THE SKULL OF THYLACOLEO CARNIFEX.

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The early descriptions of the skull of *Thylacoleo carnifex* are contained in several papers by Owen (1859–1888). The feeding habits of this marsupial have continued to arouse the interest and imagination of palaeontologists, but apart from the remarks of Anderson (1929), little additional information on the morphology of the skull has been provided. No remains of the post-cranial skeleton are known; several specimens have been attributed to *Thylacoleo*, but their association is uncertain. A bibliography of the genus has been provided by Gill (1954).

Most of the specimens referred to *Thylacoleo*, in the collections of the Queensland Museum, have been obtained from the late Cainozoic fluviatile deposits of the Darling Downs, south-east Queensland. The majority were collected by K. Broadbent and H. Hurst, collectors on the staff of the Museum, in the decade beginning 1885. A few specimens from the cave deposits of Marmor, mid-east Queensland, and Gore, south-east Queensland, also are present. The old collections are poorly documented and it is regrettable that they have not always received the attention they deserve. However, with modern treatment, they constitute a very useful collection for morphological study, and here serve as a basis for a detailed description of the skull.

The type of *T. carnifex*, which is in the collections of the Museum of the Royal College of Surgeons, London, came from the Pleistocene lacustrine deposits of Lake Colongulac, Victoria. It is apparent, from a careful check of the material from the Darling Downs with Owen's description and figures (1859), that, with the possible exception of specimens from the Chinchilla district, they are conspecific.

The use of dilute acetic acid has been found to facilitate preparation of material for this study. The soils of the Darling Downs are usually calcareous, and fossils from beds associated with them often carry strongly adherent calcareous nodular material, which is difficult to remove mechanically.

Following the removal of matrix from the undistorted cerebral cavity of one specimen, an endocranial cast in agar was prepared. The cast was removed by opening the skull along an adventitious equatorial fracture and from it a master mould in plaster was made. From this mould, casts in latex were prepared for study, and in order to minimize shrinkage, these were supported internally by a thin shell of plaster before vulcanization.

All measurements are in millimetres.

MATERIAL AND DESCRIPTION.

The description is based on the following specimens :—F. 744, nearly complete cranium with I^1, C—P^3, Pilton, Darling Downs ; artificial endocranial casts from F. 744 ; F. 754, anterior part of cranium with C, P^3—M^1, Pilton, Darling Downs ; F. 2927, right mandibular ramus with I, P_3—M_1, lacking the coronoid process, believed to belong to same individual as preceding ; F. 767, ventral part of cranium with P^2—M^1, Pilton, Darling Downs ; F. 2930, incomplete premaxillae and maxilla with I^{1-2}, C—P^3, Clifton, Darling Downs ; F. 745, nearly complete left mandibular ramus with I_1, P_3, Spring Creek, Darling Downs ; F. 2929, right mandibular fragment with P_3—M_2, aged, Gowrie, Darling Downs ; F. 2491, left mandibular fragment with I_1, P_3—M_1, juvenile, near Dalby, Darling Downs ; F. 2928, right mandibular fragment with P_3—M_1, Gowrie Creek, Darling Downs ; F. 748, left mandibular ramus with I_1, P_3—M_1, young, lacking condyle and coronoid process, locality unknown.

CRANIUM.

Measurements.

Specimen.	Length Prosthion-basion.	Width.	Length of tooth-row at alveolar margin.	Length of P^3 at alveolar margin.	Palatal width between anterior cusps of P^3.	Angle of wear of P^3 with horizontal.
F. 744	220	198	98·2	51·5	71·2	63° ; 67°
F. 754	..	196	100·7	53·8	70·9	63° ; 65°
F. 767	206	186	94·0	49·8	68·0	59° ; 64°

Broad, sub-triangular in ventral view, with rostrum, anterior to P^3, markedly concave laterally; dorsal longitudinal profile asymmetrically convex, descending gradually anteriorly from highest point on coronal suture to slightly concave rostrum.

Nasals produced to an apex anteriorly, contracted in middle, widest posteriorly above orbit ; naso-frontal suture angular, with median wedge of frontals separating nasals posteriorly ; inferior surface of nasals deeply excavated to form dorsal meatus.

Premaxillae short, high, arcuate in profile ; each separated from frontal by prominent dorsal tongue of maxilla ; antero-ventrally much thickened for incisor roots ; premaxillo-maxillar suture oblique, premaxilla expanded internally ; mesial surface crossed by longitudinal ridge, separating lateral from ventral meatus, and carrying groove for naso-lachrymal duct traceable to lachrymal foramen ; ridge extending posteriorly on to maxilla and presumably serving for attachment of maxillo-turbinal. Bar of premaxillae separating elongate oval anterior palatine foramina, intertonguing between maxillae and vomer.

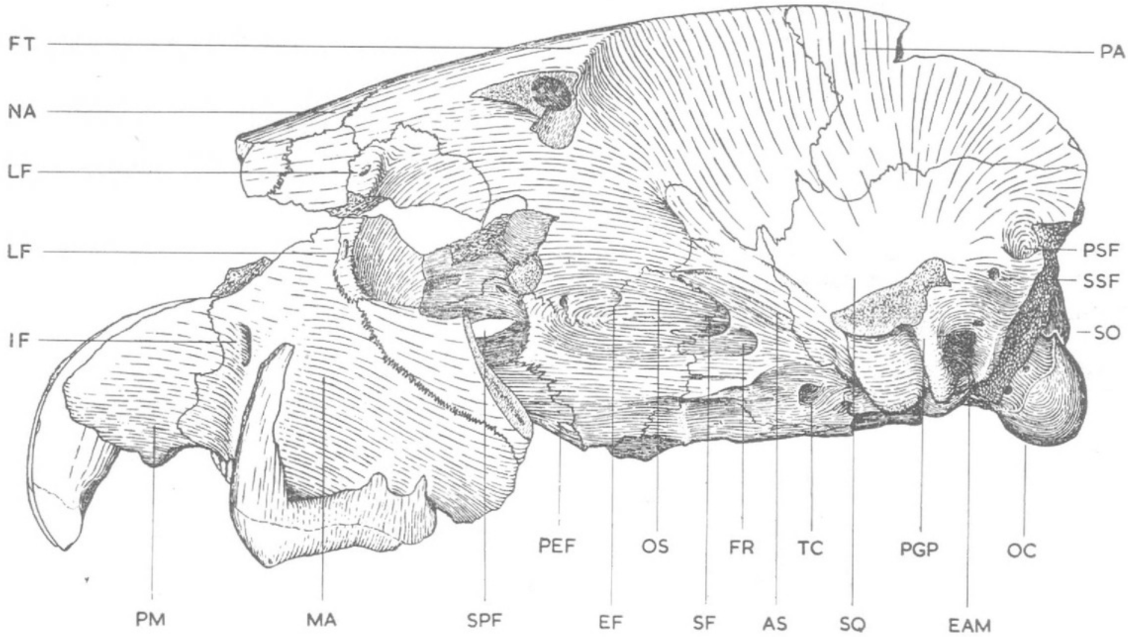


Figure 1.—*Thylacoleo carnifex* Owen. Lateral view of cranium, F. 744 (Q.M.) ; half natural size.

AS, alisphenoid
EAM, external auditory meatus
EF, ethmoid foramen
FR, foramen rotundum
FT, frontal
IF, infraorbital foramen
LF, lachrymal foramen
MA, maxilla
NA, nasal
OC, occipital condyle
OS, orbitosphenoid
PA, parietal
PEF, postero-external palatine foramen
PGP, postglenoid process of squamosal
PM, premaxilla
PSF, postsquamosal foramen
SF, sphenoptic foramen
SO, supraoccipital
SPF, sphenopalatine foramen
SQ, squamosal
SSF, subsquamosal foramen
TC, transverse canal

Maxillae short, each with the infraorbital foramen opening dorsal to anterior of P^3 ; convex over anterior root of this tooth; alveolar walls thinning, roots becoming exposed with age, with simultaneous development of an inter-rootial depression. Maxilla posteriorly forming anterior margin of temporal fossa ; postero-laterally curving to unite with jugal ; postero-mesially bounding portion of sphenopalatine foramen, extending below palatine to intersect transversely directed postero-external palatine foramen, and bounding large confluent posterior palatine vacuities laterally ; postero-dorsally flooring orbit and pierced by opening of infra-orbital canal ; relationship between maxilla and palatine above sphenopalatine foramen not observable. Maxilla much thickened above P^3, space between roots occupied by large pneumatic sinus extending posteriorly into zygomatic process. Antero-mesially, maxillae form high wide arch between third premolars.

Lachrymals, each forming narrow strip anterior to margin of orbit , with two foramina, the dorsal immediately ventral to boss close to fronto-lachrymal suture ; expanded to form much of mesial wall of orbit.

Frontals large, fused in adult ; anteriorly broad ; each with tapering ventro-lateral process abutting on post-orbital process of jugal to form post-orbital bar ; postero-dorsally narrowing, forming projecting tongue into parietals ; dorsally flattened and postero-laterally perpendicular to mesial walls of temporal fossae ; temporal line slightly rugose, extending from posterior of post-orbital bar on to parietal. Lateral wall of frontal extensive ; sutures with orbitosphenoid and palatine indistinct. Ethmoid foramen small, close to fronto-orbitosphenoid suture, posterior to small posteriorly directed foramen, near fronto-palatine suture ; canal leading from this latter foramen, with exit on palatine in nasal cavity. Frontals anteriorly roofing olfactory chamber containing ethmo-turbinal complex attached to cribriform plate anteriorly and antero-dorsally ; posteriorly excavated for pneumatic sinus system, extending posteriorly above cerebral cavity into parietals, antero-laterally into roots of post-orbital process.

Palatines, each ventrally restricted to short, vertically compressed process posterior to palatal vacuities (sufficient of these structures is preserved to indicate their union as a transverse bar) ; antero-laterally forming postero-ventral and posterior margin of sphenopalatine foramen ; postero-laterally with strong longitudinal ridge continuing on alisphenoid. Internally, palatines forming high arch over part of narial passage ; anteriorly supporting vomer ; posteriorly separated by narrow wedge of presphenoid.

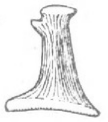
Vomer narrow, with two longitudinal grooves, lateral anteriorly, converging and becoming ventral posteriorly ; median ridge enveloping narrow anterior projection of presphenoid. Vomer laterally channelled in advance of foramen on wall of palatine in nasal cavity ; dorsally with median groove for mesethmoid.

Presphenoid dorsally fused with mesethmoid, laterally with orbitosphenoids. Orbitosphenoids small, bordering sphenoptic foramina mesially ; latter confluent through low slit.

Pterygoids each anteriorly slender, posteriorly thickened ; ventral margin posteriorly with shallow groove ; hamulae absent.

Basisphenoid fused with basioccipital. Alisphenoid wings small, relative to expanded frontal and squamosal ; each laterally with radiating ridges presumably for muscle attachment ; ventrolaterally with rugose concave area ventral to posterior continuation of prominent longitudinal ridge on palatine ; rugosity extending on to lateral wall of pterygoid. Foramen rotundum prominent, immediately postero-ventral to sphenoptic foramen. Transverse canal opening at points collinear with these foramina, but near ventral margin ; tunnelling basisphenoid and communicating with channel for maxillary nerve within cerebral cavity. Foramen ovale with tubercle at antero-lateral margin ; almost wholly within squamosal ; lipped by squamoso-alisphenoid suture. Alisphenoid postero-ventrally restricted to narrow tongue, mesial to squamosal, terminating at slit flanking petrosal in roof of eustachian canal ; no alisphenoidal bullae. Entocarotid foramen opening antero-mesiad at anterior end of canal.

Parietals fused, restricted dorsally, with temporal lines in adults converging posteriorly to form short, low sagittal crest ; concave laterally ; bounded posteriorly by sharper lambdoidal crests, extending over supraoccipital region, uniting with sagittal in smooth curves. Lambdoidal suture obliterated ; interparietal not recognised.



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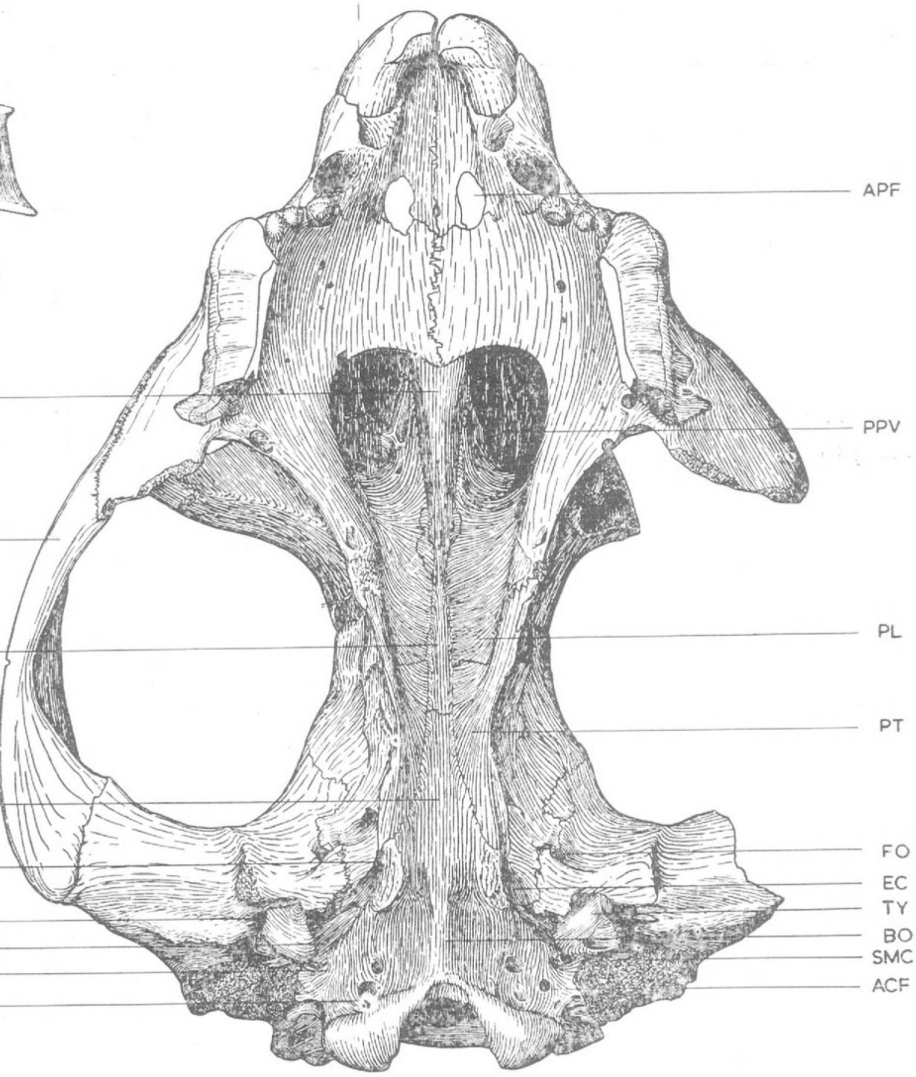

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Figure 2.—*Thylacoleo carnifex* Owen. Lateral view of stapes, F. 767 (Q.M.) ; x 5.

Figure 3.—*Thylacoleo carnifex* Owen. Ventral view of cranium, F. 744 (Q.M.) ; half natural size.

ACF, accessory condylar foramen
APF, anterior palatine foramen
BO, basioccipital
BS, basisphenoid
CF, condylar foramen
EC, eustachian canal
ECF, entocarotid foramen
FO, foramen ovale
JF, jugular foramen
JU, jugal
PE, petrosal
PGF, postglenoid foramen
PL, palatine
PPV, posterior palatal vacuity
PS, presphenoid
PT, pterygoid
SMC, stylomastoid canal
TY, tympanic
VO, vomer

Squamosals strong, expanded mesially, with subsquamosal and postsquamosal foramina variably developed, sometimes confluent. Zygomatic limb of squamosal broad and rather flattened above glenoid fossa ; becoming higher and narrower laterally, above jugal. Glenoid fossa transverse, wide and deep ; bearing surface slightly convex downwards, almost transverse ; laterally bounded by bulbous postero-ventral termination of jugal ; mesially by part of pretympanic expansion of squamosal ; posteriorly by groove, anterior, for mesial two-thirds of its course, to prominent postglenoid process. Postero-mesial margin of fossa interrupted by groove, continuing on posterior or low bullate pretympanic expansion of squamosal, forming postglenoid foramen with antero-lateral margin of tympanic. External auditory meatus deep ; bounded posteriorly by mastoid and post tympanic process of squamosal ; open dorsally to extensive sinus system in squamosal root.

Jugals, each postero-ventrally broad at union with squamosal ; anteriorly narrow and slightly longitudinally curved on lateral flank of very large temporal fossa ; antero-dorsally contributing to post-orbital bar and forming postero-ventral margin of orbit.

Tympanics relatively small, each completely exposed ventrally, not extensively united with surrounding elements ; arching below external meatus ; posteriorly perforated by groove or foramen directed dorso-mesiad.

Mastoids, each posteriorly forming oblique rugose strip on occiput, terminating dorsally at small mastoid foramen ; mesial to flange of squamosal forming ventro-lateral portion of lambdoidal crest ; anteriorly restricted in the meatus. Petrosals, each visible in contact with basioccipital in ventral view ; with fenestra rotunda at postero-lateral margin and fenestra ovalis slightly dorsal to it ; exit for facial nerve at antero-lateral margin, opening to canal passing posteriorly, dividing to form stylomastoid canal crossing mastoid and squamosal obliquely to emerge on postero-lateral margin of meatus ; with other branch crossing exoccipital ventrally, confluent with jugular foramen. Stapes columelliform, with small lateral spur immediately below head ; crura fused, bearing median groove, and thickened at attachment of slightly concave base.

Basioccipital fused with exoccipitals ; ventrally with median ridge separating two depressions, each flanked antero-laterally with rugose projection.

Exoccipitals ventrally with condylar and accessory foramina asymmetrically distributed between condyles and prominent jugular foramina ; posteriorly with venous foramina irregular distributed dorso-lateral to condyles. Condyles heavy, well rounded, separated ventrally by deep median embayment ; foramen magnum flattened oval in posterior view. Paroccipital processes incomplete in all specimens studied ; postero-ventrally directed.

Supraoccipital fused with exoccipitals ; concave with a low median vertical ridge separating two foramina ; overhung by lambdoidal crest dorso-laterally. Occipital region as a whole nearly twice as broad as high.

Endocranial Region.

Maximum dimensions of artificial endocranial cast : length, 97 ; width, 66 ; height, 46 ; volume, 131 cc.

Cast with slight axial flexure, rather compressed vertically, elongate hexagonal is dorsal view, widest across middle of hemispheres, tapering only slightly posteriorly to cerebellum. Olfactory bulbs, not markedly divergent at mid-line, high and wide, with cribriform plate, on the whole, beyond vertical; olfactory peduncle short, covered dorsally by truncated frontal poles of hemispheres. Rhinal fissures distinct only posteriorly, pyriform lobes restricted in ventral view by ventro-lateral spread of hemispheres. Hemispheres relatively extensive, moderately convoluted; dorsally with sulci as recognised by Elliot Smith (1902, p. 198); ventro-laterally with prominent, oblique sulcus (sulcus F in Elliot Smith's terminology, and possibly equivalent to postsylvian sulcus of other orders). Hemispheres separated dorso-medianly by prominent impression of superior sagittal sinus; postero-laterally in contact with cerebellum; tentorial ridge feebly impressed, cut by prominent transverse sinus, continued by low antero-mesial ridge of petrosal. Cerebellum short, medianly with high, narrow vermis; laterally broad behind postero-lateral lobes of hemispheres; floccular projection variably developed; pons with slight elevation.

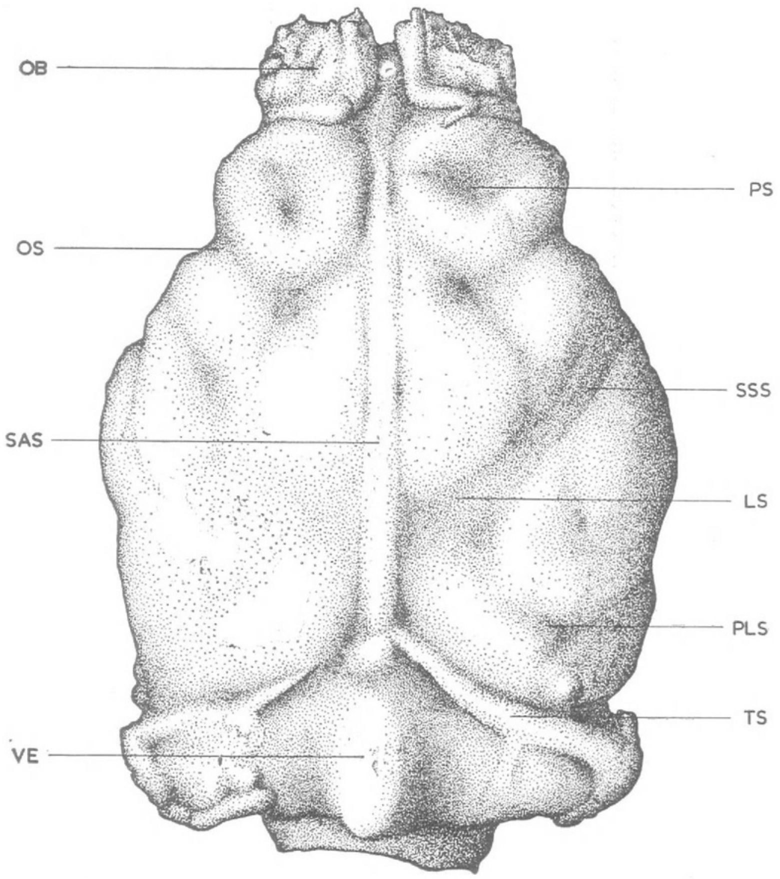
Cribriform plate well preforated for olfactory nerves. Olfactory lobes ventrally with impression of vessel traceable through canal to ethmoid foramen. Sella turcica shallow, posterior to exit of confluent optic, oculomotor, trochlear, ophthalmic and abducens; antero-medianly with small hypophysial fossa; laterally perforated for entrance of entocarotid artery, mesial to gasserian fossa. Gasserian fossa communicating posteriorly with slit in roof of eustachian canal as well as foramen ovale; flanked mesiad by groove, presumably for inferior petrosal sinus, terminating posteriorly at jugular foramen, communicating with entocarotid canal in one specimen. Internal auditory meatus piercing petrosal near antero-mesial margin. Short lateral groove, for glosso-pharyngeal, vagus and spinal accessory, passing below petrosal to jugular foramen. Internal condylar foramen for hypoglossal slightly postero-ventral to this, communicating with jugular foramen and condylar foramina. Transverse sinus passing ventrally, posterior to petrosal, emerging at jugular foramen.

MANDIBLE.

Measurements.

Specimen.	Depth of ramus posterior to P_3.	Length of crown of P_3.	Length of crown of M_1.	Angle between ramus and symphysial plane.	Angle between I_1 and base of mandible.
F. 745	50	40·7	..	30°	51°
F. 2927	44	..	13·7	28°	48°
F. 2929	44 (incomplete)	39·3	13·2 (worn)	..	..
F. 748	37	35·3	11·9	30°	48°
F. 2928	44	39·2	13·8	..	..

Rami strong, deep, diverging posteriorly at approximately 60°; longitudinal axes slightly convex laterally; symphysis not fused; symphysial plane short, sub-triangular, somewhat upturned; fossae subalveolaris deep, confluent; mental foramen prominent, ventral to anterior margin of P_3, and dorsal to junction of anterior margin and inferior surface of ramus at blunt angle; lateral alveolar walls of P_3 thinning, roots becoming exposed with age, with simultaneous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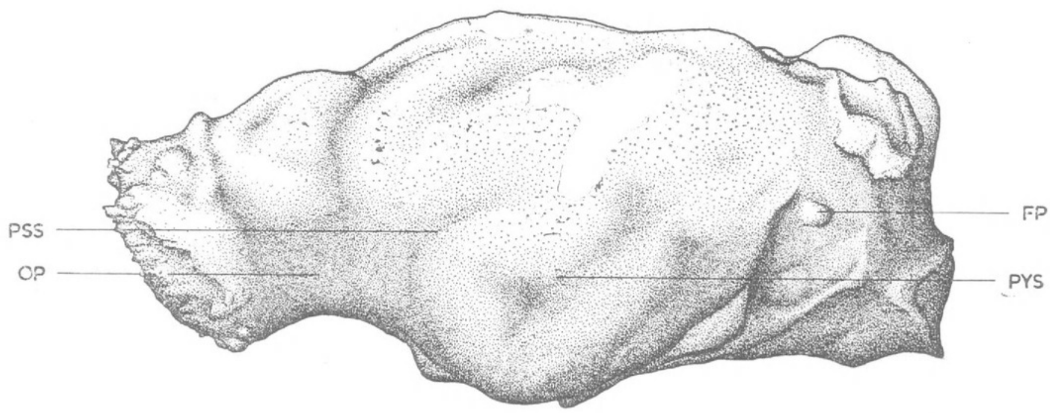
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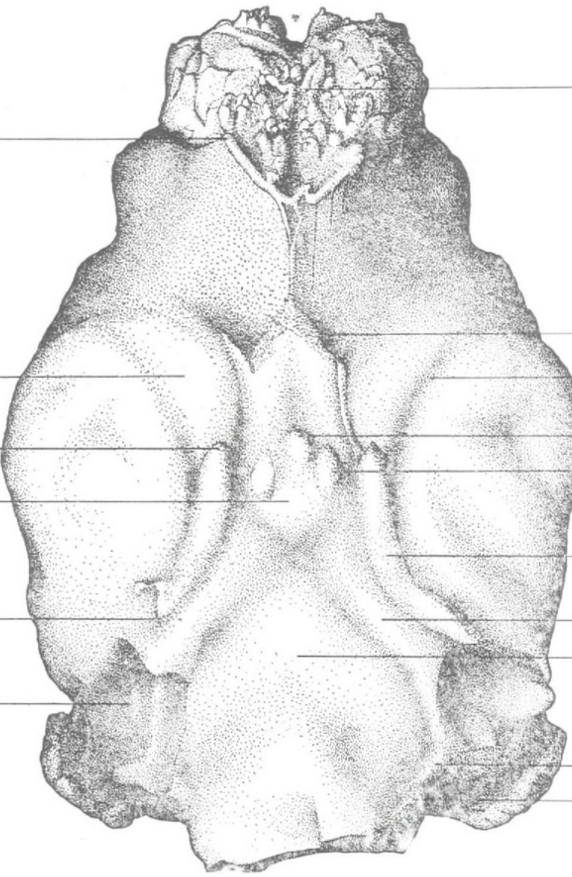

Figure 4.—*Thylacoleo carnifex* Owen. Dorsal, lateral, and ventral views of endocranial cast prepared from F. 744 (Q.M.); natural size.

EA, entocarotid artery
FP, floccular projection
GF, gasserian fossa
HF, hypophysial fossa
I–XII, cranial nerves
IPS, inferior petrosal sinus
LS, lateral sulcus
OB, olfactory bulb
OP, olfactory peduncle
OS, orbital sulcus
PL, pyriform lobe
PLS, postlateral sulcus
PO, pons
PS, prorean sulcus
PSS, pseudosylvian sulcus
PYS, postsylvian sulcus
RF, rhinal fissure
SAS, superior sagittal sinus
SSS, suprasylvian sulcus
ST, sella turcica
TS, transverse sinus
VE, vermis
VEF, vessel passing to ethmoid foramen

development of inter-rootial depression. Ramus ascending at low angle posterior to smooth, feebly developed diagastric process, ventral to M_2 ; post-alveolar ridge not prominent, ascending gradually, disappearing on mesial wall of large coronoid process. Process diverging from line of ramus, directed antero-posteriorly ; antero-dorsal margin ascending at about 45°, grooved, laterally flanged ; flange continuing ventrally on body to ramus, limiting large ectocoronoid fossa anteriorly. Wall of fossa with ridges ascending posteriorly ; ventrally perforated by two or three small masseteric foramina opening into inferior dental canal, close to mandibular foramen ; postero-ventrally limited by prominent angular process, posterior to which ramus rises steeply to condyle. Condyle broad, nearly transverse, low, without neck ; articulating surface postero-dorsally rounded ; mesially with a narrow anterior projection. Postero-mesial angle of ramus broadly inflected, thickened and rugose at margin ; pterygoid fossa very deep, produced laterally.

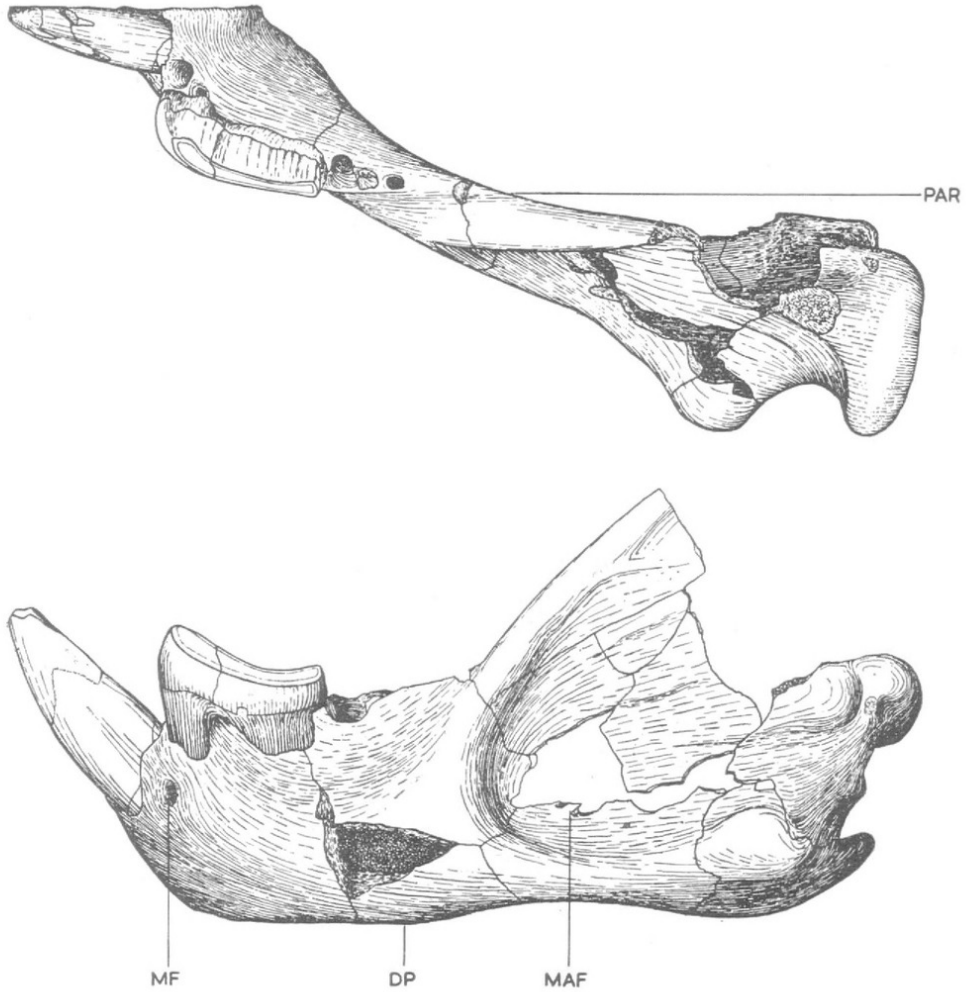

Figure 5.—*Thylacoleo carnifex* Owen. Occlusal and lateral views of left ramus, F. 745 (Q.M.) ; half natural size.

DP, diagastric process

MF, mental foramen

MAF, masseteric foramina

PAR, postalveolar process

DENTITION. $I\frac{3}{1}$, $C\frac{1}{0}$, $P\frac{3}{3}$, $M\frac{1}{2}$.

Median upper incisors large, strong, curved, laterally compressed, convergent, in contact distally, with mesial facet of wear on enamel ; crown sub-quadrantal in section, tapering distally, tips blunted by wear often involving fracturing ; posteriorly grooved by movement of I_1 ; enamel most extensive labially, postero-laterally produced to low flange ; roots open, compressed oval in section. Second incisor small, directed antero-mesiad, with lingual facet of wear. Third incisor larger, incomplete in specimens examined ; alveolus postero-lateral to that of I^2. Canine small, posterior to I^3 ; crown tapering, obliquely compressed, labially convex, lingually flattened, not descending to level of I^2 ; not functional, but occasionally damaged. First and second premolars smaller than C, set almost transversely between C and P^3 ; crowns ovate, blunt, not functional, often lost during life. Third premolars exceedingly large, sectorial, subparallel, with axes slightly convergent anteriorly ; deeply rooted ; anterior root longer, convex laterally ; posterior root directed ventro-mesiad, so crown moves in this direction during growth. Crown vertically ridged ; enamel thickened to flange on anterior edge ; widest below anterior root ; trenchant, asymmetric, with longitudinally concave labial face at much lower angle with horizontal than lingual ; main surface of wear near planar, developed dorso-mesial to cutting edge by shearing with P_3 and M_1 ; making angle of approximately 60° with horizontal, decreasing in aged individuals ; direction of movement indicated by slightly oblique surface scoring, paralleling posterior ridge due to passage of junction of P_3 and M_1 ; enamel also removed lingually at margin of crown by contact with labial side of P_3 at ultimate occlusion. Molar series reduced to M^1 ; small, set obliquely, postero-mesial to P^3 ; trapeziform in outline ; paracone predominant ; metacone reduced ; lingually low, with fine anastomosing ridges ; functional as stop for M_1, with facet of wear developing on antero-mesial surface ; tri-rooted with larger roots implanted above cusps ; other smaller, variably developed, set slightly antero-mesial to axis of tooth.

Median lower incisors similar to upper, but more compressed, less curved, making an angle of approximately 50° with base of mandible ; converging at much lower angle, approximated at tips, with development of mesial facet of wear ; tip passing posteriorly to I^1, blunted by wear, but not commonly fractured ; dorso-lateral flange of enamel worn by indirect attrition with I^2 and I^3. First and second premolars not retained in any specimen examined ; alveoli small, shallow, mesiad to anterior root of P_3. Third premolar shorter than P^3, sectorial, deeply rooted ; roots directed somewhat dorso-laterally, so crown moves in this direction during growth ; crown with enamel vertically ridged especially on lingual surface, thickened to flange on anterior edge ; asymmetric, with longitudinally convex labial face set at much higher angle with horizontal than lingual ; main surface of wear near planar, developed ventro-lateral to cutting edge by shearing with P^3 ; enamel also removed labially, at margin of crown, by contact with lingual side of P^3 at ultimate occlusion. Molar series reduced ; M_1 small, subtriangular, anteriorly with metaconid high, flanged, with short longitudinal cutting edge in functional continuity with that of P_3 ; posteriorly reduced, medianly with narrow, finely ridged area ; developing facet of wear in continuation with that of P_3, and another directed postero-laterally due to movement against M^1 ; bi-rooted, anterior larger. Second molar very small, functionless, single rooted, often lost during life.

No deciduous teeth are present in any specimen.

DISCUSSION.

The reduced state of the molar series is a unique feature of this phalangeroid marsupial. Of the premolars, the third is exceedingly large, while the others are small, functionless, and telescoped in the tooth row. These dental characters may be correlated with the relatively short rostrum, which together with the width of the temporal fossae imparts to the skull a broad subtriangular outline resembling those of some of the larger aeluroid carnivores.

The upper median and lower incisors form two laniariform structures, which, while formidable, lack the efficiency of the large canines of dasyuroid marsupial and eutherian carnivores. Anderson (1929, p. 45) has described the upper median incisors as blunt tusks, but examination of his figure of the young individual (pl. 19) does not support his statement. The tips of the lower incisors were fractured less commonly than those of the upper median incisors ; they passed behind the former in occlusion, and were attached to a less rigid structure. Anderson has claimed that the incisors meet at an angle approaching 90°, but as shown in the restored profile (fig. 6), the curved axes meets at a much greater angle. Krefft (1872, p. 181) recognised the median facet of wear at the tips of the lower incisors and concluded that the rami were loosely attached. However, the occurrence of a similar facet between the upper median incisors nullifies argument based on this observation.

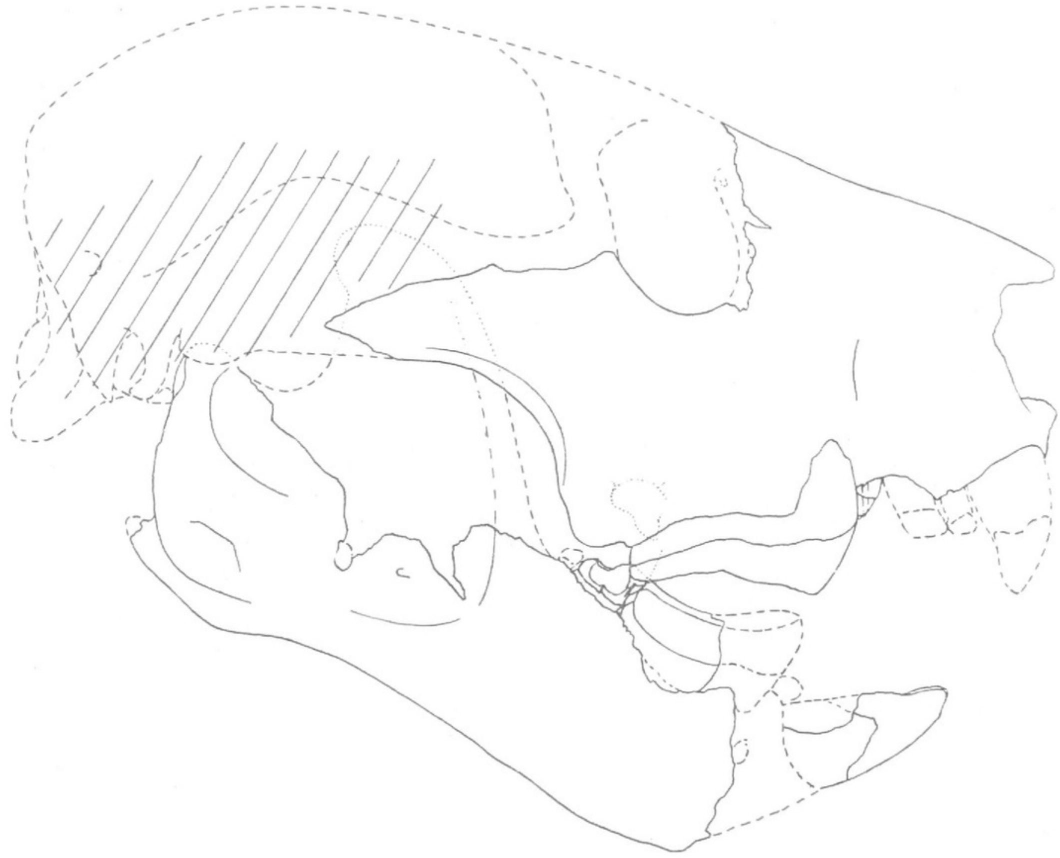

Figure 6.—*Thylacoleo carnifex* Owen. Restored profile of skull, based on F. 754 (Q.M.) and F. 2927 (Q.M.), with the area of the cerebral cavity cross-hatched ; half natural size.

Much has been written about the third premolars, but evidence of the relative motion of the teeth, afforded by the surfaces of wear, has not been examined. The slightly oblique posterior ridge on the upper tooth was made by the junction of the lower third premolar and first molar by upward and slightly forward movement in the arc of closure of the mandible. The development of this structure and the parallel scoring on the facets of wear on the teeth shows that they were opposed in a shearing movement and, contrary to the suggestion of Anderson (p. 43), there could have been no propalinal or rotational motion of the mandible. The upper third premolar is opposed to the lower third premolar and first molar, and they resemble the upper and lower carnassials of some of the eutherian carnivores. This structural convergence is continued in the disposition of the upper first molar, which functions as a stop for for its lower homologue and prevents propalinal motion.

In measuring the attitudes of the facets of wear on upper premolars, it is impossible to obtain comparable results unless sufficient of the skull is preserved to assure uniform orientation. For similar measurements involving lower premolars, the mandibular remains must be oriented in the position of occlusion. Results suggest that an angle of approximately 60° with the horizontal was maintained during much of adult life, before it decreased in aged individuals. Teeth opposed during life wore at the same angle. Gill (1954, p. 20) makes a statement to the contrary but his remarks are based on an upper left tooth opposed to a right lower tooth reversed (pl. 4).

Growth of the oblique roots of these premolars had the effect of moving the cutting edge of the upper premolar ventro-mesiad and that of the lower premolar dorso-laterally. This balanced the effect of wear and tended to keep the cutting edges opposed vertically at the commencement of occlusion so that the bite involved an efficient shearing motion. Furthermore, the facets of wear formed by the mutual attrition of the teeth were kept at a moderately high angle and the resultant cutting edge was sharp. The progressive exposure of the roots of these teeth with age, and the simultaneous development of an inter-rootial fossa were due to the growth of roots and the closure of the alveolus between them, following the emergence of the crown.

Additional structural convergence with some of the aeluroid carnivores is exemplified in the disposition, relative to the temporal fossa, of the shearing teeth at occlusion. The longitudinal axes of the teeth tend to lie in the plane of the coronoid process which bisects the fossa, and the zygomatic arch anteriorly joins the skull in the region of implantation of the roots of the upper tooth. Shearing, therefore, is activated by a relatively efficient lever, and the skull is also locally strengthened to resist the confined reactionary stresses transmitted by the upper tooth.

An extensive area of attachment existed for the apparently powerful temporal muscle. The masseter muscle, with the exception of the superficial layer, was also well developed. The ventro-lateral groove on the jugal is reduced and the ventrally projecting boss of the maxilla, usually conspicuous in phalangeroid marsupials, is absent. The areas of attachment for the pterygoid muscle indicate that the medial pterygoid, especially, was well developed. No satisfactory explanation of this structure is proposed; clearly, there was no rotational movement of the mandible, but the fact that the lower sectorial teeth lie mesiad to the upper teeth at ultimate occlusion indicates that there was a component of movement in this direction. It is possible that the pterygoid muscle balanced the action of the masseter in the control of this movement. In the temporomandibular joint, mesial movement of the condyle was limited by the wall of the fossa which otherwise reflects the phalangeroid affinities of the genus, and among living forms, resembles most closely that of *Phascolarctos*. The significance of the structure of the condyle was discussed by Owen (1888, p. 2).

As in *Phascolarctos*, the tympanics are small, not transversely elongated and not united extensively with the surrounding elements to form the floor of much of the meatus. Instead of the bullate pretympanic expansion of the alisphenoid, there is a rather similar structure formed by the mesial extension of the squamosal. In this feature the resemblance exists with the Phascolomidae. Of the auditory ossicles, only the stapes is preserved and its simple fused columelliform structure recalls those of *Phascolarctos* and *Phascolomis* as figured by Doran (1879, pl. 64).

In his examination of endocranial casts from marsupials Gervais (1869, p. 236) made a generalized comparison between those of *T. carnifex* and *P. ursinus*. Elliot Smith (1902, p. 189) extended that comparison with a survey of the indications of dorsal sulci on the cast, but he does not mention the prominent impressions of the superior sagittal and transverse sinuses. These impressions, although less conspicuous, are also recognisable in skulls of Phascolomidae. They suggest that the tissues superficial to the brain were thin.

Owen (1871, p. 263) concluded some of his remarks on *Thylacoleo carnifex* with the statement that " a great proportion of the fair edifice of Palaeontology still rests upon a scaffolding of wise and well-founded conjecture." That the animal was carnivorous is still unproved, but on an analysis of the morphology I consider that this conjecture is well founded. Owen (1871, p. 246; 1888, p. 2) and Bensley (1903, p. 203) both recognised this example of the adaption of the diprotodont dentition for a carnivorous function. That the dental specialization would function efficiently in this way has been questioned by Anderson (p. 45) who pointed out the lack of a transverse incisor row for the stripping of flesh. This argument may be countered by reference to felines with large carnassial teeth which, as Owen (1871, p. 242) mentions, are applied to food when the mouth is turned sideways. Furthermore, he stresses the absence of a cingulum on the premolars and molars, but the inclination of the crowns of the teeth in question is such that any bone splinters would be readily diverted from the gums. It cannot be expected that the replica of structures of an eutherian carnivore will be observed in a phalangeroid marsupial, even if they involve functional similarity. Study of the post-cranial skeleton may help solve the problem of whether *Thylacoleo* sought live prey or was a carrion-feeder. Both types of food would have been readily available during the Pliocene and Pleistocene, and indeed, the marsupial fauna would have been markedly unbalanced if the large herbivorous diprotodontids sustained carnivores no larger than *Thylacinus*. If *Thylacoleo* is included with the carnivores, it does not appear likely that it would be reduced to chewing the bones left by more active predators. Every carnivore encounters some bone in its diet, and the evidence of occasional damage to the functionless canine and anterior premolars of *Thylacoleo*, suggests that hard and irregular objects passed beneath its palate.

Nothing is known of the phylogeny of *Thylacoleo carnifex*. Described specimens are believed to be of Pleistocene age and in view of the specialization of many features of the species, inferences based on comparisons with other Quaternary marsupials must be generalized if they are not to be erroneous.

A NOTE ON FRAGMENTARY REMAINS OF *THYLACOLEO* FROM THE CHINCHILLA FORMATION.

The Chinchllla Formation of the north-western Darling Downs, differs lithologically and palaeontologically from the superficial fluviatile deposits of the south-eastern Downs, and appears to be older, possibly of Pliocene age. Fossil remains are usually harder and more mineralized than material preserved in the beds to the south-east. Bone is usually lustrous, but occassionally exhibits limonitic staining. The stratigraphic distinction of the beds was discussed with Dr. R. A. Stirton, of the University of California, during his recent visits to Australia, and he, too, was impressed with the differences noted.

In maxillary fossils, no difference is apparent in the third premolar, and the preservation of the material does not allow any comparative series of measurements to be made. Two specimens display the first molar more distinctly tri-rooted and the base of the crown wider than in the later forms.

Mandibular remains differ in that the longitudinal concavity of the mesial side of the ramus is less pronounced and the ramus is wider in the region of implantation of the first molar. The third premolar is only well preserved in two individuals, and they indicate that this tooth is relatively broader posteriorly and displays a stronger longitudinal convexity on the labial side. The posterior root of the first molar is wider, and in two specimens which are without data but have the characteristic preservation of the Chinchilla fauna, the posterior part of the crown of the tooth is comparable with the size of the root and exhibits a much wider median ridged area. The second molar is rarely preserved. It is variable in development, but appears to be stronger and the alveolus is partially divided by a vertical ridge on the lateral wall. In a large specimen, there is a depression immediately posterior to the relatively large second molar. This is interpreted as the alveolus of a very small third molar.

It appears that the thylacolean population of the Chinchilla Formation, while showing considerable variability in its dental characters, differs from typical representatives of *T. carnifex* in that the molar series is less reduced both in size and numbers. This is precisely what would be expected after considering the suggested time relationship of the faunas, and a specific distinction may have to be recognised.

LITERATURE CITED.

Anderson, C., 1929. Rec. Aust. Mus., 17, pp. 35–49, pls. 17–23.

Bensley, B. A., 1903. Trans. Linn. Soc. Lond. (Zool.), ser. 2, 9, pp. 83–217, pls. 5–7.

Doran, A. H. G., 1879. Trans. Linn. Soc. Lond. (Zool.), ser. 2, 1, pp. 371–497, pls. 58–64.

Elliot Smith, G., 1902. Catalogue of the Museum of the Royal College of Surgeons. Physiological Series 2, pp. 1–518.

Gervais, P., 1869. Nouv. Arch. Mus. Hist. Nat., Paris, 5, pp. 229–251, pls. 13–14.

Gill, E. D., 1954. Vict. Nat., 71, pp. 18–35, pls. 1–12.

Krefft, G., 1872. Ann. Mag. Nat. Hist., ser. 4, 10, pp. 169–182, pls. 11–12.

Owen, R., 1859. Phil. Trans., 149, pp. 309–322, pls. 11–15.

——— 1871. Phil. Trans., 161, pp. 213–266, pls. 11–14.

——— 1888. Phil. Trans., 178, B, pp. 1–4, pl. 1.