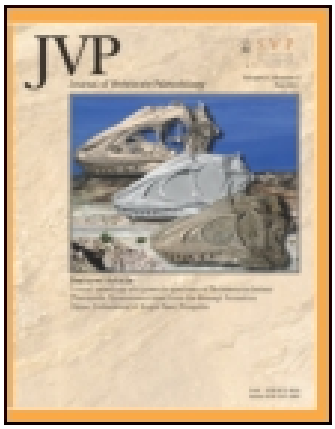

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Pedal morphology of the marsupial lion Thylacoleo carnifex (Diprotodontia: Thylacoleonidae) from the Pleistocene of Australia

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SHORT COMMUNICATION

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

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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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