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PALÆONTOLOGICAL NOTES No. 1.

MACROPUS TITAN OWEN AND *THYLACOLEO CARNIFEX* OWEN.

By

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(Plates xvii-xxiii.)

Macropus titan *Owen.*

(Plates xvii-xviii.)

Macropus titan Owen, *in* Mitchell's Three Expeditions into the Interior of Eastern Australia, 2nd Edit., ii, 1838, p. 360.

Macropus titan Lydekker, Brit. Mus. Cat. Foss. Mamms., Part v, 1887, p. 225.

Macropus magister De Vis, Proc. Linn. Soc. N. S. Wales, x, 1894, p. 120.

On a recent visit to the Wellington Caves, New South Wales, a well known depository of fossil marsupials, Mr. G. C. Clutton of the Museum Staff and myself obtained the greater part of a macropod skull, which was firmly embedded in the red cave earth at a depth of about seventy feet. On examination this was found to conform closely to Owen's description of *Macropus titan*, a species first recorded from the same locality. Our specimen, though it belongs to a young individual and has several marks of immaturity, is highly interesting in that certain features are preserved which have not been previously described. The opportunity has also been taken to examine other cranial remains of this form and to review De Vis' species *Macropus magister,* which I find to be a synonym of *M. titan.*

Skull (Pl. xvii, figs. 1-3).—The skull (F.18665) lacks the occipital bones and most of the basicranial region, the anterior part of the nasals and the incisor teeth. In profile it ascends gently from the interparietal to the coronary suture, in front of which it is almost straight dorsally. The walls of the nasal chamber are slightly swollen, the sides of the muzzle almost parallel; the nasals expand only slightly posteriorly. The opening of the lachrymal canal lies wholly in the lachrymal bone but close to the maxillo-lachrymal suture. Supraorbital edges not sharp, but continued backwards in temporal ridges, which bound a median depressed

area; no sign of a postorbital process; intertemporal constriction slight (a mark of youth).

Anterior palate with moderately sharp edges, its least breadth (20·6 mm.) going less than two and a half times into the diastema. Posterior palate, so far as preserved, complete except for a small slit near the palato-maxillary suture. Anterior palatine (incisive) foramina slightly longer than m^1, commencing in front of the middle of i^3 and extending back to the maxillo-premaxillary suture. In the premaxilla, external to and slightly behind the incisive foramen, and in contact with the maxillo-premaxillary suture, is the outlet of the alveolar branch of the infraorbital nerve, from which it comes off in the infraorbital canal. Wood Jones has stressed the diagnostic importance of the position in relation to the incisive foramen of this opening,[1] which he terms the anterior palatine or naso-palatine foramen. This, however, is an unsuitable name, for the naso-palatine nerve does not, as he supposes, emerge through this outlet but from the incisive foramen. I would suggest the name *inter-alveolar foramen* for this opening, which is a conspicuous feature in all macropodine skulls; its position in *Macropus titan* approaches that seen in *M. giganteus*.

Dentition.—As shown by the alveoli i^1 is larger than i^2, and i^3 is long antero-posteriorly, its alveolus measuring approximately 13 mm. The cheek teeth present are p^3, mp^4, m^1, m^2 (in *alveolo*).

The third premolar (Pl. xviii, figs. 4, 5), which is slightly worn on the internal cusps, is shorter than m^1, hour-glass shaped, the constriction in front of the middle, the posterior segment wider than the anterior. Buccal edge trenchant, with two cusps, the posterior the larger. The lingual margin is shelf-like, with anterior and posterior cusps and a low tubercle in the valley between. The fourth premolar (secator) was extracted from its crypt and examined (Pl. xviii, figs. 6, 7); the roots are not completely formed but the characters of the crown are distinctive. Its antero-posterior length somewhat exceeds that of p^3, but it has less width. There are two external cusps, the anterior pyramidal, though slightly compressed laterally, the posterior sharp-edged and connected with the single postero-internal cusp by a ridge, behind which is a basin.

The first true molar (Pl. xviii, figs. 1-3) is practically unworn and displays very distinctly the characters of the upper molars of *Macropus titan*. The anterior shelf is short, bounded in front by a well marked ridge, which is connected to the anterior loph by a conspicuous bridge (fore link of Owen); the prebasal ridge at its highest point and the fore link are as high as the mid link. The latter is well developed, and shows a slight notch behind the middle.

[1] Wood Jones.—Proc. Zool. Soc., 1924, i, p. 457; Mammals of South Australia. Part ii, pp. 249, 254 (Adelaide, Govt. Printer, 1924).

The posterior loph has a greater transverse curvature than the anterior, and the "pocket" on the posterior aspect of the tooth described by Owen,[2] and formed by the continuation backward, upward, and outward of the inner end of the posterior loph as a "postbasal" ridge which ends at the postero-external margin of the base of the crown, is well marked, as is also the vertical groove near the lingual margin of this posterior fold.

The collection contains an imperfect skull of a mature *Macropus titan*, obtained from the Wellington Caves and figured but not described by Ramsay[3]; this affords a useful comparison with the immature skull described above. The anterior part of the facial region is wanting, and the zygomatic arch of the right side is incomplete, but the cheek teeth are well preserved, particularly on the right side, which shows p^4 and four molars, the fourth very slightly abraded, so that it may be assumed that the animal was not quite full grown. The intertemporal constriction is relatively much more marked, and there is a slight sagittal crest where in the young specimen there is a depressed area on the parietal vertex. The anterior opening of the infraorbital canal is well forward (about 24 mm. in front of the level of the lachrymal foramen), and six mm. behind the lower edge of the antorbital foramen is the opening leading down into the maxilla are described by Owen.[4] This opening is not present in the skull of the younger specimen, and it is not shown by all maxillary fragments in the collection, so that, apparently, it is not a constant feature. The teeth of this more mature individual conform so closely to those of the recently discovered skull that there can be no doubt concerning the specific identity of the two specimens.

From the collection contained in the Museum two maxillæ, each with a complete cheek series but of different ages, were selected for comparison; both are from the Wellington Caves. One (F.20887) is not quite adult, as p^3 has not been shed and m^4 has not erupted, the other (F.20886) is "aged," and apparently slightly older than F.7273. Measurements of the teeth were made and are embodied in the subjoined table of dimensions; the breadth of premolars was taken across the (wider) posterior portion, of molars across the anterior loph.

The name *Macropus titan* was established by Owen on portion of the right ramus of the mandible of a young animal with mutilated m_1 and m_2 and p_4 (*in alveolo*). Subsequently he described a number of specimens, chiefly from Queensland localities, including a fine skull from King's Creek, Darling Downs,[5] which he assigned

[2] Owen.—Phil. Trans., clxiv, 1874, p. 252; Extinct Mamms. Australia, p. 404 (London, 1877).
[3] Ramsay.—Exploration of the Caves and Rivers of N. S. Wales, p. 45 (N. S. Wales Votes and Proceedings, 1882, v, pp. 551-602).
[4] Owen.—Phil. Trans., clxiv, 1874, p. 254; Extinct Mamms. Australia, p. 405-6.
[5] Owen.—Phil. Trans., clxvi, 1876, pp. 204-209; Extinct Mamms. of Australia, pp. 435-439 (London, 1877).

to this species. The late C. W. De Vis held the view that the Queensland specimens described by Owen under this name are not conspecific with the Wellington Caves form, and for them he proposed the new specific name *Macropus magister*.[6] He based his argument chiefly on the ratio of breadth to length of the lower molars, but he seems to have overlooked the fact that in the type specimen, now in the British Museum, the two molars are both incomplete, m_1 lacking the front loph and m_2 part of the hind loph, so that his comparative measurements are unreliable. By the courtesy of Mr. H. A. Longman, Director of the Queensland Museum, I have been enabled to examine a number of maxillary and mandibular fragments identified by De Vis as *Macropus magister*, and after careful comparison and a study of Owen's descriptions and figures, I find that *M. magister* agrees in all essential features with *M. titan*. As Owen had for examination a part of an upper jaw accompanied by an almost entire lower jaw, apparently of the same individual,[7] there is no good reason for doubting the correctness of his identifications and association of maxillary with mandibular teeth, which moreover were accepted by Lydekker when preparing his catalogue.

At my request Mr. A. T. Hopwood, Geology Department, British Museum, examined the type of *Macropus titan*, and estimates that the width of m_2 is 64 per cent. of its length, while in other mandibular specimens relegated by Owen to this form the

	I.	II.	III.	IV.	V.	VI.	VII.
Zygomatic breadth ..	101·5	64·7	130·0	102·0	—	—	—
Inter-temporal breadth ..	32·7	18·2	31·0	—	—	—	—
Palatal breadth outside m^1	51·0	32·0	58·0	47·5	—	—	—
Palatal breadth outside m^2	—	—	63·6	52·2	—	—	—
Diastema..	48·0	19·0	—	56·8	—	—	—
p^3	10·1× 7·6	7·5×4·3	—	—	—	10·2× 6·7	—
mp^4	12·3× 9·2	8·0×6·0	—	—	—	11·2× 9·2	—
p^4	11·1× 6·5	8·3×4·0	9·5× 5·4	8·0× 5·0	9·3× 6·0	11·2× 5·6	9·2× 5·2
m^1	14·8×10·5	9·3×7·0	12·5× 9·7	9·1× 8·0	12·0× 9·5	13·8×10·5	12·0× 8·9
m^2	—	—	15·1×11·5	11·2× 9·3	14·1×11·1	15·6×12·2	14·0×10·5
m^3	—	—	15·5×12·5	12·7× 9·4	14·8×11·8	17·0×13·0	14·6×11·0
m^4	—	—	16·1×12·1	13·5×10·0	16·6×11·9	—	15·0×11·0
m^1–m^3 ..	—	—	43·1	33·0	40·9	46·1	40·6
Foramen incisivum	12·0	8·3	—	10·2	—	—	—

I. *Macropus titan*, juvenile, Wellington Caves (F.18665).
II. *Macropus robustus*, approximately same age as F.18665.
III. *Macropus titan*, Wellington Caves (F.7273).
IV. *Macropus giganteus*, approximately same age as F.7273.
V. *Macropus titan*, Wellington Caves (F.20886).
VI. *Macropus titan*, Wellington Caves (F.20887).
VII. *Macropus magister* (=*M. titan*), Darling Downs, Queensland (F.19646).

[6] De Vis.—Proc. Linn. Soc. N. S. Wales, x, 1894, p. 120.
[7] Owen.—Phil. Trans., clxiv, 1874, p. 253; Extinct Mamms. of Australia, p. 405.

mean percentage is 63. In *M. magister*, according to De Vis, the mean ratio of length to breadth in m_2 is 100 : 62. Mr. Hopwood, to whom I am greatly indebted for the trouble he has taken, agrees with me that *M. magister* is a synonym of *M. titan*.

This large extinct kangaroo, which considerably exceeded any existing species in size, belongs to the small-premolared group, and in its skull characters and dentition it most resembles *Macropus giganteus*, as has already been pointed out by McCoy[8] and Lydekker.[9] Its molars are slightly more complicated in structure than those of the latter, and it does not seem that the two species "pass imperceptibly into one another," or that *M. giganteus* is a direct descendant of *M. titan*. It was one of the commonest species in the Pleistocene period, and widely distributed on the Australian continent, for it has been found in various localities in Queensland, New South Wales, and Victoria, and has also been recorded from Western Australia.[10]

Genus THYLACOLEO *Owen*.

Thylacoleo Owen, *in* Gervais' Zool. et Pal. franc., 1st Edit., 1849-1852, pt. 1, p. 192; Proc. R. Soc., ix, 1858, p. 585.

Schizodon Stutchbury, Parl. Blue Book, Dec., 1854, p. 52.

Thylacopardus Owen, Proc. R. Soc. xlv, 1888, p. 99 (*nom. nud.*).

Id. Trouessart, Cat. Mamm. tam. Viv. quam Foss., nov. Edit., ii, 1898-1899, p. 1156. *Id.* Zittel, Handb. d. Pal., iv, 1891-1893, p. 110.

THYLACOLEO CARNIFEX *Owen*.

(Pls. xix-xxiii.)

Thylacoleo carnifex Owen, Proc. R. Soc., ix, 1858, p. 585; Phil. Trans., cxlix, 1859, p. 309; Extinct Mamms. Austr., p. 107 (London, 1877). *Id.* Lydekker, Brit. Mus. Cat. Foss. Mamms., pt. v, 1887, p. 189.

Thylacoleo oweni McCoy, Prodromus Palæont. Vict., Decade iii, 1876, p. 9.

Thylacopardus australis Owen, Proc. R. Soc. xlv, 1888, p. 99 (*nom. nud*).

Few mammals living or fossil have excited more interest and discussion than the so-called Marsupial Lion, both as regards its affinities and its food habits. Broom[11] has given an excellent sum-

[8] McCoy.—Prodromus Palæont. Vict., Decade vi, 1879, p. 6.
[9] Lydekker.—Brit. Mus. Cat. Foss. Mamms., Part v, 1887, pp. 225-6.
[10] Glauert.—Rec. West. Aus. Mus., i, 2, 1912, p. 61.
[11] Broom.—Proc. Linn. Soc. N. S. Wales, xxiv, 1898, pp. 57-74.

mary of the stages by which our present knowledge of this animal has been attained, and it is not necessary to traverse the ground again. Briefly, it may be stated that *Thylacoleo* is now generally placed in a sub-family Thylacoleoninæ of the family Phalangeridæ,[12] or in a separate family Thylacoleontidæ,[13] though by Trouessart it is catalogued in a sub-family Thylacoleoninæ of the family Dasyuridæ.[14]

As regards its food habits the opinion has now gained ground, chiefly on account of the strong arguments advanced by Broom,[15] that Owen was right in regarding it as a carnivore. Marrett Tims and Hopewell-Smith, however, still hold that the balance of evidence is against Owen's view.[16] This question will be briefly discussed subsequently. Whether it is possible to recognise more than one species of *Thylacoleo* is doubtful. The type is the mutilated skull discovered at Lake Colungoolac, eighty miles south-west of Melbourne, by Mr. W. Adeney in 1846, and McCoy considered that this is distinct from the New South Wales and Queensland form, for which he proposes the specific designation *oweni*.[17] But the points of difference on which he relies (chiefly the size and form of the third maxillary tooth and the course of the premaxillo-maxillary suture) are not conclusive when comparison is made with Wellington Caves specimens in our collection. In view of our limited knowledge of possible variations due to sex and age, it seems preferable to include all the known specimens in the species *T. carnifex*.

In 1888 Owen communicated to the Royal Society a paper entitled "Description of the Skull of an Extinct Carnivorous Mammal of the Size of a Leopard (*Thylacopardus australis* Owen), from a recently opened Cave near the Wellington Caves Locality, New South Wales."[18] This paper was never published, but on communicating with Mr. F. A. Towle, Assistant Secretary of the Royal Society, I was informed that Owen's manuscript is still in existence, and that four plates had been prepared by Erxleben to illustrate the paper. I am extremely grateful to Mr. Towle and the Council of the Royal Society for the opportunity of obtaining and making use of a copy of Owen's manuscript, and photographic reproductions of Erxleben's drawings, which, like all that artist's work, are beautifully executed. The skull on which Owen's description was based is in the Mining and Geological Museum, Sydney, and by the kindness of the Under-Secretary for Mines, Mr. F. S. Mance, Trustee, and the Government Geologist, Mr. E. C. Andrews, Trustee,

[12] Zittel.—Grundzüge d. Pal., Abt. ii, 1923, p. 435; Zittel-Eastman, Text-book Pal., iii, 1925, p. 29.
[13] Bensley.—Trans. Linn. Soc., Zool., ix, 1903, p. 203, Gregory.—Bull. Amer. Mus. Nat. Hist., xxvii, 1910, p. 217.
[14] Trouessart.—*Loc. cit.*, Suppl., 1904-1905, p. 846.
[15] Broom.—*Loc. cit.*
[16] Marrett Tims and Hopewell-Smith.—Tomes' Manual of Dental Anatomy, 7th Edit., 1914, p. 418.
[17] McCoy.—*Loc. cit.*
[18] Owen.—Proc. R. Soc., xlv, 1888, p. 99 (title only).

I have been permitted to obtain a loan of the specimen. I am indebted to Mr. W. S. Dun, Palæontologist, Geological Survey, New South Wales, for calling my attention to this fine skull and its history. This skull is briefly discussed below and Erxleben's drawings are reproduced (Pls. xix-xxii); I find that there is no good reason for regarding it as generically or specifically distinct from *Thylacoleo carnifex*.

One of the curiosities of zoological nomenclature is revealed by the history of a supposed marsupial fossil *"Thylacodes,"* presumed to belong to the same family as *Thylacoleo*. In 1888, at a meeting of the Linnean Society of New South Wales, the late Dr. J. C. Cox exhibited "a Tertiary fossil from Wildhorse Plains, which he believed to be identical with *Thylacodes decussatus* Gm., a living Port Jackson species"; this name is synonymous with *Vermetus decussatus*, which is a marine mollusc. By some unfortunate mistake this note led to the tentative recognition of a new genus of fossil marsupial, ? *Thylacodes* Cox, which is listed in Roger's "Verzeichnis der bisher bekannten fossilen Säugetiere."[19] Trouessart places it with *Thylacoleo* in the family Phalangeridæ, sub-family Thylacoleontinae, and, in the supplement to his well-known catalogues, in the family Dasyuridæ.[20]

This peculiar mishap can be accounted for only by the similarity in the first part of the names *Thylacodes* and *Thylacoleo*, and the fact that both records are Australian. Trouessart naïvely states in a footnote, "Ce genre ne figure pas dans: Palmer, Index generum Mammalium (1904); c'est vraisemblablement un *nomen nudum*."

Cranial Osteology of Thylacoleo.

Owen in his several papers in the Philosophical Transactions, reproduced in his Extinct Mammals of Australia,[21] has discussed the skull and dentition of *Thylacoleo* at great length, and only a few details are now lacking. On our visit to the Wellington Caves, Mr. G. C. Clutton and myself were fortunate enough to obtain a fine skull, and, using this and other specimens contained in the Museum collection, Mr. J. Kingsley, Assistant Articulator, has prepared a model of the skull and mandible (pl. xxiii). In the course of the work some interesting points in the skull structure were discovered.

One feature in which *Thylacoleo* differs from all marsupials, recent or extinct, is the presence of a postorbital bar. In marsupials a slight postorbital process is sometimes present on the frontal, and, in the Polyprotodonts particularly, the malar also sends up a post-

[19] Roger.—Ber. d. Naturw. Verh. f. Schwaben u. Neuburg, 1896 (p. 9).
[20] Trouessart.—Cat. Mamm., ii, 1898-9, p. 1156; Suppl. 1904-5, p. 846.
[21] Owen.—Phil. Trans., cxlix, 1859, pp. 309-322; clvi, 1866, pp. 73-82; clxi, 1871, pp. 213-266; clxxviii, B, 1887, pp. 1-3; Extinct Mamms. Austr., pp. 107-188 (London, 1877).

orbital apophysis, but these are separated by a wide gap. In *Thylacoleo*, however, these two processes join to form a complete though rather slender bar. Gregory suggests that the prominent postorbital apophysis on the malar of carnivorous marsupials may possibly be a remnant of the postorbital bar in the Cynodonts.[22] In any case the presence of a complete postorbital bar in *Thylacoleo* emphasizes the aberrant character of the animal. Whether it has preserved a feature which was present in ancestral marsupials, or developed the bar since it branched off, one may judge that the *Thylacoleo* line has long been distinct, and that it has no close affinity with any existing family. Its resemblance to the Phalangeridæ is probably the result of convergence.

A striking feature of the skull, which has not been alluded to by previous writers, is the large opening in the region of the spheno-palatine foramen, due to which there is wide communication between the orbito-temporal fossa and the nasal cavity. This opening is oval in shape, the long axis approximately parallel to the long axis of the skull, and it measures as much as 27 × 15 mm. in a medium-sized skull; in a large tiger, in which the skull is about twice the size of that of *Thylacoleo*, the spheno-palatine foramen is no more than 10 mm. in greatest diameter. In *Thylacoleo* the lower margin of this opening forms the lateral boundary of the posterior palatal vacuity, so that these two openings may be described as confluent. In no land mammal with which I am acquainted is the spheno-palatine foramen so large relatively as it is in this marsupial, though in the sheep and certain other ruminants it attains a considerable size. In the Pinnipedia, however, there is a large vacuity in this region. I am unable to suggest what may be the significance, if any, of the unusually large size of this opening in *Thylacoleo*.

In marsupials generally the optic and anterior lacerate (sphenorbital) foramina are not separated, and the opposite sphenoptic foramina (using the term suggested by Kesteven[23]) are confluent, so that at this point a bristle may be passed through the skull perpendicular to the sagittal plane. In *Macropus* and most diprotodonts the fissure formed by the confluent foramina is widely open, but in polyprotodonts and *Phascolarctos* it is much smaller, a mere slit in the median septum. In *Thylacoleo*, so far as can be judged from the specimens available to me, either the opposite sphenoptic foramina are not confluent, each running backward separately to open into a common fossa in the brain cavity, or the fissure uniting them is very small.

The "transverse canal," which tunnels the basisphenoid a little in advance of the entocarotid foramen, is well developed and sends

[22] Gregory.—Bull. Amer. Mus. Nat. Hist., xxvii, 1910, p. 220.
[23] Kesteven.—Jour. Anat., lii, 1918, p. 466.

off a branch on each side, which runs forward to emerge in the foramen rotundum. This transverse canal is poorly developed or even absent in diprotodonts, but is prominent in polyprotodonts, particularly in *Thylacinus*, in which the forwardly running branch leads, not to the foramen rotundum as in *Thylacoleo*, but to the sphenoptic fissure.

The mode of articulation of the lower jaw is of great importance from the point of view of food habits, the features characteristic of flesh-eaters and of vegetable-feeders being well known. In *Thylacoleo* the condyle is low, being about on a level with the cutting edge of the large premolar, and it is without neck. It is transversely elongated, the longer half on the lateral side of the ramus. The articulating surface faces upwards, not backwards as in typical carnivores. The glenoid facet is convex downwards in fore and aft direction (the skull being held in the natural position), and is not a transverse hollow but extends some distance forwards. Apparently the mandible was capable of some degree of propalinal motion and of some rotation as well, though lateral movement of the jaws can not have been very extensive. The post-glenoid process is a comparatively weak structure, thin and almost scroll-like, its lower edge curving over the auditory meatus; apparently it was co-ossified with the tympanic ring.

The dentition has been so fully described by Owen that a brief outline only will be given here. The front incisors in the upper jaw are large, tusk-like, blunt, and somewhat procumbent, separated at their bases and approximated at the tips. A facet of wear soon develops on the tip, and the lower incisor scores a vertical groove on the postero-internal surface, indicating that the lower teeth pass inside the upper. There is no interlocking of the upper median incisors and the lower incisors, which Owen regarded as the grasping and piercing teeth, corresponding to the canines of placental carnivores and marsupial carnivores of the ordinary type. It seems that as the jaws closed the mandible moved backwards slightly. The two succeeding incisors, the canines, and the two foremost premolars of the upper jaw are of relatively small size, trenchant or pointed when unworn, but becoming blunted later, so that they evidently served some useful purpose. The fourth (or it may be the third) upper premolar is an enormous blade-like tooth, with a fore and aft length of as much as 5 cm. For about two-thirds of its length its cutting edge is practically straight, but the posterior third takes a pronounced bend outwards. This edge is irregularly concave and the medial margin becomes abraded by attrition against the outer margin of the similar lower premolar, which develops a corresponding facet of wear. This shows that the two large premolars, above and below, acted exactly like a pair of shears, the lower passing inside the upper, mutual attrition maintaining a chisel edge on both throughout life or until extreme old age. Succeeding the trenchant premolar in the upper jaw is a

tubercular molar, the crown much lower than that of pm^4; it is placed medial to the posterior end of that tooth, the long axis of its occlusal surface almost at right angles to the long axis of the latter. It evidently acted partly as a stop for the large lower premolar.

The pair of lower incisors are placed close together in the middle line, their medial surfaces in contact for their entire length so that they presented practically a single point. They sweep upwards in a gentle curve, their long axis having an angle of about 125° to the axis of the mandible. They are more pointed than the median upper incisors, although they become blunted with use. Close behind the incisors are two small rounded premolars, situated medially to the large premolar and apparently functionless. The fourth premolar in the mandible resembles the corresponding tooth in the maxilla, but it is shorter antero-posteriorly, measuring about 3·8 cm. in this direction. Its cutting edge curves regularly in the antero-posterior direction, the concavity being on the lingual side, and it has also a downward concavity. Behind this tooth are two molars, the first fairly large, the anterior part of its crown as high as that of the trenchant premolar, but sloping posteriorly; its edge forms a continuation of that of pm_4, making this tooth about equal in length to the corresponding upper premolar. The second molar, which is separated from m_1 by a slight interval, is small and pointed.

A cast of the brain cavity of *Thylacoleo* has been described by Gervais,[24] who found that in its cerebral form it closely resembles the wombats and differs from the macropods, phalangers, and dasyures.

Food Habits.

Thylacoleo has been regarded as a carnivore (Owen,[25] Broom[26]), an egg-eater (Cope[27]), a gnawer of bones (De Vis,[28] W. Anderson,[29] Spencer and Walcott,[30] Glauert[31]), and as a vegetable feeder, which might on occasions devour a bird or a small mammal (Krefft,[32] Flower,[33] Lydekker[34]). Bensley[35] and Abel[36] are of opinion that

[24] Gervais.—Nouvelles Arch. Mus. d'Hist. Nat. Paris, v, 1869, pp. 236-237, pl. xiv, fig. 1.

[25] Owen.—Phil. Trans., cxlix, 1859, pp. 309-322; clvi, 1866, pp. 73-82; clxi, 1871, pp. 213-266; clxxiv, 1883, pp. 575-582; clxxviii, B, 1887, pp. 1-3; Extinct Mamms. Austr., pp. 107-188 (London, Erxleben, 1877).

[26] Broom.—Proc. Linn. Soc. N. S. Wales, xxiii, 1898, pp. 57-74.

[27] Cope.—Amer. Nat., xvi, 1882, pp. 521-2; xviii, 1884, pp. 696-7.

[28] De Vis.—Proc. Linn. Soc. N. S. Wales, viii, 1883, pp. 187-190; Proc. Roy. Soc. Vict., xii, 1, 1899, pp. 83-4; Ann. Q'land Mus., 5, 1900, pp. 7-11.

[29] Anderson (W.).—Rec. Geol. Surv. N. S. Wales, i, 2, 1899, pp. 122-3.

[30] Spencer and Walcott.—Proc. Roy. Soc. Vict., xxiv, 1911, pp. 92-123.

[31] Glauert.—Rec. West. Austr. Mus., i, 2, 1912, pp. 55-60.

[32] Krefft.—Ann. Mag. Nat. Hist., (3), xviii, 1866, p. 148; (4), x, 1872, pp. 169-182; Trans. Roy. Soc. N. S. Wales, 1873, p. 138.

[33] Flower.—Quart. Journ. Geol. Soc., xxiv, 1868, pp. 307-319.

[34] Lydekker.—*In* Nicholson and Lydekker, Manual of Palæontology, ii, 1889, p. 1285; Royal Nat. Hist., iii, 1894, p. 264; Allen's Naturalists' Library (Marsupials and Monotremes), 1894, p. 260.

[35] Bensley.—Trans. Linn. Soc., (2), Zool., ix, 3, 1903, pp. 161-2, 203.

[36] Abel.—Palæobiologie, p. 502 (Stuttgart, 1911).

Thylacoleo, from the omnivorous stage, had proceeded some distance along the evolutionary path leading to herbivority but reverted to a flesh diet, and, as its canines had already become so reduced that they were no longer capable of being utilised or modified as grasping and lacerating teeth, the incisors took on this function; in fact that *Thylacoleo* affords an example of the operation of Dollo's law.

Where opinions are so diverse, a natural deduction is that the available evidence is insufficient or conflicting, and it is probable that until additional material is procured, for example, limb bones undoubtedly thylacolean, the wisest course is to suspend judgment. A few points, however, which have a bearing on this question may be discussed here.

Cope's suggestion, that *Thylacoleo* subsisted on eggs, may, I think, be dismissed. It is difficult to see why an egg-eater should be provided with such large and trenchant premolars. Nor does the hypothesis that it was a sort of marsupial hyæna commend itself, although several writers have described fossil bones which exhibit what they suppose to be tooth marks of *Thylacoleo.* An animal adapted for a bone diet has broad strong teeth with several cusps, and a well developed cingulum on the molars and premolars, the purpose of which is to protect the gums from injury by splinters of bone. The teeth of *Thylacoleo* are not of this type; nor is such a cingulum to be found on them.

If Bensley and Abel are right in their interpretation of the dentition of *Thylacoleo,* we should find in its skull and teeth a number of characters recalling its incipient herbivority, overlain by features imposed by its later developed carnivority, and, if it was the fell and destructive beast that Owen pictured it, its flesh-eating and predatory character should be unmistakable. In some respects, however, *Thylacoleo* was but poorly equipped for killing and devouring animals, at any rate animals of a size at all approaching its own.

The median incisors of the upper jaw were blunt tusks rather than piercing implements, they early developed signs of wear, and there was no interlocking of upper and lower incisors to enable the animal to get a firm and deadly grip of its prey. The upper median incisors were slightly procumbent and met the lower pair at an angle approaching 90°. We should expect that in an efficient carnivore the upper and lower grasping and piercing teeth would have their long axes approximately parallel. It is to be noted that there is a resemblance between the upper median and the lower incisors of *Thylacoleo* and *Nototherium,* in which these teeth are tusk-like and meet at approximately the same angles as do those of *Thylacoleo.* In *Procoptodon,* an extinct genus of the family *Macropodidæ,* the lower incisors incline upwards at an angle of about 135°, and are of a pointed piercing type; the upper incisors of *Procoptodon* seem to be unknown.

Nor did *Thylacoleo* possess a convenient provision for removing the flesh of its victim. Typical placental and marsupial carnivores are provided with transverse incisor rows above and below, which enable them to tear the flesh from their prey, but *Thylacoleo* had no teeth adapted for this purpose.

Owen emphasized the low position of the mandibular condyle and its sessile condition. But this is a primitive character, and, moreover, some undoubtedly vegetarian marsupials, such as *Petaurus breviceps* and *Potorous tridactylus* also have a relatively low condyle without neck. The shape of the condyle and of the glenoid facet in *Thylacoleo* (Pl. xxi, fig. 1, *g*) is not at all what we should expect in an habitually carnivorous animal, and recalls that of certain phalangers such as *Trichosurus vulpecula* amongst living marsupials.

The evidence to be derived from the muscular system, so far as that may be reconstructed from a study of the cranial and mandibular osteology, is conflicting. It is evident that in *Thylacoleo,* as in typical carnivores, the temporal muscle was large and powerful, as Broom maintains, although even in old animals the lambdoidal and sagittal crests are only of moderate size and in younger examples are practically absent. The masseter, judging by its impression on the zygoma, was not a large muscle, as we should expect in a vegetable feeder. On the other hand, the pterygoids were apparently well developed, as indicated by the long pterygoid crest and the strongly inflected angle of the jaw, which forms a broad shelf with a deep depression on its upper surface. Powerful pterygoids suggest that the mandible was capable of lateral and rotational movements, and are characteristic of phytophagous animals.

The zygomatic arches are wide and strong, but this, as Osborn[37] points out, is no proof of carnivorous habits, and it is well known that in the Nototheres, particularly Euryzygoma,[38] there is an enormous expansion of the zygomatic arches.

The absence of effective grinding teeth is the strongest argument against the view that *Thylacoleo* was a herbivore; it is obvious that it did not live on grass, roots, leaves, or any ordinary vegetable food. Are we then driven to the conclusion that it was a carnivore, or is it possible that it subsisted on some unusual type of vegetable food? Is it not possible that its food consisted of some sort of vegetable or fruit with a tough hard rind, which would be cut by the enlarged blade-like premolars, and a soft pulpy interior which did not require mastication? I have made inquiries from Mr. Edwin Cheel, of the Botanic Gardens, Sydney, who has an intimate knowledge of Australian plants, whether there is at the present time any plant of

[37] Osborn.—Amer. Nat., xxxiii, 1899, pp. 174-5.
[38] Longman.—Mem. Q'land Mus., vii, 12, 1921, pp. 65-80.

this kind widely distributed in Australia and occurring in sufficient quantity to render plausible the supposition that *Thylacoleo* may have been able to obtain an adequate supply. One may be justified in assuming that in Pleistocene times, when *Thylacoleo* lived, the general character of Australian vegetation was not greatly different from what it is now. He suggests that possibly the members of the family *Cucurbitaceæ* might fulfil requirements. There are several species of the cucumber family indigenous to Australia, and the fruit of some kinds is of fair dimensions, up to two and a half or three inches in diameter, with a hard rind and succulent interior. The seeds, which have a high food value, may well have been swallowed without mastication. The fruit, according to Mr. Cheel, lies on the ground for months, and it is conceivable that *Thylacoleo* may have been able to obtain a sufficient quantity all the year round. We may suppose that the front incisors were employed to pick the fruit, that the small teeth between these and the large premolars were used to hold it, that it was then passed back to the sectorial premolars by which the rind would be cut so that the contents might be utilized. It is also possible that *Thylacoleo* fed on the starchy pith of certain cycads, such as *Zamia* and *Macrozamia*, which would be cut into chunks by the large premolars and swallowed practically without mastication.

It is realised that this suggestion is no more than tentative, and that there are difficulties in accepting the view that *Thylacoleo* could obtain an adequate food supply from these sources.

"THYLACOPARDUS AUSTRALIS."

(Pls. xix-xxii.)

From Owen's manuscript we learn that this skull was discovered in "a small cave near Mitchell's 'Breccia Cavern,' 100 feet below the surface in Wellington Valley. A shaft had been sunk which led to the discovery of a series of small caverns, which were reached at a depth of 83 feet below its present surface." In describing it he says: "It is the skull, lacking the lower jaw, but with the teeth of the upper jaw characteristic of the genus *Thylacoleo*, but differing in size from those figured in Plates xvi and xvii of the work above quoted,[39] and with the addition of a small molar or molariform prominence (Pl. xxi, fig. 1, *m*) in a position which justifies a generic distinction, the dentinal structure being demonstrated. I have been favoured with the loan of the original specimen, with permission to make the section requisite for demonstration of the structure."

Examination of the specimen and the figure shows conclusively that "the small molar or molariform prominence" is merely the

[39] Owen.—Extinct Mamms. Australia (London, 1877).

truncated end of the bar which bounds the posterior palatal vacuity behind. In *Thylacoleo* as in *Phascolarctos* and *Phascolomys* this bar is slender; it is seldom preserved unbroken, and in no specimen that I have seen is there any indication of a septum dividing the palatal vacuity into two halves, though it is probable that it was so divided. When the post-palatal bar is broken the two lateral ends are left as small processes, but it is surprising to find that Owen could have mistaken these for dentinal structures.

Owen is justified in calling attention to the relatively small size of the skull. He gives a table of measurements, comparing the dimensions of this specimen and of a skull of *Thylacoleo carnifex,* evidently that from the Condamine River, Queensland.[40] This table is copied below, inches and lines being converted into millimetres.

	"Thylacopardus."	*Thylacoleo carnifex.*
Length from occipital condyles to the fore part of the sockets of the front incisors	168	248
Length of the facial part anterior to orbit ..	64	77
Breadth across zygomata	154	205
Length of temporal vacuities	60	92
Length of alveolar series in a straight line ..	77	103
Breadth of bony palate at fore part of palato-nares	73	90
Breadth of the pair of palatal vacuities ..	47	56
From occipital crest to postorbital process ..	81	128
Vertical diameter of orbit..	38	45
Breadth across paroccipital processes	72	128

These figures establish a considerable discrepancy in size, but it seems probable that *"Thylacopardus"* was a young individual, the trenchant premolar showing but little wear. If Owen had measured the premolars, which do not vary in size with age, he would probably not have stressed the differences in size between his supposed new genus and *Thylacoleo carnifex.* In *"Thylacopardus"* these teeth measure in antero-posterior length at the base of the crown 50·75 mm., and their greatest thickness is 15·5 mm.; in three other skulls of considerably larger dimensions these measurements are respectively 49·8, 50·35, 50·65 and 15·8, 15·25, 15·3, showing the essential agreement in the four specimens.

As therefore, apart from its smaller dimensions, Owen's *"Thylacopardus"* exhibits no features which distinguish it from *Thylacoleo carnifex,* I have little hesitation in including it in that species.

[40] Owen.—*Loc. cit.,* p. 123, pls. xvi-xviii.

SUMMARY.

A skull of *Macropus titan* Owen, recently discovered at the Wellington Caves, N. S. Wales, is described, and some additional data are given regarding its cranial osteology and dentition. *Macropus magister* De Vis is shown to be a synonym of *M. titan.*

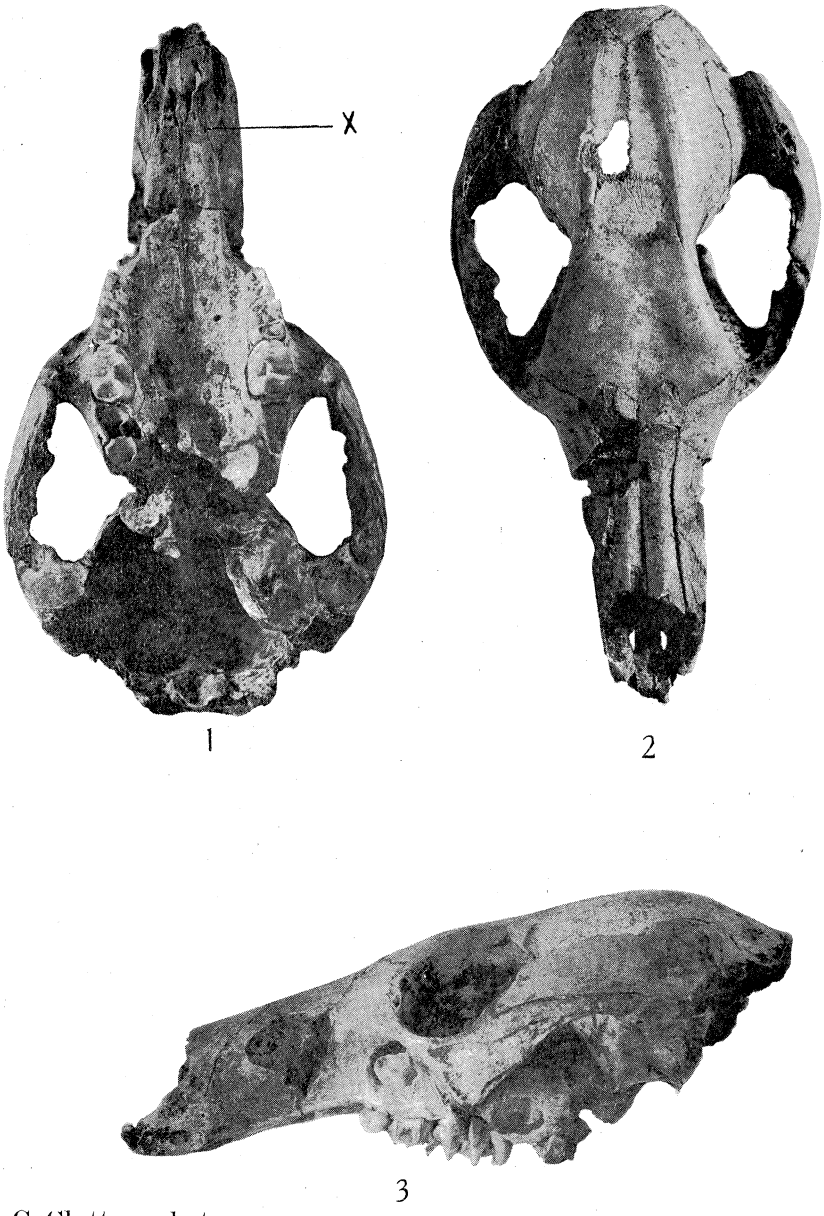
Some notes are given on the skull and dentition of *Thylacoleo carnifex* Owen, and its food habits are briefly discussed. It is shown that the animal was not well equipped for a flesh diet, and the tentative suggestion is made that it may have fed on some such vegetation as the fruit of the *Cucurbitaceæ.*

The type of *Thylacopardus australis* Owen (*nom. nud.*) is examined, and that name is found to be a synonym of *Thylacoleo carnifex.*

It is pointed out that *Thylacodes decussatus,* which has been listed as an extinct marsupial allied to *Thylacoleo,* is a mollusc (= *Vermetus decussatus*).

EXPLANATION OF PLATE XVII.

Macropus titan Owen; skull, Wellington Caves, New South Wales. A.M. No. F.18665. In Fig. 1 the bone has been cut to expose the unerupted fourth premolar. In Fig. 3 × indicates the interalveolar foramen. Slightly more than half natural size.



G. C. Clutton, photo.

EXPLANATION OF PLATE XVIII.

Teeth of *Macropus titan* Owen.

Fig. 1. Right first molar, occlusal surface, inside of tooth to right.

Fig. 2. Right first molar, outside view.

Fig. 3. Right first molar, posterior view.

Fig. 4. Left third premolar, inside view.

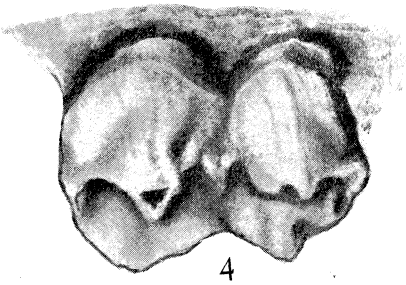
Fig. 5. Left third premolar, occlusal surface, inside of tooth to left.

Fig. 6. Left fourth premolar, inside view.

Fig. 7. Left fourth premolar, occlusal surface, inside of tooth to left.

All figures × 4 natural size.

1



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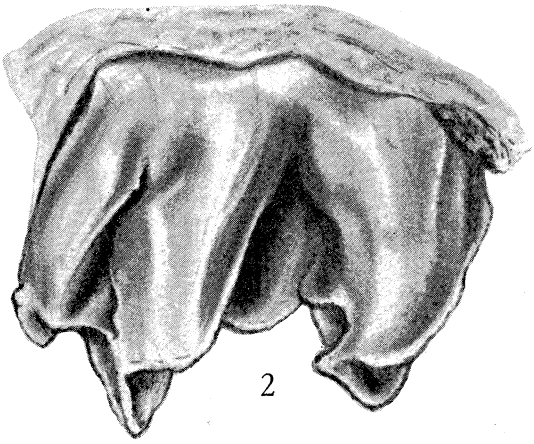

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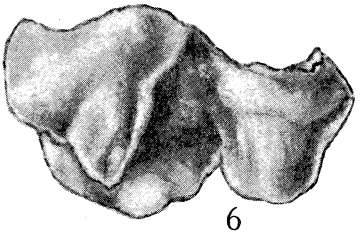

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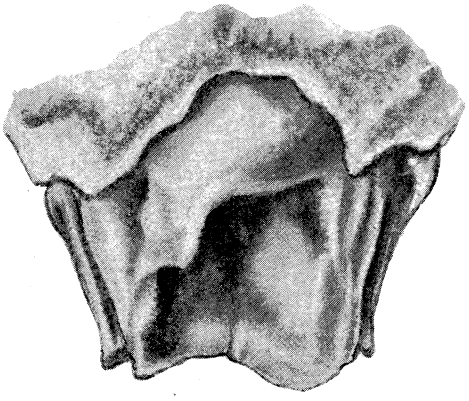

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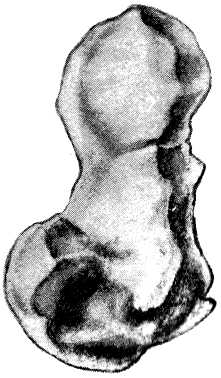

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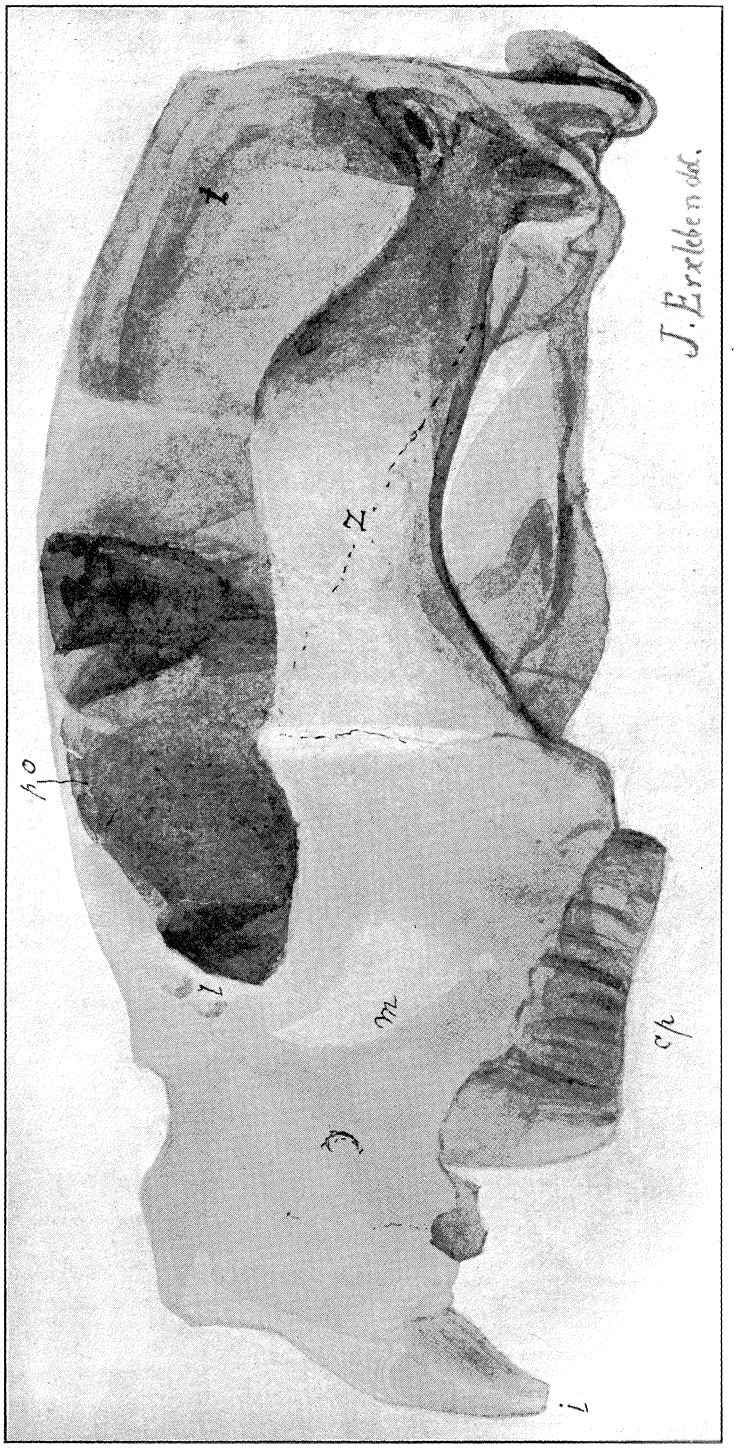
Joyce K. Allan, del.

EXPLANATION OF PLATE XIX.

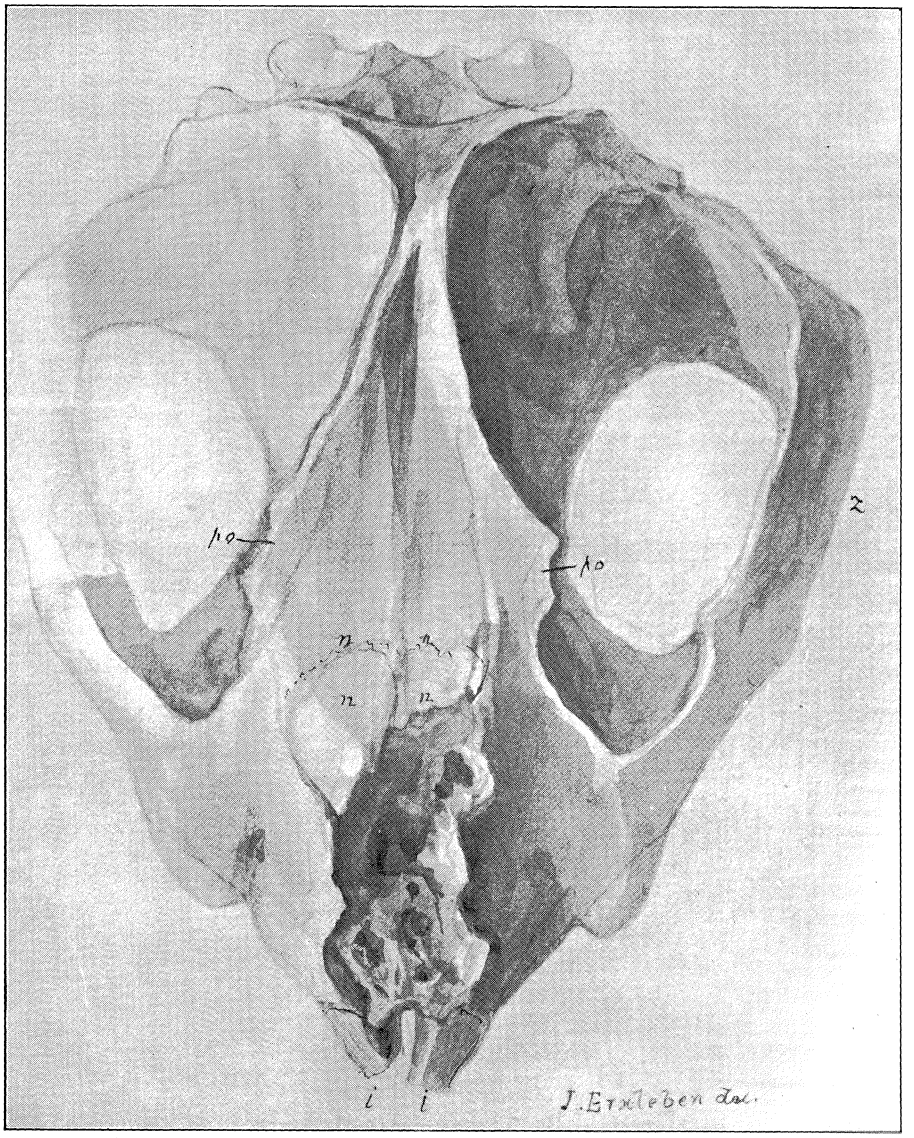
"Thylacopardus australis" Owen (= *Thylacoleo carnifex* Owen). Skull, Wellington Caves, New South Wales. Natural size.



J. Erxleben, del.

EXPLANATION OF PLATE XX.

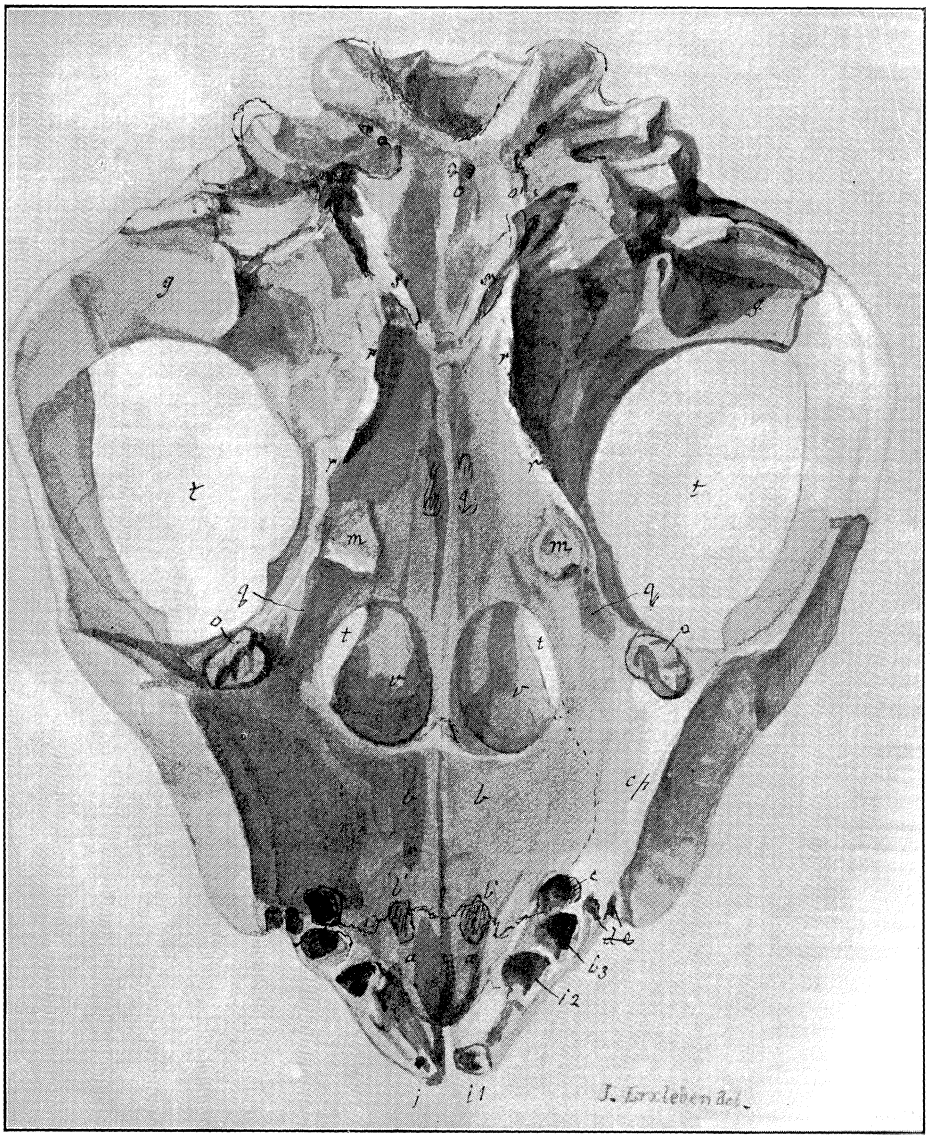
"Thylacopardus australis" Owen (= *Thylacoleo carnifex* Owen). Skull, top view. $\frac{3}{4}$ natural size approx.



J. Erxleben, del.

EXPLANATION OF PLATE XXI.

"Thylacopardus australis" Owen (= *Thylacoleo carnifex* Owen). Skull, palatal view. The drawing is deceptive, as the palatal portion of maxilla appears to be on the same plane as the vomer, presphenoid and basisphenoid; *m, m* are the remains of the post-palatal bar, thought by Owen to represent a "small molar or molariform prominence." $\frac{3}{4}$ natural size approx.



J. Erxleben, del.

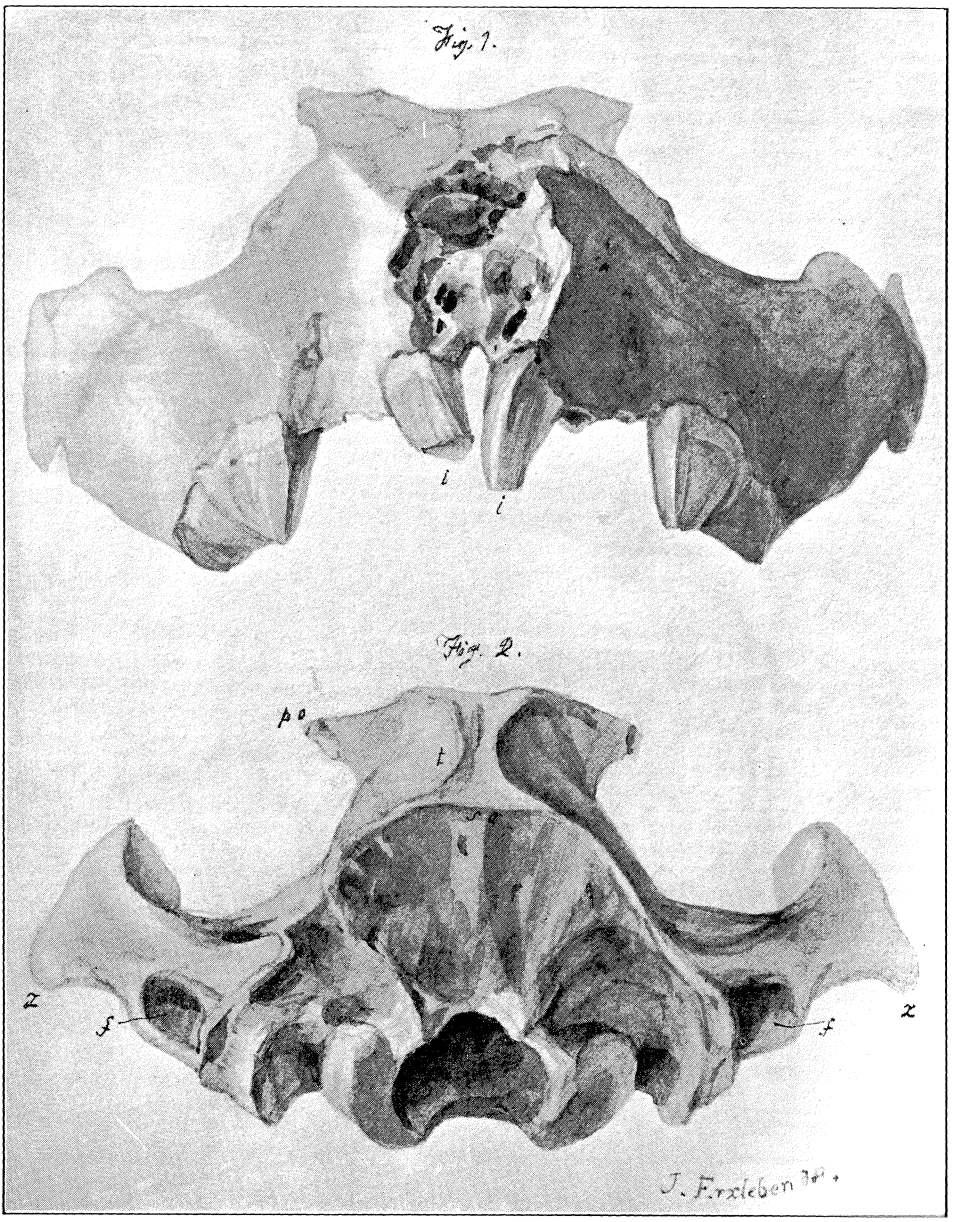
EXPLANATION OF PLATE XXII.

"Thylacopardus australis" Owen (= *Thylacoleo carnifex* Owen).

Fig. 1. Skull, front view.

Fig. 2. Skull, back view.

$\frac{3}{4}$ natural size approx.



J. Erxleben, del.

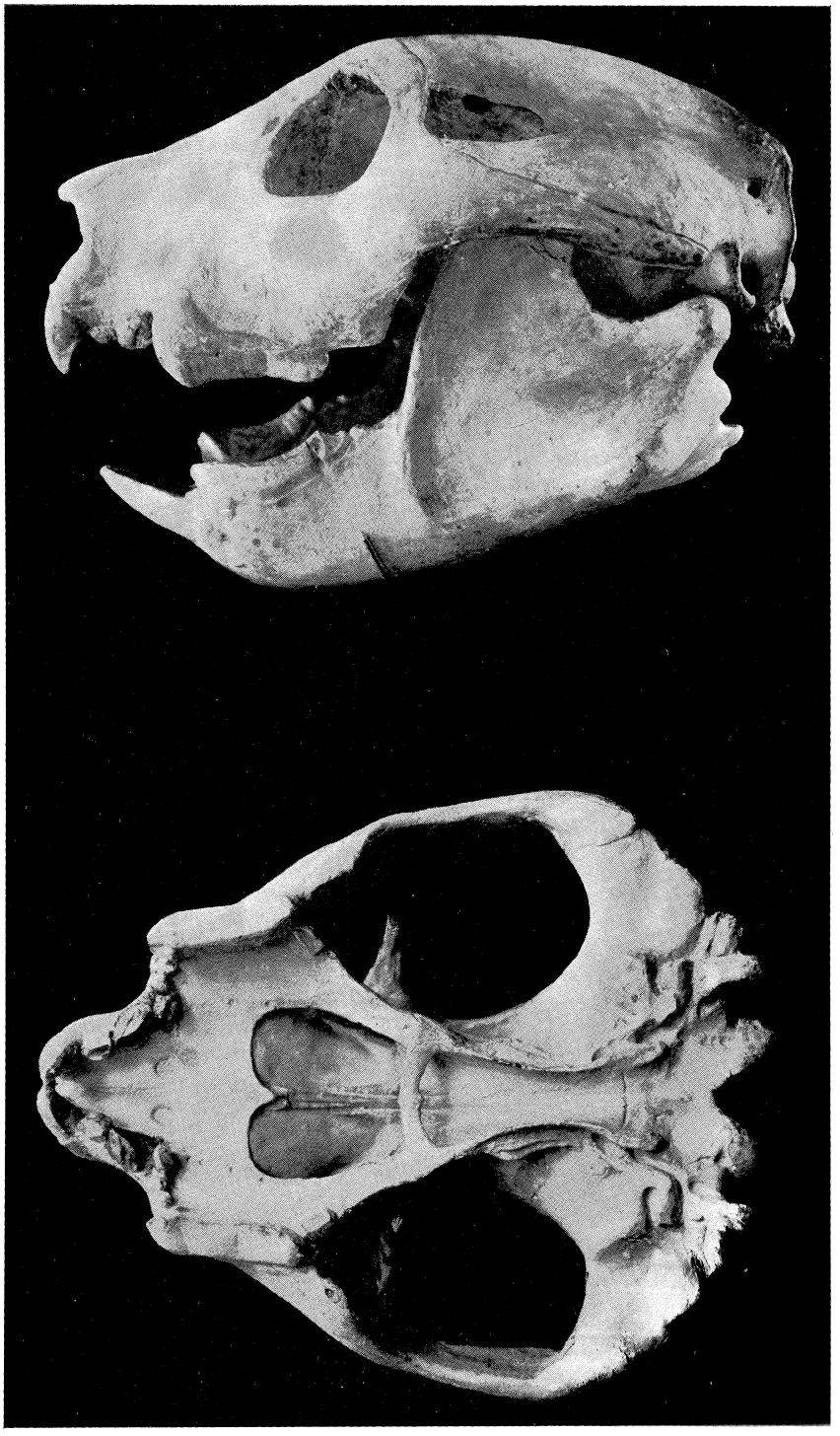
EXPLANATION OF PLATE XXIII.

Thylacoleo carnifex Owen. Skull and mandible, from a model by J. Kingsley.

Fig. 1. Side view of skull and mandible; in the photograph, the lower incisors appear slightly more procumbent than they are in reality.

Fig. 2. Palatal view. The posterior palatal vacuity is shown as undivided; the septum is not preserved in any of the specimens examined, but there is little doubt that an undamaged skull would show a narrow bar dividing the vacuity into right and left halves.

$\frac{3}{7}$ natural size approx.



G. C. Clutton, photo.