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PEDAL MORPHOLOGY OF THE MARSUPIAL LION *THYLACOLEO CARNIFEX* (DIPROTODONTIA: THYLACOLEONIDAE) FROM THE PLEISTOCENE OF AUSTRALIA

RODERICK T. WELLS,[*,1,2] PETER F. MURRAY,[3] and STEVEN J. BOURNE[4]; [1]School of Biological Sciences, Flinders University GPO Box 2100 Adelaide South Australia 5001, Australia; [2]Palaeontology, South Australian Museum, North Terrace, Adelaide 5000 South Australia, Australia, Rod.Wells@flinders.edu.au; [3]Museum of Central Australia, Larapinta Drive, Alice Springs, Northern Territory 0871, Australia, Peter.Murray@nt.gov.au; [4]Dept. for Environment and Heritage, Naracoorte Caves, Naracoorte, South Australia 5271, Australia, Bourne.Steven@saugov.sa.gov.au.

INTRODUCTION

Thylacoleo carnifex, the so-called marsupial lion, is arguably the most enigmatic of all Australia's extinct marsupials. It was the last and most derived member of an entire family of extinct marsupials that included the small Oligo-Miocene form *Priscileo* and the Oligo-Miocene dog-sized species of *Wakaleo*. Dog to lioness-size Plio-Pleistocene species of *Thylacoleo* were the largest and principal mammalian carnivores of the Australian late Cenozoic and among the most widely distributed of the so-called megafauna species. Clearly derived from a diprotodontian ancestry, species of *Thylacoleo* have evolved to hyper-carnivory through pronounced development of upper and lower third premolars as extreme carnassials with a concomitant reduction in the molar tooth row. Paralleling these changes has come a foreshortening and broadening of the palate along with frontation of the orbits to produce a skull architecture reminiscent of felids, no doubt giving rise to Owen's 'lion' analogy (Owen, 1871). Paradoxically they retain the diprotodontian incisor configuration to form an almost parrot-like beak while the upper canines persist as vestigial stumps within a very short diastema (Wells, Horton and Rogers, 1982).

Diprotodonty is the condition found in all herbivorous marsupials and deemed by many (Flower, 1868; Gregory 1951; Gill, 1954) an unsuitable substitute for interlocking canines used by carnivores in the capture and killing of prey. Wells and Nichol (1977) went some way to solving the question of prey capture with description of the manus and a partial pes of *T. carnifex*. Of particular significance was the large slashing/grasping unguis of the pollex. Wells, Horton and Rogers (1982) elaborated on the dentition, jaw mechanics and the role of the forearm in prey capture. On the basis of the hind limb structure and an incomplete pes they speculated on the climbing ability of *T. carnifex* and proposed a leopard-like niche for this species. They drew attention to the possum-like structure of the syndactylous pes and noted that Wells and Nichol (1977) had described a medial tuberosity on the navicular which suggested the presence of a divergent hallux reminiscent of climbing mammals. The leopard analogy has been challenged (Finch and Freedman 1988; Wroe et al., 1999) on the basis of the body weight estimates, the assumption being that at around 100–130 kg adult weight *T. carnifex* would have been too heavy to climb trees notwithstanding that bears of similar weight do and even gorillas at almost double the estimated weight build sleeping nests in trees.

The pes described by Wells and Nichol (1977) was incomplete, missing were the cuneiform bones of the distal row of the tarsus, the first metatarsal, all the phalanges and any associated sesamoids. Wells and Nichol (1977) noted a marked similarity in form and structure between the pes of *T. carnifex* and the Brush-tailed Possum, *Trichosurus vulpecula.*

Finch and Freedman (1986) carried out a comparative and functional analysis of the vertebral column in *T. carnifex* concluding that it was more lion-like (*Panthera*) in proportions than possum-like (*Trichosurus*). They drew attention to the high neck mobility as well as the robust nature of the sacrum implying powerful hind limbs. However the lumbar sagittal stress curve values turned out to be lower than expected and they concluded that the animal probably had a robust counterbalancing tail. Finch and Freedman (1988) furthered their studies with a functional morphological analysis of the limbs of *T. carnifex*. Among Australian marsupials the limb indices (proximal to distal ratios) were most similar to those of the Tasmanian Devil (*Sarcophilus harrisii*) and again the authors drew attention to similarities with the African lion (*P. leo*) concluding that *T. carnifex* was a "...slow medium cursor, possibly capable of leaping" with a scapula better adapted to walking and trotting rather than climbing. Further they noted that the small claws on digits II–V of the manus "...do not appear sufficiently powerful to support a weighty animal when ascending a tree" and that "...pedal morphology would provide very useful evidence" (Finch and Freedman, 1988:270).

Missing from all specimens used in these reconstructions have been complete hind feet and tail. In June 2005 quarrying activities at Henschke's Quarry, Naracoorte in south-eastern South Australia intercepted a hitherto unknown cave some 11 metres below the surface. Fragmented bone material was visible and the undisturbed section of the exposed cave was almost filled with sediment. The quarry owners, the Henschke brothers, immediately notified one of us, (SJB), and a 'rescue' operation was mounted. Over the next two years, all sediment and fossil material was removed and access gained to a further extension of the cave along the talus slope. The cave was mapped and registered as 5U240 Komatsu Cave with the Cave Exploration Group of South Australia. Partially exposed in the sediment cone were incomplete but articulated skeletal remains of a number of individuals of *T. carnifex* including an adult (?) female and young. The remains included complete hind feet and some caudal vertebrae.

In this article, we describe the hitherto-unknown pedal elements and provide a functional analysis based on comparison with extant ambulators, cursors, and scansors. The two components of this study are (1) the description and comparative morphology of the pes elements and (2) a functional inference based solely on measurement and a physical and mechanical analysis of arthroses. We have avoided making behavioural inferences that rely on higher-order neural processing and integration.

MATERIALS AND METHODS

The presence of articulated skeletal material required particular care in excavation. Soft powdery grey silt and sand was gently

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[*]Corresponding author.

brushed away from the specimens that were then photographed in situ. The exposed bone mass was soaked in a polyvinyl butyral (MOWITAL) solution in acetone and allowed to harden. This served to hold the articulated portions together as they were removed to the Naracoorte Caves on-site laboratory for careful cleaning and reassembly. Specimens include a number of partial skeletons of *T. carnifex* along with macropodine and sthenurine macropodids, vombatids, phalangeridans, peramelids and species of *Thylacinus, Dasyurus, Sarcophilus, Diprotodon, Zygomaturus, Megalibgwilia*; for a complete species list see Reed and Bourne (2009).

The complete hind feet of *T. carnifex* from the partial skeleton of a single individual were of particular interest. The skeleton from which the feet are described is registered with the South Australian Museum (**SAM**) palaeontology collection as P43220. The partial skeleton included all the bones of left and right pes with the exception of the distal phalange I of the hallux and some sesamoids, viz: talus (astragulus); calcaneus; cuboid; navicular; ento-, meso-, and ecto- cuneiforms; metatarsals I,II,III,IV, V; proximal, medial and distal phlanges II,III,IV,V; some phalangeal sesamoids. The right pes from a second individual was also recovered, this was near complete, lacking only the talus, entocuneiform and sesamoids and the distal phalange of the hallux. This specimen is registered as **SAM** P43221. Terminology is based on the Terminologia Anatomica 1998.

DESCRIPTION

Description and Comparison of the Pes

The assembled left pes with tibia and fibula attached is shown in Figure 1. The most salient features include a sub equal development of the robust fibula and tibia; a plantigrade stance; a narrow foot with long slender digits II–V each with recurved clawed distal phalanges, those of II & III being hooded; and a divergent hallux. The pes comprises the tarsus, metatarsus and phalanges. The most proximal element of the tarsus is the talus.

Talus (Astragalus)—The talus takes part in three joints. On its dorsal aspect is the 'supratalar joint' or ankle articulation with the tibia and fibula; on its ventral aspect the 'subtalar joint' is the articulation with the calcaneus; on its anterior aspect, the 'pretalar joint', is the articulation with the navicular. The supratalar surface is convex when viewed laterally (Fig. 2B, D). It is divided into three facets (Fig. 2A). The larger medial facet, facet medialis malleolus, is in the form of a shallow saddle-shaped groove, the trochlea tali, upon which articulates the distal end of the tibia. The trochlea is mildly wedge-shaped tapering posteriorly. A smaller facet medial to the trochlea, the facet medialis malleolus, articulates with the internal malleolus of the tibia providing stability to the ankle during flexion and extension. Lateral to the trochlear groove is the convex articulating facet, the facet lateralis malleolus, for the distal end of the fibula with a

FIGURE 1.   Dorsal view of distal fibula, tibia and assembled left pes of *Thylacoleo carnifex* from Komatsu Cave Naracoorte, South Australia, SAM P43220. Scale bar equals 5 cm.
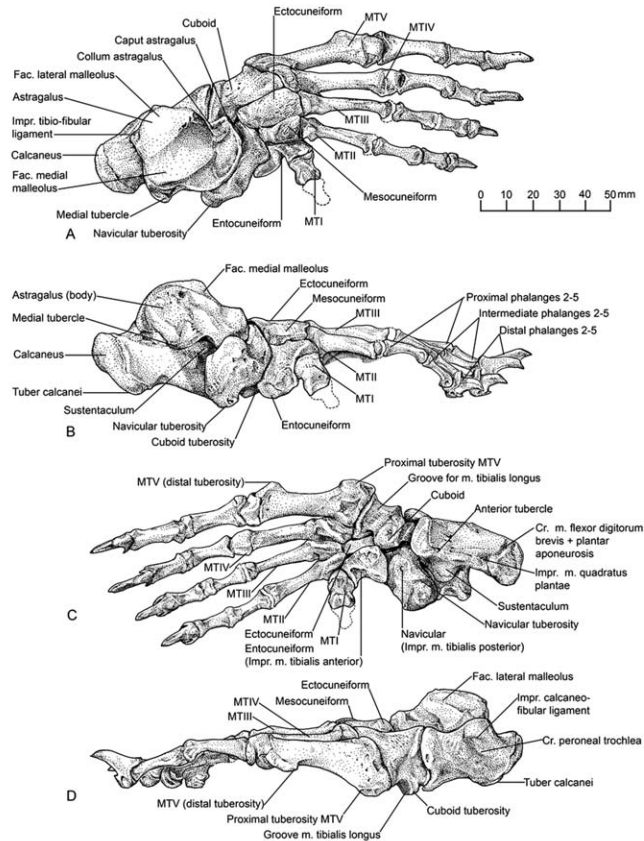

FIGURE 2.   Assembled left pes of *Thylacoleo carnifex*. **A** dorsal aspect, **B** medial aspect, **C** ventral aspect, **D** lateral aspect. **Abbreviations: Cr**. crista; **Fac**. facies; **Impr**. impression; **m**. musculi; **MT** metatarsal.

smaller facet for the external malleolus of the fibula. The fibula facets are subequal to the tibial facets reflecting the well developed fibula in *T. carnifex*. The ankle thus shares greatest structural similarity to that of fossorial wombats in contrast to the sagitally constrained ankle of terrestrial macropodoids (see Bishop, 1997). It differs from vombatids, *Lasiorhinus latifrons* and *Vombatus ursinus*, in that the trochlear groove is proportionally longer and more tapered indicative of a slightly more elevated heel in the resting position, similar to the condition in arboreal/terrestrial primates such as *Pan troglodytes* (Sondaar and Van der Greer, 2002). It differs from arboreal species such as *Trichosurus vulpecula* in that the medial trochlear ridge is less acute and the convex articulating surface less rounded. The structure of this ankle joint is such as to allow for limited flexion and extension as well as some inversion and eversion.

The subtalar joint with the calcaneus is divided into medial and lateral facets which when articulated with matching facets on the calcaneus, form a tunnel comprising the sulcus tali and the sulcus calcanei. The tunnel so formed serves for attachment of the strong interosseus ligaments (posterior synovial cavity of the ankle joint as shown in Fig. 3). The convex pretalar facet articulates almost exclusively with the concave posterior facet of the navicular although there is some overlap with the posterior medial face of the cuboid (Fig. 2A). Ventral and posterior to the trochlear and bounded by the medial tubercle lies a groove contiguous with the sustenaculum tali through which pass the tendons responsible for the downward flexion of the foot and toes, the sulci flexores digitorum (Fig. 3).
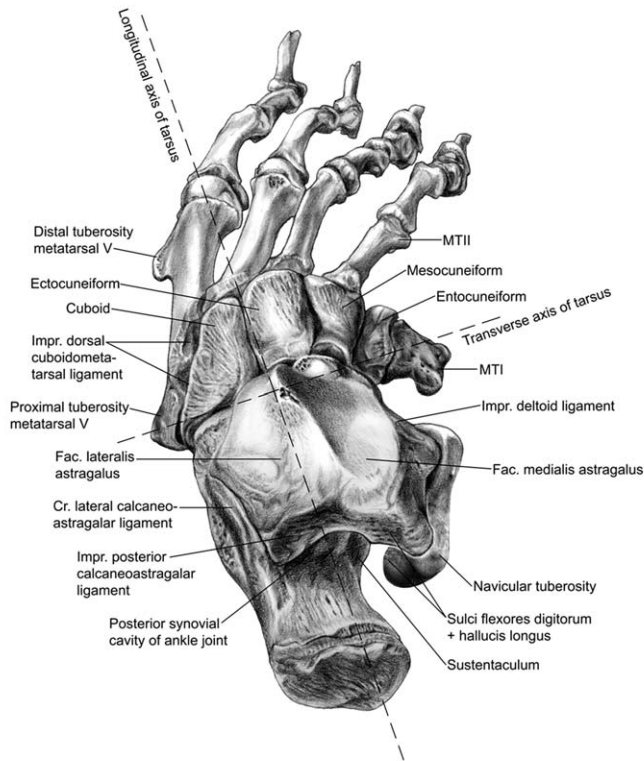
FIGURE 3. Oblique dorsal view of assembled left pes of *Thylacoleo carnifex* showing position of longitudinal and transverse axes of the tarsus. **Abbreviations: Cr**. crista; **Fac**. facies; **Impr**. impression; **m**. musculi; **MT** metatarsal.

FIGURE 4. Plantar view of the assembled right tarsus and metatarsus of *Thylacoleo carnifex*. **Abbreviations: Cr**. crista; **Fac**. facies; **Impr**. impression; **m**. musculi; **MT** metatarsal.

Calcaneus—The calcaneus is the largest element in the pes and forms the second of the first row of tarsal elements. It articulates dorsally with the talus and anteriorly with the cuboid (Fig. 2A, D). The astragular facets are aligned obliquely at approximately 45^0 to the longitudinal axis of the calcaneus. The shaft of the calcaneus has both a slight medial inflection as well as some axial rotation of the longitudinal axis relative to the saggital plane reminiscent of both the pigeon-toed condition in vombatids *L. latifrons* and *V. ursinus* and the axial rotation seen in arboreal species such as the *Phascolarctos cinereus* and *T. vulpecula*. The transverse axis of the tarsus is aligned at right angles to its longitudinal axis (Fig. 3). The anterior face of the calcaneus is deeply notched to receive the posterior face of the cuboid thereby restricting movement along the transverse axis.

Cuboid, Navicular, and Cuneiforms—The second tarsal row includes the cuboid, navicular, and the endo-, meso-, ento-cuneiforms. All these elements have plantar tuberosities, that of the cuboid in line with the posterior and anterior tuberosities of the calcaneus; those of the navicular and endo-cuneiform form a second parallel row (Fig. 4). The talar facet articulates with an extended sulcus in the navicular indicating a capacity for further inversion of the pes. The articulation of the navicular with the cuneiforms allows for both rounding and flattening of the tarsal arch with a concomitant contracting or flaring respectively of the digital array (Figs. 3, 4). The ventral tuberosities of the cuboid form a deep groove for the m. Peroneus longus tendon; a muscle associated with flexion of the first digit. This suggests that the first digit may have been used as a comparatively strong grasping mechanism. The navicular also displays a large tibial facet; among extant diprotodontians this character is only seen in scan-
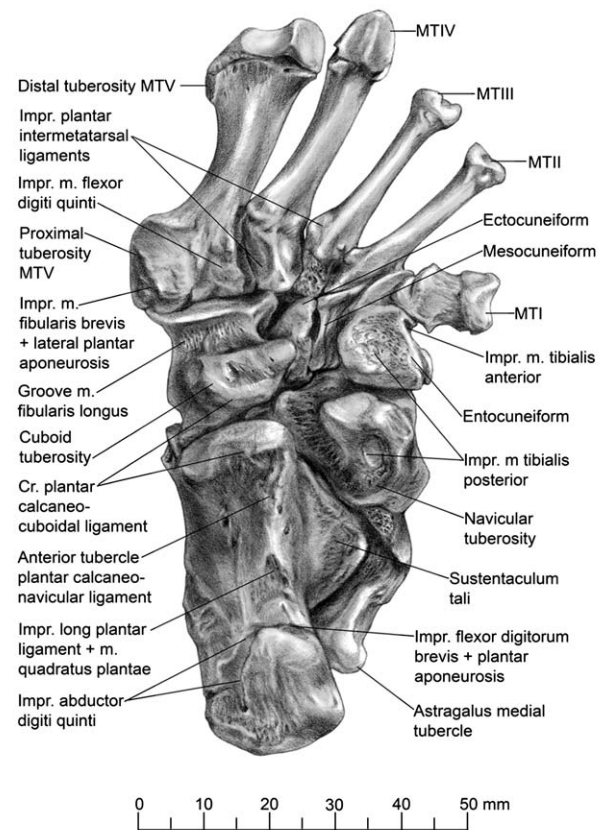
sorial or arboreal species such as possums (*T. vulpecula*) and the koala (*P. cinereus*) (Aaron Camens pers. comm., August 2008). The chord of the carpal arch measures 50mm with a depth of 8 mms which computes to a circle diameter of 86 mms.

Metatarsals—The third tarsal row comprises metatarsals I–V and associated phalanges where present. They range in length in descending order V–I. The tarsal/metatarsal articulations form a compact arch anchored laterally by a large basal tuberosity on V and medially by the basal tuberosity on the entocuneiform (Fig. 4). The metatarsals and phalanges V–II form an arched, medially directed fan-like array. V is flared laterally at both proximal and distal extremities, areas for attachment areas of the peroneal muscles. Metatarsal V is the largest and bears a prominent lateral and rearward facing tubercle with a broad plantar surface (Fig. 2C, D).

Although metatarsals V–II are similar in form, II–III are more slender forming a syndactylous-like pair (Figs. 2A, 4). Metatarsal I is short broad and divergent. The proximal facet on metatarsal I is wedge-shaped and articulates with a concave saddle-like sulcus on the distal medial aspect of the entocuneiform imparting considerable mobility to the hallux (Fig. 4).

The distal epiphyses of metatarsals II–V have keeled articulating surfaces for the proximal phalanges (Figs. 2A, 4, 5A), those of II and III are not illustrated. In lateral aspect these describe a full 180^0 arc from ventral to dorsal allowing extension of the digits as the tarsus is raised (Fig. 2D). Small sesamoid bones, also not illustrated, flank either side of the central keel of these metcarpal phalangeal joints. The distal epiphysis for metarsal I
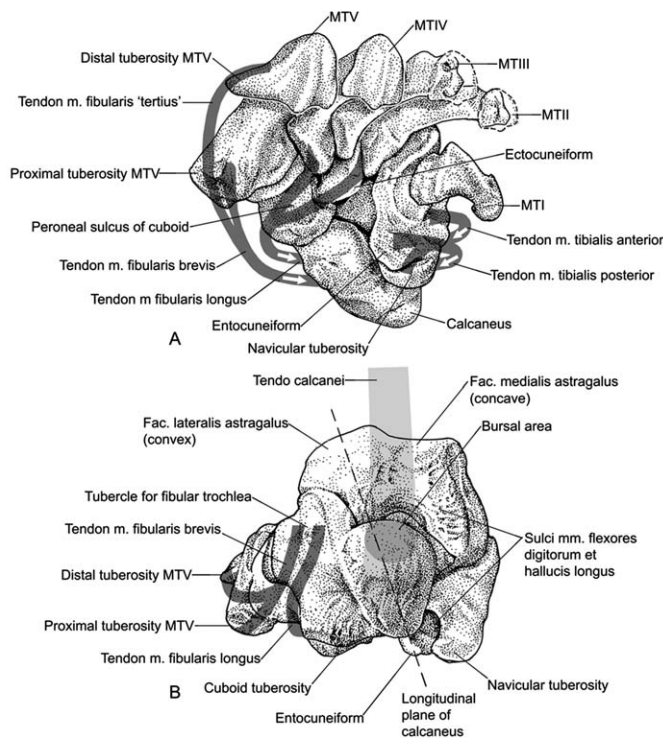
FIGURE 5. Anterior view **A**, posterior view **B**, of assembled right tarsus and metatarsus of *Thylacoleo carnifex* illustrating path of the flexor tendons. **Abbreviations: Cr**. crista; **Fac**. facies; **Impr**. impression; **m**. musculi; **MT** metatarsal.

FIGURE 6. Medial lateral view of the assembled left pes of *Thylacoleo carnifex* with digits in flexed position. Proximal and distal phalanges of hallux are missing in this specimen.

is broad and saddle shaped similar to that in *L. latifrons* and *V. ursinus* (Figs. 2C, 4).

Phalanges—The distal and proximal phalanges of metatarsal I have not been recovered. The proximal and medial phalanges of digits II–V are all similar in form (Fig. 2A–D). They are dorso-ventrally compressed in mid shaft. The medial phalanges are shorter than the proximal and together they form a size gradient in decreasing order V–II. Medial phalange V is ventrally keeled. In lateral aspect the distal epiphyses of both proximal and medial segments describe an arc approaching 270^0 beginning at the dorsal surface and terminating on the plantar surface allowing for considerable flexion of the toes. The distal phalanges of digits IV–V are laterally compressed and recurved showing greatest similarity in form to the claw base of the domestic cat (Fig. 2A–D). They lack a hooded sheathing base and are proportionally longer and more laterally compressed than those of digits II–III. They have pronounced basal tuberosities providing a strong lever arm for the digital flexor. Digits II–III retain hooded sheathing bases for the unguis and are smaller than those of digits IV–V. The curvature of all claws is similar. The concave proximal articulating surface aligns the claws along the longitudinal axis of the digits. They can be dorsally rotated to elevate the claw tip. There is no evidence of the eccentric offset of the inter-phalangeal joint as seen in the retractable claws of felids (Gonyea and Ashworth, 1975). Figure 6 shows the pes assembled with unguals in the fully-flexed position

The length of the dorsal arc of the ungual divided by the depth of the ungual base (variable UD, ungual phalanx depth, after Van Valkenburgh 1987, fig. 1A: 166) is shown in Figure 7 with measurements listed in Table 1, as is the curvature of the dorsal

arc measured as the ratio of chord length to maximum arc height (variable ARCH, curvature of dorsal arc, after Van Valkenburgh, 1987 fig. 1B:166).

The toes II–V fan out in an arched array. When flexed, the hallux is pseudo-opposable to the proximal plantar tuberosity on metatarsal V.

Tarsal, Metatarsal, and Phalangeal Ratios—Table 2 compares the input/output lever of the gastrocnemius for selected scansorial, arboreal and fossorial quadrupedal marsupials. The values were calculated by measuring the distance from tip of longest digit, excluding the unguis, to the mid-point of the ankle and from this position to the gastrocnemius insertion on the calca neus of adult skeletons; the smaller the value the greater the power. *Thylacoleo carnifex* ratios fall between those of the terrestrial/fossorial vombatids and the arboreal/scansorial *P. cinereus* and *T. vulpecula*.

DISCUSSION

The complete pes confirms speculation by Wells and Nichol (1977) about the presence of a divergent hallux and syndactyly. The tarsus and metatarsus show greatest similarity in form to vombatids. The limited flexion/extension of the ankle combined with capacity for inversion/eversion is a functional constraint shared with fossorial and scansorial species such as vombatids and phalangerids.

The bulk of the pes is confined to the tarsus and metatarsus. The phalanges, comprising approximately the last third of the pes length are relatively gracile. The pattern of plantar tuberosities on the tarsus indicates a resting plantigrade stance with a foot pad arrangement resembling that of vombatids. When viewed
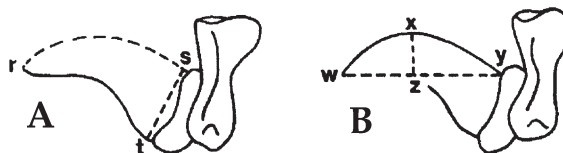

FIGURE 7. Ungual phalanx shape after Van Valkenburgh 1987 fig.1 P. 166, where **A** phalanx depth is represented by length of dorsal arc 'rs' and phalanx depth 'st' and **B** phalanx curvature is represented by chord length 'wy' and maximum arc height 'zx.'

TABLE 1. Measurements of ungual curvature following Van Valkenburgh 1987 where 'rs' length of the dorsal arch divided by 'st' depth at ungual base equals ungual phalanx depth UD see Fig. 7 (A); where 'wy' equals chord length divided by xz arc height equals curvature of the dorsal arc ARCH see Fig. 7 (B).

Ungual	rs	st	UD	wy	xz	ARCH
II	10.65	7.00	1.52	9.30	3.50	2.65
III	11.90	7.45	1.59	10.50	4.23	2.48
IV	15.10	9.80	1.54	15.60	5.40	2.88
V	16.00	10.15	1.57	15.90	6.20	2.56

laterally, the arc of the metacarpal/phalangeal articulation on each toe allows the heel to be raised while the toes remain in contact with the substrate. The body weight would then be borne by pads beneath the sesamoids. The extent to which the heel could be raised would be limited by the rather restricted flexion of the ankle due to its tapering trochlea.

The foot would be capable of moderate grasping via the lateral arching of the metatarsal array and ventral flexing of toes II–V combined with medial and ventral rotation of the hallux about the saddle-shaped articulation with the entocuneiform (Fig. 6). This grasping would be facilitated by limited inversion of the pes at the tibio-talar joint as indicated by the concave tibial facet and convex fibular facet in the tranverse plane. The distal and proximal phalanx of the hallux is unknown but the broad shallow sulcus on the distal end of metatarsal I indicates a similarity in form to the clawless nubbin found in vombatids. There is no evidence of opposability of the first digit as in *P. cinereus*. Indeed the base of the first digit is relatively short and broad. Its function would more likely be as an aid in stabilising the tarsus when moving or grasping on a curved substrate. When flexed it is pseudo-opposable to the large tuberosity on the proximal plantar surface of metatarsal V which presumably bore a substantial foot pad. Gebo (2005) considers the I–V opposable grasp in primates ancestral to the I–II grasp and concludes that large bodied forms using the former were '... probably not able to use vertical supports frequently.'

The laterally compressed and recurved claws of digits II–V with their strong lever arms for the digital flexors are ideally adapted for penetration into a compliant substrate. The hooded sheathing bases on unguals II–III serve to increase the anchorage area for the nail. The keeled medial phalange of digit V is suggestive of greater bending stresses on this digit during flexion and claw penetration. Flexion of the digits would serve to deepen the arch of the foot. When the ungual curvature (ARCH) is plotted against ungual depth (UD), as in Van Valkenburgh's figure 4, *T. carnifex* sits comfortably with *Prionodon linsang*

(the Oriental Linsang) and *Felis wiedii* (the Margay Cat), both expert climbers.

All evidence points to a pes adapted to bearing much of the body weight along the lateral margin of the foot and the base of the tarsus. The slightly bowed tarsal arch mirrors that of the carpus (Wells and Nichol, 1977). The digits of both manus and pes, when moderately flexed would be ideally adapted to clasping a cylindrical shape as small as 90 to 100 mms diameter such as a tree trunk or large branch as in possums or perhaps the body trunk of a prey victim. The low gearing of the gastrocnemius is consistent with a climber requiring power for thrusting the body up vertical surfaces. Conversely on a flat substrate the hind feet would settle to a plantigrade somewhat pigeon-toed stance reminiscent of vombatids. We speculate that *T. carnifex* may have been able to tripod on tail and hind feet freeing the forelimbs for dealing with prey. This interpretation is supported by the comparatively horizontal talar facet of the calcaneus, suggesting much of the weight could be born by the latter. Pes mechanics geared for anchoring and pushing a heavy body up a tree may also equally serve to anchor the hind feet when manipulating prey. Notwithstanding the rather vombatid-like ankle, the laterally flattened ungual bases and the narrow recurved unguals were unlikely to support a fossorial shovel-like nail. Clearly in the *T. carnifex* pes we have all the features required for a climbing scansorial syndactylous marsupial. At the time of writing we have uncovered more articulated skeletal material including the undescribed tail, clavicles and sternabrae. These too are indicative of a scansorial habit and will be the subject of our next paper.

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TABLE 2. Comparison of ankle gearing, (in/out ratios for gastrocnemius) of wombat, koala, possum, and *Thylacoleo carnifex* expressed as ratio of distance from heel to ankle axis/ankle axis to tip of longest digit x 100

Species	Habit	Longest Digit	In/out Ratio X 100
Vombatus ursinus (Common Wombat)	Fossor	IV	25.2
Lasiorhinus latifrons (Southern Hairy-nosed Wombat)	Fossor	III	23.8
Thylacoleo carnifex (Marsupial Lion)		V	17.2
Phascolarctos cinereus (Koala)	Arboreal	IV	15.1
Trichosurus vulpecula (Brush-tailed Possum)	Scansor	III	13.6

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