement of teeth:" which averment Dr. FALCONER reiterates and "calls special attention to," in X. p. 365, XI. p. 451. For if, in place of assuming *Plagiaulax* to be the earliest mammal, and, as such, with the full complement of teeth, or "the oldest well-ascertained herbivorous mammal," it be viewed as no more than it is, viz. a geologically earlier form than *Thylacoleo* with a dentition similarly modified for carnivority, the degree of difference between the two members of the *Paucidentata* is affirmatory instead of contradictory, in relation to the rule in question, rightly stated.

§ 18. *Relation of Size to Carnivority.*—One other argument against the predatory way of life of the subject of the present Paper remains for notice, although its very suggestion implies a sense of the insecurity of the grounds on which the herbivorous habits and affinities of *Plagiaulax* and *Thylacoleo* have been advocated.

They are affirmed to have been animals too small, too feeble, to have preyed upon others, especially when much larger than themselves.

Whoever has witnessed the well-known zoological phenomenon of the pertinacious pursuit and fatal attack of a hare by the diminutive weasel would pause, however, before venturing on such grounds of objection.

Dr. FALCONER, selecting for his purpose the most diminutive of the species of *Plagiaulax*, affirms: "The entire length of the specimen, including the six molars and premolars, together with the procumbent incisor (according to the metrical line *e*), does not exceed ·4 of an inch, of which the six cheek-teeth united make only about two and a half lines (·25 inch). I ask any zoologist or comparative anatomist to look at it, and say whether the dental apparatus of this extremely minute creature is competent to perform the duties required of a predaceous carnivore. Magnitude in this case is an important ingredient, as it necessarily involves measure of force. Could *P. minor* have preyed on small Mammals and Lizards? Is it not more probable that this pigmy form was itself an object of prey in the Purbeck fauna?"*

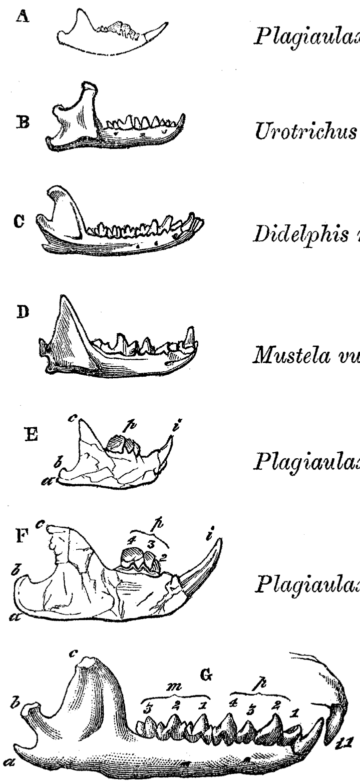
To this I reply, that I have now before me the original of fig. 15, *Plagiaulax minor* of the Quarterly Journal of the Geological Society of London for August 1857, xiii. p. 281, reproduced in the subsequent paper of Dr. FALCONER in Quarterly Journal &c. for June 1862 (X. p. 367), and copied in pl. 34. fig. 2 of the posthumous work (XI. p. 416).

The specimen (fig. 20, A) shows two molars and four premolars; the incisor is neither chisel-shaped nor procumbent, but rises with a slight curve to its pointed apex at an angle of 120°, with the line of the molar alveoli. The length of the dental series from the apex of the laniariform incisor to the hind part of the second molar is seven-sixteenths of an English inch, precisely the length of the dental series in *Urotrichus talpoïdes* (ib. B), a ferine mammal, 5 inches long from the snout to the tip of the tail, with a skull 1 inch in length, and an approximate pair of lower pointed incisors upcurved at the same angle as in *Plagiaulax minor*, but relatively less and shorter.

* X. p. 363; XI. p. 448.

Some Opossums, *e. g.* the murine and dorsigerous Philanders (fig. 20, C)*, have the mandible intermediate in size between that in *Plagiaulax minor* (A) and in *Plagiaulax Becklesii* (F); it is both shorter and weaker than in the latter species. A naturalist and good observer (Dr. CARTER BLAKE, F.G.S.) has expressed to me his surprise at witnessing, while in Central America, the disproportion of size between those mouse-like predaceous Marsupials, and the Lizards and Snakes on which they prey.

Fig. 20.



A. *Plagiaulax minor.*
B. *Urotrichus talpoïdes.*
C. *Didelphis murina.*
D. *Mustela vulgaris.*
E. *Plagiaulax Falconeri.*
F. *Plagiaulax Becklesii.*
G. *Potamogale velox.*

The above figures of the mandible and mandibular teeth are of the natural size.

I am not cognizant of any grounds afforded by zoology which forbid the supposition that a mammal of five inches in length, with the carnivorous type of dentition of *Plagiaulax*, may have been able to capture and kill the diminutive Lizards (*Saurillus*, *Macellodus*, *Nuthetes*†, &c.) abundantly associated with *Plagiaulax* in the Purbeck shales. Comparative anatomy suggests that the modifications of the dentition of *Plagiaulax minor*, as compared with the similarly sized Shrew (*Urotrichus*, fig. 20, B) and Opossum (*Philander murinus*, ib. C.), would give the Purbeck marsupial both the disposition and power to attack and prey upon animals of a larger size and higher organization than worms and insects. But the question of the carnivority of *Plagiaulax*, if weighed by

* In *D. dorsigera*, from tip of incisors to condyles, 10 lines; in *D. murina* $11\frac{1}{2}$ lines.

† OWEN, 'Quarterly Journal of the Geological Society,' 1854, vol. x. p. 420.

"magnitude as a measure of force," is not fully or fairly tested by the exclusive example of the most diminutive species.

In *Plagiaulax Falconeri* (Ow.*, fig. 20, E) the extent of the dental series, lower jaw, is six-sixteenths of an inch; in *Plagiaulax Becklesii*, Fr. (fig. 20, F) it is ten-sixteenths of an inch. The entire length of the mandible in this species, inclusive of the incisor, in a straight line, is 1 inch two-sixteenths; the depth of the ramus at the back part of the large carnassial is five-sixteenths of an inch.

In the Weasel (*Mustela vulgaris*, Cuv., fig. 20, D) the extent of the dental series, lower jaw, is eight-sixteenths of an inch; the depth of the ramus at the back part of the large carnassial is two-sixteenths of an inch.

With the greater relative depth and consequent strength of the jaw of *Plagiaulax* a greater size and strength of both laniary and carnassial teeth are concomitant. The condyle, which is on the level of the dental series in the Weasel, is below that level in *Plagiaulax*. Every modification of the small marsupial by which it departs from the little blood-thirsty Placental is in the direction of greater carnivority.

In *Phascogale penicillata* the extent of the dental series, lower jaw, is fourteen-sixteenths of an inch. It has four true molars in such lateral series, with relatively smaller laniaries and still smaller sectorial premolars than in *Plagiaulax*; the mandibular condyle is raised a little above the dental line; the carnivorous adaptation of both jaw and teeth is less marked than in the Purbeck marsupial. But what is the testimony in regard to the habits of the existing pouched carnivore no bigger than a rat?

Gould, who would be the last to repeat testimony to which zoology and comparative anatomy ran counter, writes "*Phascogale penicillata*, small as it is, comparatively, is charged with killing fowls and other birds"†.

I can bear personal testimony, and that to my own loss, of the attack and slaughter of nearly full-grown Shanghai Pullets by *Mus decumanus*. Comparative anatomy lends more aid to the credibility of the predatorial powers of the carnivorous marsupial than of the equally small rodent; but that both of them do attack and destroy animals more than twice their size and weight is a zoological fact.

Though magnitude may be, in one sense, a measure of force, it by no means necessarily implies the application of such force, and consequently is any thing but "an important ingredient" in the question of the carnivority of *Mus*, *Mustela*, *Phascogale*, and *Plagiaulax*.

But whatever bears on the interpretation of the singular dentition of the small "paucidentate" marsupial, logically applies to the larger one.

Mr. Krefft gives drawings of sections of the "lower incisor of *Thylacoleo*, *Nototherium*,

* Monograph of the Fossil Mammalia of the Mesozoic Formations, p. 84, plate iv. figs. 16, 16 A.

† "Mammals of Australia," fol. Introduction, p. xviii. Mr. Waterhouse remarks, "In the Phascogales, where the two foremost of the lower incisors are large, their increased development is, as it were, at the expense of the posterior incisors, which are very small, and the canine which follows them is but moderately developed."—Nat. History of the Mammalia, vol. i. (1845) p. 256.

Diprotodon, *Thylacinus*, and *Sarcophilus*," also of what he terms the "upper incisor and lower incisor of *Felis tigris*,.... showing the relative size of the teeth in these animals, and proving sufficiently that the *Thylacoleo* was far inferior in strength to a modern Tiger, and no match for ponderous Diprotodonts and Nototheriums"*.

If the carnassial tooth were selected instead of an incisor, it would show on the above basis that *Thylacoleo* was "far superior in strength and carnivority to the modern Tigers and Lions." But I would submit that the test of relative size of a single tooth, if even the answerable or homologous one were recognized by the tester, is not a decisive or sufficient one in the present question.

It is evident that Mr. KREFFT's figures 7 & 8 are sections of the canine, not the incisor, of the Tiger. But if that tooth in the *Hippopotamus* were exemplified by a similar section, it would be no element, or a very deceptive one, in concluding as to strength or carnivority. The canines of *Moschus* and other like instances will at once suggest themselves to the competent Comparative Anatomist.

To the assertion of the "gigantic herbivorous *Nototherium*" &c. being "many times as large as the *Thylacoleo*"†, I will oppose a few matters of fact and mensuration. The length of the skull of the largest species of *Nototherium* (*N. Mitchelli*) is 1 foot 6 inches ‡; that of the skull of *Thylacoleo carnifex* is 10 inches 8 lines: were the occipital ridge and spine entire in the specimen measured (Plate XIV.) it might be set down at 11 inches. It will be within the bounds of accuracy to say that the Notothere was twice as large as the *Thylacoleo*, not more. The skull of the *Diprotodon* is 3 feet in length; it is, however, large in proportion to the trunk and limbs; bulk for bulk, it was probably not much larger in comparison with the *Thylacoleo* than is the Giraffe in proportion to its destroyer the Lion. The disproportion between the Wolverene (*Gulo luscus*) and its prey the Reindeer must be greater than that which the dimensions of the known fossils of *Thylacoleo* and *Diprotodon* suggest. The length of a Lion's skull before me is 1 foot; that of the skull of a South-African Giraffe is 2 feet 2 inches. If we next compare, not a single tooth merely, but the whole lethal tooth-weapons of *Thylacoleo* and *Felis tigris*, we get the following results. The length from the fore part of the laniary to the hind part of the carnassial, upper jaw, is in *Felis tigris* 3 inches 7 lines; in *Felis spelæa* 4 inches; in *Thylacoleo carnifex* 4 inches 3 lines. In the lower jaw the proportions are reversed; but the difference affords no reasonable ground for inferring such inferiority of strength or destructive power as to support the inference that *Thylacoleo* was incapable of playing the same part in relation to the *Nototheres* and *Diprotodons* as the Lion now performs in relation to the Buffaloes and Giraffes.

* "On the Dentition of *Thylacoleo carnifex* (Ow.)," in Annals and Magazine of Natural History, Third Series, vol. xviii. 1866, p. 148.

† Professor FLOWER, F.R.S., however, adopts the argument from size, and rejects the hypothesis "that *Thylacoleo* was the destroyer of the gigantic herbivorous Marsupials (many times as large as itself) with which its remains are found associated, the Diprotodons and Nototheres."—XII. p. 318.

‡ OWEN, "On some Outline-drawings and Photographs of the Skull of *Nototherium*," Quarterly Journal of the Geological Society of London, vol. xv. p. 173, pl. vii. (1858).

The remains of the large extinct *Herbivora* of the Pleistocene period in Britain, which have been found in the limestone-caves of Weston-super-Mare, Torquay, Pickering, &c., are held to have been parts of animals which have fallen a prey to the contemporary *Carnivora*, now also extinct. The caves of the limestone-district of Wellington Valley, Australia, reveal phenomena of extinct animal life closely analogous. I infer that the fossils, always more fragmentary than those from the tranquil freshwater deposits, of the Diprotodons, Nototheres, large Kangaroos, and Wombats, surpassing in size any existing species, were remains of animals which had fallen a prey to contemporary *Carnivora*, and by them had been dragged into the cave.

Now, no predaceous species bearing such proportion to the *Diprotodon* and *Nototherium* as the spelæan Lion, Bear, and Hyæna bore to the Mammoths, Rhinoceros, Oxen, &c., has hitherto been detected in Australian bone-caves, save the *Thylacoleo carnifex*. To its associated fossils, the Thylacine or the Dasyure (*Sarcophilus*), the objection of defective strength and bulk might be specious; but it is inapplicable to the *Thylacoleo*.

§ 19. *Conclusion.*—In the main the descriptions or definitions of the characters of the fossil remains of *Thylacoleo* and *Plagiaulax* by my antagonists and myself are the same; and the chief difference herein is that I interpret the fractured surface of the angle of the jaw in a specimen of *Plagiaulax* as indicative of that part being bent inward immediately below the neck of the condyle as in *Sarcophilus* and *Thylacinus*, whilst Dr. FALCONER contends that the part broken away descended below the condyle as in the mandible of the Aye-aye. And so, with regard to *Thylacoleo*, I interpret the evidences of its fossil mandible as indicative of an agreement with that in existing Marsupial *Carnivora* in the form and proportions of the coronoid process and in the position of the transversely extended condyle. Messrs. KREFFT and FLOWER restore the mandible of *Thylacoleo*, in regard to these light-giving structures, according to the analogies of the carpophagous Phalangers and Koalas and the poëphagous Potoroos, assigning to the upper jaw the same incisive formula, for dissenting from which I have given reasons.

I cannot find better words to express my conviction of the state of the question as now analyzed and tested than those of the gifted and lamented Palæontologist, whose criticisms, as reproduced in his posthumous work, reiterated, as it were, from the grave, have overcome the reluctance which, till now, has kept me silent. In those words, therefore, I venture to remark, that, if my inferences and conclusions be favoured by acceptance, it will not imply that my opponents had "fallen into errors of observation and description"*, so much as it will expose "the fallacious train of reasoning which had led them astray"†.

Should *Thylacoleo* be permitted to rest, after the facts and inferences from the scanty fossil evidences at my command, in the section of diprotodont Marsupials, with *Plagiaulax*, amongst the predaceous feeders on flesh, and not with *Hypsiprymnus* amongst the harmless *Herbivora*, it will only be further proof of the worth and truth of the principle which CUVIER laid down as our guide in such dark routes in Palæontology.

* X. p. 350; XI. p. 433. † Id. ib.

Already, since writing the above, evidence has reached me, in the last Packet from Sydney, which I shall probably be not the only one to hail as undesigned witness to what I deem the truth of the matter.

Amongst the fossils obtained by Professor THOMSON and Mr. KREFFT from the breccia-caves of Wellington Valley were several ungual phalanges, some of which, equalling or surpassing those of a Lion, were compressed, the vertical exceeding the transverse diameter, and being considerable in proportion to the length: these phalanges are curved and pointed, but the point is more or less blunted or broken, apparently after interment. They supported a claw, and in most there are traces more or less plainly discernible of a bony sheath which bound or strengthened the attachment of the base of the claw. These specimens, at present, I know only by photographs of the natural size.

Plate XIII. fig. 12 is of one of these ungual phalanges, 1 inch 9 lines in length, 1 inch 3 lines in basal depth. The articulation (*a*) occupies the upper half of the basal surface; it is concave and divided by a median vertical ridge, adapting it to the pair of convexities on the distal end of the penultimate phalanx. A strong tuberous process (*b*) for the insertion of the flexor tendon projects from the lower part of the basal half of the bone. A ridge (*c*) anterior to the joint may indicate the attachment of the sheath broken away.

Figure 14 gives an under view of this phalanx, showing the breadth of the apophysial part of the base, and the compressed character of the decurved claw-bearing part of the phalanx.

Figure 13 is a side view of a similar phalanx, 1 inch 8 lines in length, 1 inch in basal depth. The upper part of the articular surface (*a*) is more produced, or better preserved, than in figure 12; and the indication of the sheath (*c*, *c*) is more considerable and begins more in advance. The insertional tuberosity (*b*) also extends rather more forward.

In the next photograph (ib. fig. 11) the bony basal claw-sheath (*c*, *c*) is evidently preserved; its anterior margin is 1 inch 3 lines in advance of the hind part of the phalanx; but this, as well as the under surface of the back part, appears to be mutilated. One half or side of the sheath has been broken away, exposing the core of the claw (*d*), the pointed termination of which is better preserved than in the preceding specimens.

From these specimens may be inferred a spelæan animal with subcompressed decurved pointed claws, equalling or exceeding those of the Lion or Tiger in size, but supported by phalanges resembling those of *Thylacinus*, *Dasyurus*, and the Opossums in being non-retractile, or wanting the characteristic low position of the joint in the sheathed claw-bones of placental Felines, but resembling those phalanges, rather than the non-retractile ones of the Marsupials above mentioned, in the proportion of depth to length and breadth.

A claw may be adapted to pierce, retain, and lacerate (as, for example, the large sheathed one of *Myrmecophaga jubata*), and be used as a weapon against a mammal of equal or superior size only in defence (as when the great Anteater causes the death of its assailant the Jaguar by the tenacity of its grip). So, likewise, may the claws of the Megatherioids have been put to such occasional defensive uses against their probable assailant the *Machairodus neogæus*, although, as in the Anteater, the habitual service of the claws may have related to insects or vegetable diet.

One is guided in a conjecture as to the uses of claws by the evidence afforded by the associated fossils of the animals which, if unguiculate, would have had claw-bones of the size of those under consideration.

No evidence of a Megatherioid or other Edentate animal has been had from any cave or fossiliferous deposit in Australia. The shape of the ungual phalanges in Kangaroos and Wombats is known. The ungual phalanges (Plate XIII. figs. 12–14) are too small for *Nototherium* and *Diprotodon*, if even one were to entertain the idea of those huge Marsupial *Herbivora* having had sheathed, compressed, decurved, pointed claws, like those which the plalanges in question plainly bore. These phalanges are as much too large for the *Thylacinus* and *Sarcophilus*. But there is no other associated Carnivore corresponding in size with that of the animal indicated by them, save the *Thylacoleo*.

It is open to any one to repeat, with respect to these phalanges, the remark which has been made on the fossil metacarpal of the carnivorous type from Australia, the size of which is such, as the articular surfaces (*a* in figs. 11, 12 & 13, Plate XIII.) show to have entered into the formation of the paw terminated by such claw-phalanges, viz. "That the metacarpal bone figured in Phil. Trans. 1859, Plate XIII. belonged to the same animal as the skull is only conjectural"*.

All that has been above advanced in searching out the nature of the ungual phalanges made known to me by photography is conjectural; but if a Palæontologist or Comparative Anatomist is willing to lend friendly aid in such difficult gropings after the things of the past, he should point out in what particulars he deems the grounds of the conjecture to be defective.

A great proportion of the fair edifice of Palæontology still rests upon a scaffolding of wise and well-founded "conjecture."

Description of the Plates.

PLATE XI.

Fig. 1. Portion of right upper jaw-bone (*maxilla*) and teeth, outer side view.

Fig. 2. Portion of right upper jaw-bone (*maxilla*) and teeth, inner side view.

Fig. 3. Portion of right upper jaw-bone (*maxilla*) and teeth, under view with working-surface of teeth: the relative size and position of the tubercular is shown at m_1.

Fig. 4. Portion of right upper jaw-bone (*maxilla*) and teeth, front view.

Fig. 5. Portion of right upper jaw-bone (*maxilla*) and teeth, hind view.

Fig. 6. Crown of a less worn upper laniary (i_1), outer side; from a breccia-cave.

* XII. p. 309.

Fig. 7. Upper laniary (i_1), front view; from a breccia-cave.
Fig. 8. Part of crown of upper laniary (i_1), inner side view; from a breccia-cave.
Fig. 9. Second incisor (i_2), outer side; from a breccia-cave.
Fig. 10. Right upper canine (c), outer side; from a breccia-cave.
Fig. 11. Left upper canine (c), outer side; from a breccia-cave.
Fig. 12. *a*, right upper canine (c), inner side: *b*, ib. hinder side; from a breccia-cave.
Fig. 13. First upper premolar, outer side; from a breccia-cave.
Fig. 14. Second upper premolar, side view; from a breccia-cave.

The foregoing figures are from *Thylacoleo carnifex*, nat. size.

Fig. 15. Second upper carnassial, *Machairodus*, inner side view, nat. size.
Fig. 16. Second upper carnassial, *Machairodus*, working-surface, nat. size.
Fig. 17. Right upper premolar, inner side view, nat. size, *Hypsiprymnus*.
Fig. 18. Right upper premolar, working-surface, nat. size, *Hypsiprymnus*.

PLATE XII.

Fig. 1. Left mandibular ramus, wanting the "rising branch," outer side view; ib. i'', a section of fractured laniary.
Fig. 2. Left mandibular ramus, wanting the "rising branch," inner side view.
Fig. 3. Left mandibular ramus, wanting the "rising branch," upper view, with working-surface of carnassial.
Fig. 4. Under view of beginning or fore part of the inflected angle.
Fig. 5. Back view of fractured ditto.
Fig. 6. Lower carnassial tooth (p_4), outer side, with fangs exposed.

The foregoing figures are from *Thylacoleo carnifex*, nat. size.

Fig. 7. Lower carnassial, outer side, *Machairodus*, nat. size.
Fig. 8. Left lower premolar, outer side, *Hypsiprymnus*, nat. size.
Fig. 9. Left lower carnassial, inner side, *Machairodus*, nat. size.
Fig. 10. Left lower premolar, inner side, *Hypsiprymnus*, nat. size.
Fig. 11. Working-surface of lower carnassial, *Thylacoleo*, less worn than in fig. 3, nat. size.
Fig. 12. Working-surface of lower carnassial, *Hyæna*, nat. size.
Fig. 13. Working-surface of left lower premolar, *Hypsiprymnus*.

The line I indicates the total length of the mandible of *Thylacoleo* when entire.

PLATE XIII.

Fig. 1. Horizontal ramus of right mandible, with teeth, outer side view, nat. size; from a "photograph." (Original, a cave-specimen in the Museum of Natural History, Sydney, New South Wales.)

Fig. 2. Fore part of mandibular ramus, showing depth of implantation of laniary (i), and part of socket of carnassial (p_4); from a "photograph." (Id. ib.)

Fig. 3. Front view of mandible and teeth; the bone in outline: from original fossils.

Fig. 4. Right lower incisor, inner side view; from a "photograph." (Original, a cave-specimen in the Museum of Natural History, Sydney, New South Wales.)

Fig. 5. Right lower incisor, from a breccia-cave in Wellington Valley, outer side view.

Fig. 6. Right lower incisor, from a breccia-cave in Wellington Valley, inner side view.

Fig. 7. Right lower incisor, from a breccia-cave in Wellington Valley, back view.

Fig. 8. Right lower incisor, from a breccia-cave in Wellington Valley, transverse section, one-third from apex of crown.

Fig. 9. Right lower incisor, from a breccia-cave in Wellington Valley, transverse section of base of crown.

The subjects of the foregoing figures are from *Thylacoleo carnifex*, nat. size.

Fig. 10. Left mandibular ramus and teeth, *Bettongia*, nat. size.

Fig. 11. Inner side view of a sheathed ungual phalanx (claw-core exposed by the removal of part of bony sheath) of an unguiculate mammal.

Fig. 12. Outer side view of a similar ungual phalanx, with more of the bony sheath preserved.

Fig. 13. Side view of a similar ungual phalanx; sheath mutilated.

Fig. 14. Under view of the same phalanx.

(From "photographs:" the originals in the Museum of Natural History, Sydney, New South Wales, were obtained from the same breccia as the subjects of figs. 1 and 2, and are from a large carnivore, probably of the same species.)

PLATE XIV.

Section of the skull of *Thylacoleo carnifex* as at present known, showing the cerebral cavity and the entire dentition from nature, nat. size. Owing to the crowding of the abortive premolars ($p_{1, 2, 3}$) to the inner side of the functional one (p_4), a complete view of the dental system cannot be had from the outer side of the jaws: if illustrated from that point of view it must be more or less diagrammatically; this Plate is, therefore, added, to be contrasted, as to number and relative size and position of the teeth, with the restorations which have been published in support of the herbivorous hypothesis of *Thylacoleo*. I have refrained from completing anatomically the articular part and ascending ramus of the mandible: one cannot doubt but that, ere long, an entire mandibular ramus of *Thylacoleo carnifex* will be obtained. The section of the cerebral cavity confirms the ascription of the extinct carnivore to the Lyencephalous subclass. The cerebellum, as in *Dasyurus*, rises wholly behind the cerebrum, with apparently the interposition of part of the mesencephalon. The prosencephalon (*pr*) is very small when its proportion to the entire skull is compared with that in the Lion or Tiger. The rhinencephalon (*rh*), projecting and conspicuous anterior to the cerebrum, is characteristically large. A "sella" (*h*) is plainly indicated at the part of the basisphenoid where that cavity is "indicated only by the internal orifices of the entocarotid canals" in *Thylacinus* *. The chiasmal fossa is shown at *o*: the precondylar foramen at *p.c.*

The symbols, letters, and numerals are explained in the text.

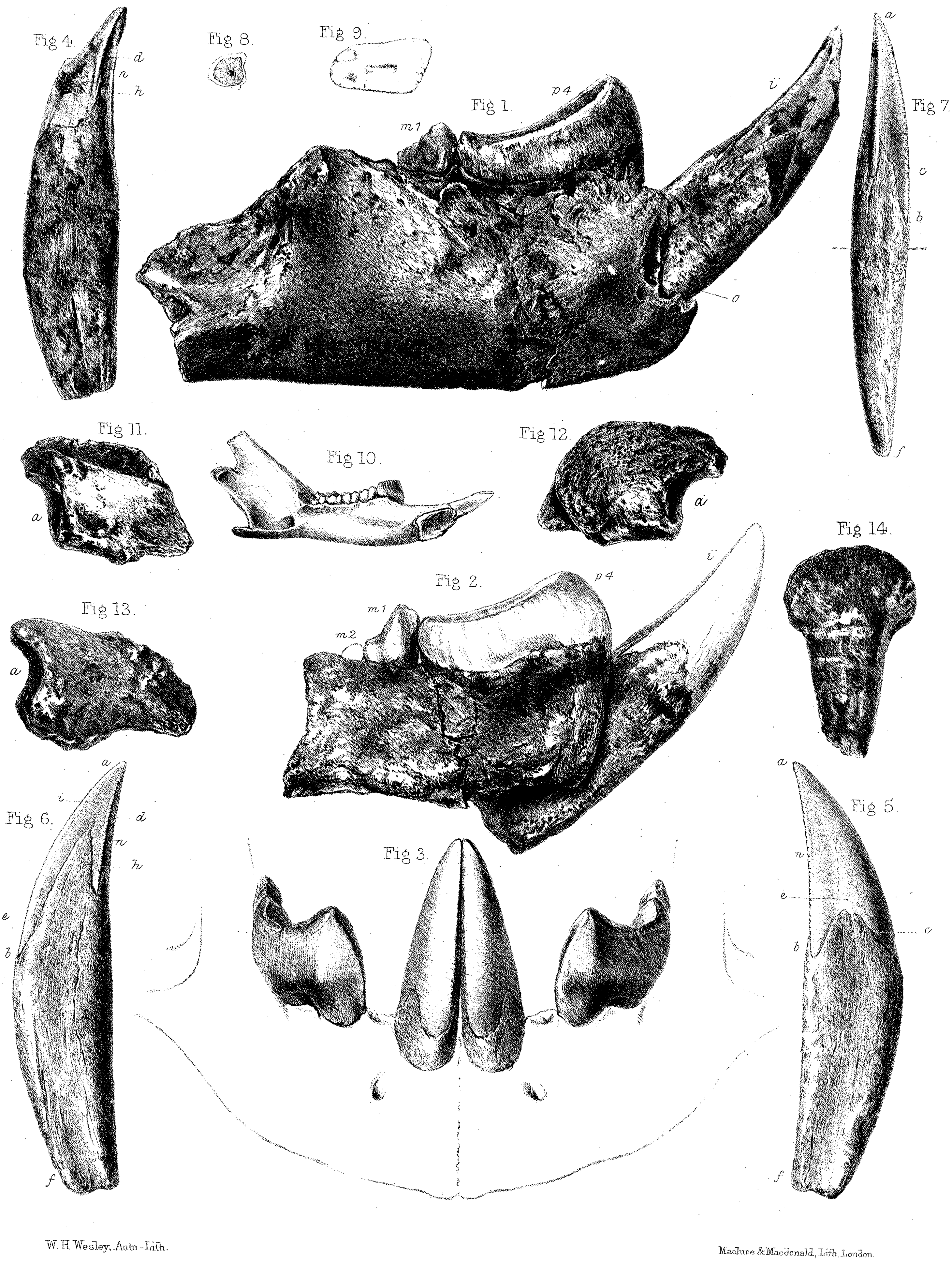
List of Woodcuts.

* Descriptive Catalogue of the Osteological Series, &c., 4to, p. 349.


Fig 12.
Fig 6.
Fig 1
Fig 7.
Fig 4.
Fig 5.
Fig 10.
Fig 9.
Fig 8.
Fig 2.
Fig 13.
Fig 11.
Fig 17.
Fig 15.
Fig 3.
Fig 14.
Fig 16.
Fig 18.

W. H. Wesley, ad nat, Auto-Lith.

Maclure & Macdonald, Lith, London.



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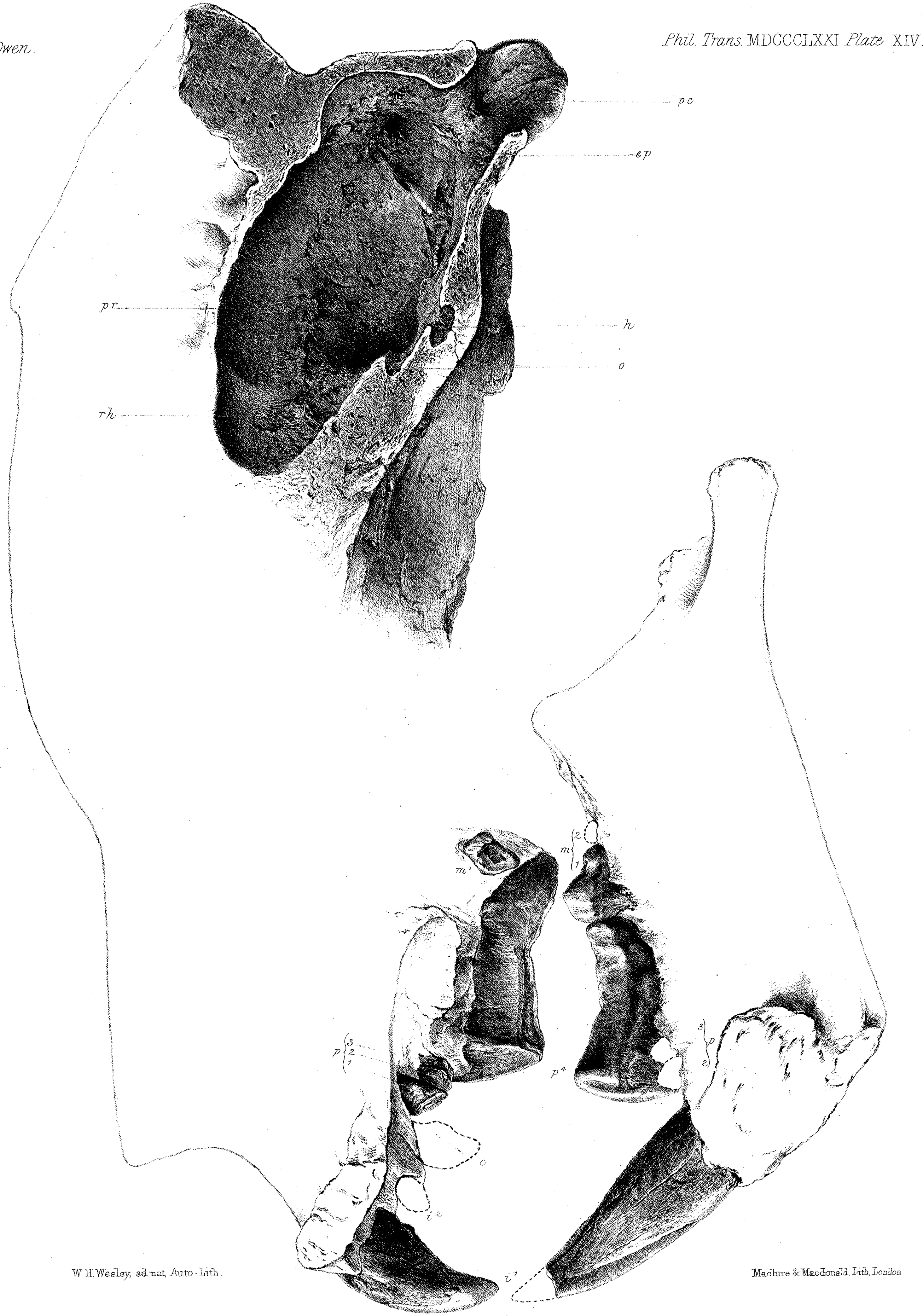

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