CATCHING the MARSUPIAL 'LION' by the TAIL: *THYLACOLEO CARNIFEX* and the NARACOORTE CAVES

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"Thylacoleo exemplifies the simplest and most effective dental machinery for predatory life and carnivorous diet known in the Mammalian class. It is the extreme modification, to this end, of the Diprotodont type of Marsupialia."

Owen (1866)

Introduction

Of all the extinct Australian Pleistocene megafauna species, *Thylacoleo carnifex* (the marsupial 'lion') has captured the imagination and interest of people more than any other. Perhaps it is the allure of its predatory habits, (Australia's Pleistocene answer to *T. rex*); or the intriguing notion that it used caves as dens (Lundelius, 1966). It is certainly an enigma and, as Owen (1866) suggested, an extreme and meat-eating version of the otherwise herbivorous diprotodont marsupials. Spectacular fossil finds over the past few decades have put to rest much of the speculation regarding its habits and morphology. Fossil remains found in caves at Naracoorte in South Australia have played a central role in solving the puzzle of *Thylacoleo*. Likewise, this iconic marsupial has been integral to the history, science, tourism and interpretation of the Naracoorte Caves. The aim of this paper is to explore the discovery of *Thylacoleo carnifex* at Naracoorte Caves and how this has influenced the scientific and social history of the park.

Discovery

The first recorded fossil material of *Thylacoleo carnifex* was recovered by Major Thomas Mitchell at Wellington Caves in New South Wales in the 1830s (Figure 1). It consisted of only a few isolated teeth and was not immediately identified (Gill, 1954). Lake Colongulac, near Camperdown, in Western Victoria, some 150km east of Naracoorte, bore the first remains to be formally described by science. The eminent palaeontologist, Sir Richard Owen, received the fossils in 1855 and described the bones (parts of the cranium), in 1859. He interpreted the remains as those of a great marsupial carnivore and was sufficiently impressed by its carnassial-like premolars to assert that *"…it was one of the fellest and most destructive of predatory beasts*." (Owen 1859). Almost at once, controversy ensued.

William Sharp Macleay, an entomologist with a keen interest in Australian Natural History, lashed out in the Sydney Morning Herald convinced of Owen's folly, defending *Thylacoleo* as "A very gentle beast, and of good conscience" (Macleay 1859). Macleay based his argument on *Thylacoleo's* relationship with other Diprotodont marsupials, most of which are herbivores. Gerard Krefft, Curator of the Australian Museum, was almost equally as unimpressed with *Thylacoleo's* carnivory, opining that it *"…was not much more carnivorous than the Phalangers (possums) of present time."* (Krefft, 1866). Owen, meanwhile, had received an almost complete skull from the Darling Downs, in Queensland and published a more detailed paper, further describing the skull and teeth of *Thylacoleo*, acknowledging its diprotodont affiliation but more convinced than ever of its carnivorous habits (Owen, 1866). The debate raged back and forth in both the popular media and scientific literature for some years (for example see Broom 1898). While there was not enough evidence to settle the debate, *Thylacoleo* had captured the imagination of the public and scientific community.

The controversy did not end with *Thylacoleo's* diet. Krefft further proposed that an unusually large, clawed distal phalanx found at Wellington Caves belonged to an Australian Megatherium (giant sloth), and proposed the name *Mylodon australis* (Krefft 1870 - republished in Mahoney and Ride, 1975 page 198). Owen, who received photographs of the ungual from Krefft, referred the claw to *Thylacoleo*, almost purely by the deduction that it belonged to a carnivore, stating there was "No evidence of a Megatheroid…in Australia" and that "there is no other associated Carnivore corresponding in size…save the *Thylacoleo*" (Owen 1871; Figure 2)). Owen later received and described (again from Wellington Caves), a mandible, radius, ulna and a similar distal phalanx (Owen, 1883a) as well as a partial pelvis (Owen, 1883b), which he attributed to *Thylacoleo*. However, as an articulated skeleton was yet to be found, there was still a question whether these elements were from *Thylacoleo* at all. In 1888, Owen presented to the Royal Society a new Genus in the Thylacoleonidae, although the paper was never published (Anderson, 1929). He had received a skull (much smaller than those recovered earlier), from a newly found cave near Wellington. He named the species *Thylacopardus australis*, an allusion to the animal's size being more leopard-like, than lion-like.

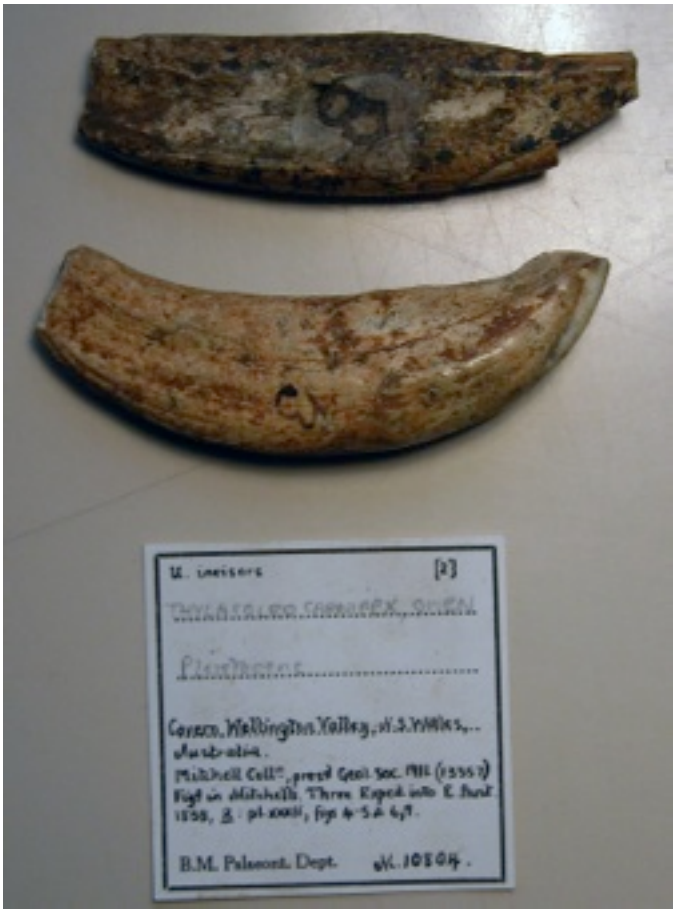


Figure 1 - Thylacoleo incisors collected by Mitchell and sent to Owen at the Natural History Museum, London Photo: Steve Bourne

Early Discoveries at Naracoorte

Father Julian Tenison-Woods was the first person to describe any fossil material from Naracoorte Caves; however, he did not report any material attributable to megafauna species (Woods, 1858; Reed, 2012; Reed & Bourne, 2013). There can be little doubt he yearned to find megafauna animals, as he devoted an appendix in his 1862 book to the fossil discoveries of Wellington Caves (Woods, 1862). While, he had some success in finding isolated specimens in other sites around the southeast of South Australia, he never found them at Naracoorte. What Woods couldn't know was that the remains he sought lay as little as one metre below his feet as he explored Blanche Cave (Reed and Bourne, 2013).

William Reddan (caretaker of Naracoorte Caves from 1886 to 1919) was the first to discover Thylacoleo fossil remains at the caves. In Specimen Cave, he found skull and jaw bones of an unusual animal with "large tusks protruding" (Anonymous 1908a,b). He forwarded the bones to his department and they were subsequently presented to Dr Edward Stirling, Director of the South Australian Museum (SAM). Stirling identified the remains as belonging to *Thylacoleo* and was keen to visit

Figure 2 - The type of "Thylacoleo oweni" in the Natural History Museum, London. Photo: Steve Bourne

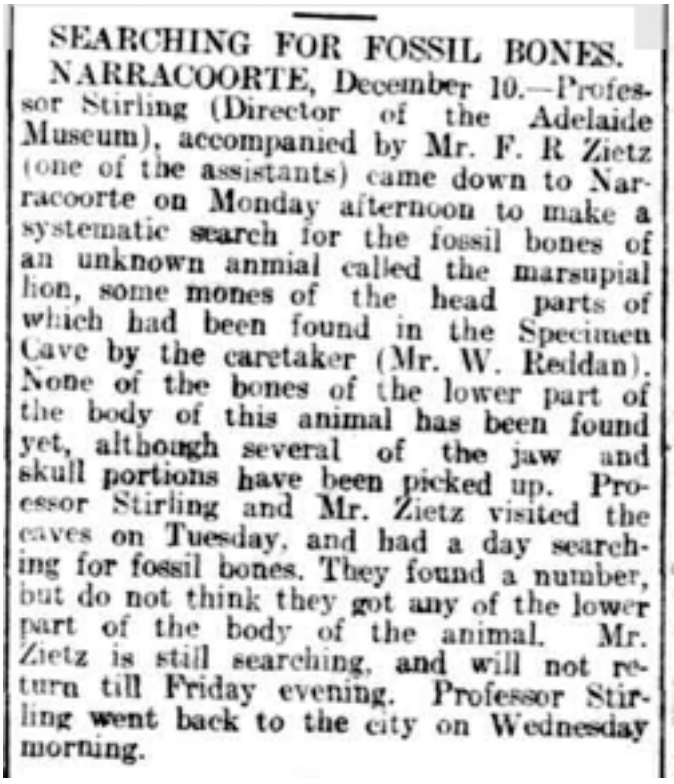
the site to determine if bones of the post-cranial skeleton were present in the cave. Fifty years after Owen's papers, very few bones of the skeleton were yet known to science, so the opportunity to expand knowledge of the species was too good for Stirling to pass up. He decided to do a systematic search for fossils and arrived at the caves on Monday 14th of December 1908, accompanied by his assistant, Fritz Zietz. They began their search the next day and found numerous bones, which were taken back to the museum for further study (Figures 3 and 4). Stirling later reported on the finds in reports to the museum board (Stirling, 1908, 1912). Reddan made some further finds in the newly discovered Alexandra Cave and these bones were also forwarded to the museum. Unfortunately Stirling never published the material.

Renewed interest in the science of Naracoorte Caves came in the 1950s, with the formation of the Cave Exploration Group of South Australia (CEGSA). Members of the group continued systematically exploring, mapping and surveying the caves. During these surveys, fossil material (including *Thylacoleo*) was discovered scattered throughout the system, adding numerous specimens to Naracoorte's collection; but in 1956, an amazing cave deposit was about to come to light in a somewhat unconventional way.

The James' Quarry *Thylacoleo*

During quarrying operations, Mr Amos James, the proprietor of Naracoorte Quarry, opened up a previously unknown cave (5U29) during blasting operations. Within a small cave he discovered an unusual skeleton and reported the find to staff at the SAM, who dispatched Norman Tindale (Curator of Anthropology) and fossil preparator, Paul Lawson, to investigate. Tindale, an

Top. Figure 3 - Specimens collected by Reddan and Zietz in the South Australian Museum; Photo: Liz Reed.
Below. Figure 4 - Newspaper article recording the Museum visit to Naracoorte Caves to collect Thylacoleo specimens. The Register, Saturday December 12th 1908 pp. 4.



SEARCHING FOR FOSSIL BONES.

NARRACOORTE, December 10.—Professor Stirling (Director of the Adelaide Museum), accompanied by Mr. F. R Zietz (one of the assistants) came down to Naracoorte on Monday afternoon to make a systematic search for the fossil bones of an unknown anmial called the marsupial lion, some mones of the head parts of which had been found in the Specimen Cave by the caretaker (Mr. W. Reddan). None of the bones of the lower part of the body of this animal has been found yet, although several of the jaw and skull portions have been picked up. Professor Stirling and Mr. Zietz visited the caves on Tuesday, and had a day searching for fossil bones. They found a number, but do not think they got any of the lower part of the body of the animal. Mr. Zietz is still searching, and will not return till Friday evening. Professor Stirling went back to the city on Wednesday morning.

accomplished anthropologist and entomologist, had previously published papers on the nearby Tantanoola Caves (Tindale, 1933) and excavated megafauna fossils at Rocky River on Kangaroo Island (Hall et al, 1935); a site that was later to bear *Thylacoleo* fossils of its own. Lawson was also experienced with Pleistocene megafauna, having recently accompanied the American palaeontologist Ruben Stirton to Lake Callabonna in the state's northeast, where they famously excavated large numbers of Diprotodon fossils embedded on the lake's shore (Anonymous, 1953).

Unfortunately, Tindale and Lawson arrived a little too late. With the best intentions, Mr James had covered the well preserved skull of the animal with a hessian bag to protect it from the weather. They arrived to find the skull in pieces, crushed under the weight of the rain soaked bag, scattered amongst the talus at the base of the quarry face (Daily, 1960). What remained in the cave was the well-preserved post-cranial skeleton of *Thylacoleo carnifex*, which Lawson painstakingly retrieved from the sandy sediment of the alcove while balanced on a wooden ladder some 4 metres above the quarry floor.

The post-cranial skeleton of *Thylacoleo*, which had remained elusive since description of the skull by Owen almost a century before, had finally been discovered. Previous attribution of post-cranial material to *Thylacoleo* by Owen was now confirmed. It was the start of a rewarding few years for palaeontologists. CEGSA members found the skull of a juvenile *Thylacoleo*, along with some skeletal elements (SAM P12902, P12911), in Cathedral Cave (5U12), which is now part of the Naracoorte World Heritage area. Ruben Stirton and Richard Tedford found another partial skeleton near Lake Menindee in NSW (Daily, 1960). In 1959, blasting at James' Quarry opened a second cave, in close proximity to 5U29. Another partial skeleton, comprising most of the front half of the animal and including a complete – albeit disarticulated - left manus, and complete forelimb, was added to the museum's collection (SAM P2910, Figure 5). Stirton and Tedford took the material back to UC Berkeley with the intention of describing the post-cranial skeleton. Unfortunately this did not eventuate and Gill (1973) suggests that the task was passed on.

Curiously, despite the excitement of the long awaited finds, research on the post-cranial skeleton was not to be published for almost two decades. The material and inspiration for this research was to come not from the James' Quarry specimens but from another Naracoorte cave, Victoria Cave 5U1. Two scientists, who were also avid cavers, were to make a remarkable discovery that would highlight the scientific importance of the Naracoorte Caves to the world.

Victoria Fossil Cave

Discovered by Reddan in 1894 and opened to the public in 1897 (Anonymous 1897), Victoria Cave (now Victoria Fossil Cave) is one of the main Naracoorte tourist caves.

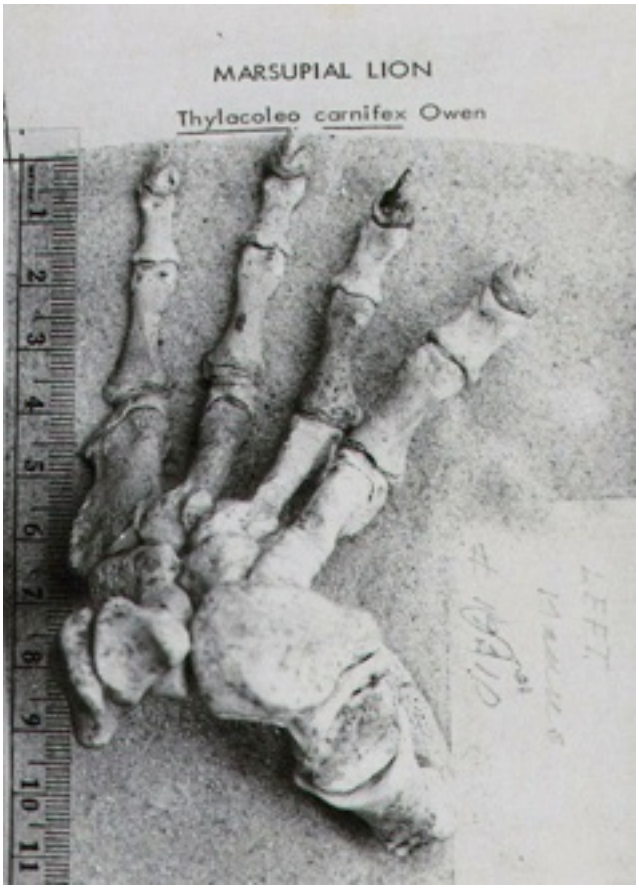


Figure 5 - James Quarry Thylacoleo manus specimen. Photo of image held in the South Australian Museum collection - Photo: Liz Reed

During explorations in 1969, Grant Gartrell and Rod Wells (members of CEGSA) pushed through a 10 m long, low rocky passage located about halfway through the known cave and found a chamber filled with countless fossils. Limb bones, skulls and other elements could be seen lying on the surface and poking through the sediment (Wells, 1975). As Gartrell explored the cavern, Wells scanned the sediment from a ledge at the front of the deposit where he found an encrusted *Thylacoleo* skull lying at his feet (Figure 6). Gartrell found another skull lying on a rock pile about halfway along the chamber (Wells, pers. comm. 2014). Over the next few years, the remains of at least 18 individual *Thylacoleo* were collected from the deposit (Wells et al., 1984). The chamber contains a sediment cone, which was deposited through an entrance hole located above the northeast end of the chamber. That entrance is now blocked, but once acted as a "pitfall" trap, collecting and preserving large numbers of animals over a period of more than 200,000 years (Wells, 1984; Reed, 2008).

It would be difficult to overstate the significance of the discoveries in Victoria Fossil Cave. The Main Fossil Chamber is massive, some 54 metres long, about 16 metres at its widest point and at least 3 metres deep (Reed, 2008). The accumulation dates from around 213,000 to as far back as 478,000 years ago (Reed and Bourne, 2009). The sediment deposit contains a diverse assemblage of fauna, with over 100 species of vertebrates

Figure 6 - Thylacoleo skull in situ, Fossil Chamber, Naracoorte Caves
Photo: Rod Wells

recorded (Reed and Bourne, 2000). Numerous important *Thylacoleo* specimens have been recovered from this rich deposit, including the articulated right and left manus and an almost complete pes; which were recovered by Wells soon after the chamber was discovered (Wells, 1975). Grant Hall, a chamber located just beyond the Fossil Chamber and discovered in 1975, covers a period from around 70,000 to 93,000 years ago (OSL chronology), providing an almost complete chronology of the late Pleistocene fauna (Macken et al., 2011). The Upper and Lower Ossuaries, located through low passages beyond the main Fossil Chamber, contain breathtaking fossils littering the sandy-clay floor of a chamber covering an area of around 450 m^2 (Reed, 2006). The Ossuaries are so remarkable, that David Attenborough filmed the cave for his "Life on Earth" series, which aired in 1979 (Nolan, 1977, Figure 7).

He also mentioned them in his book of the same name (Attenborough, 1979). As the chambers contain relatively pristine sediment floors, they are protected as a "Reference Area" for the Naracoorte Cave system – no excavation has taken place in the chamber and no research is allowed without special permission and strict conditions. Fossils of *Thylacoleo*, *Megalibgwilia*, *Zygomaturus* and *Thylacinus* are spread across the surface, but they are overwhelmed by the number of Sthenurine kangaroos – which account for almost 60% of the visible material (Reed, 2006). Butch and Lake Chamber, a small chamber adjacent to the Main Fossil Chamber has also provided *Thylacoleo* fossil material.

An underground museum

The scientific value of the Victoria Fossil Cave deposits was recognised at once by Rod Wells, who wrote in a special report to the Deputy Director of the South Australian Government Tourist Bureau strongly recommending the area be protected, as "*…it could yield a considerable amount of scientific information if studied by qualified zoologists and palaeontologists*". *Furthermore if properly developed it could also be of educational value to the general public*" (report by Wells September 1969 –

R. Wells pers. comm. 2014). Tours in Victoria Cave had occurred since its discovery and had focussed on the impressive speleothem formations in the cave; but the idea of the deposit being an underground museum for communicating the scientific value of the fossil deposit was novel, and one that would shape the future of tourism at Naracoorte. In 1970, Dr Richard Tedford,

Figure 7 - David Attenborough with Thylacoleo skull in the Ossuaries, Victoria Fossil Cave, Naracoorte Photo: Rod Wells

Curator of Vertebrate Palaeontology from the American Museum of Natural History in New York visited the site. He was quoted in the Canberra Times (July 18 1970 page 13) to have remarked - "*From these exceptionally rich deposits we may get some answer to the puzzle of why so many forms of large animal life became extinct*". Tedford also noted that ".. similar bone caves in the United States and Europe had provided excellent tourist attractions".

By the mid to late 1970s, the Tourist Bureau had installed electric lighting at the excavation area and was conducting tours to the site for the general public. Part of the ticket office at the caves was made available for Rod and his team to use as a field laboratory and by 1971 Rod was working together with Ern Maddock of the Tourist Bureau to develop displays for visitors. One of these was a silhouette image of *Thylacoleo*, that Rod had reconstructed based on the two known skeletons of the time. The focus of guided tours shifted to discussions of the significance of the deposit and on vertebrate palaeontology of the late Pleistocene in Australia. A workbench had been set up at the dig and fossils were used as props by cave guides. The Tourist Bureau improved facilities at the park in preparation for the increased numbers of visitors the new site had attracted.

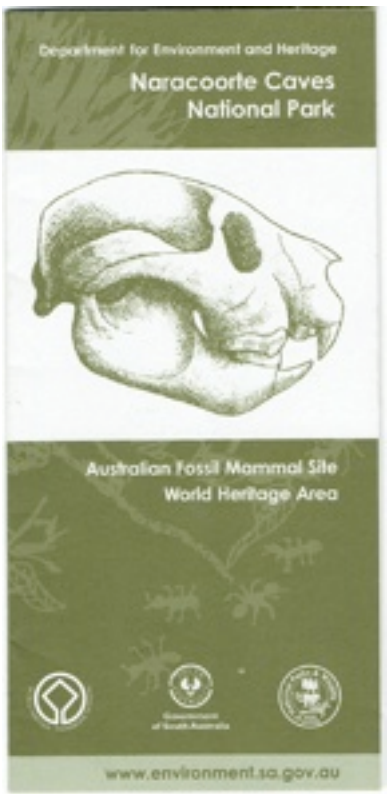
Currently a 60 minute tour runs at least twice daily through Victoria Fossil Cave. The tour includes a 30 minute talk held in the Fossil Chamber, just above the Excavation Site A (Wells et al., 1984), where a purpose built viewing and seating area supports up to 25 visitors. Immediately below the viewing platform, hundreds of exposed skeletal elements are visible in the pit, relieved out *in situ*. A full skeletal cast of *Thylacoleo carnifex*, as well as *Simosthenurus occidentalis*, is mounted on display at the front of the platform (Figure 8). The cast of *Thylacoleo* is a composite model, reconstructed from a number of individual specimens which have been excavated from the Fossil Chamber. The hands and forelimbs, pelvis and hind limbs of the model were cast from those used by Wells and Nichol (1977). The vertebrae were cast from individual bones found associated with a *Thylacoleo* skull in the Fossil Chamber (R. Wells, pers. comm. 2014). Casting of the manus and pes was done by Rod Wells, limbs and vertebral column by Ed Baily and the skull and dentaries by Peter Daenke at Flinders University. The cast is posed in a somewhat aggressive stance, and is striking and photogenic, appearing in numerous photos on popular photography websites, such as Flickr and is currently featured on the Wikipedia entry for the Naracoorte Caves (2014). *Thylacoleo* has also featured on various tourist websites, brochures and information boards for the region (Figure 9a,b).

A second cast from the same material is on display at the caves visitor centre, the Wonambi Fossil Centre, where the reconstruction is "struggling" with the extinct madtsoiid snake, *Wonambi naracoortensis*. This reconstruction is the centre piece of the visitor centre foyer, and accompanies two other reconstructions of *Thylacoleo*; both animatronic, life models. The original robotic model is located in the diorama, along with a number of other life-sized Pleistocene reconstructions, such as *Diprotodon optatum*, *Zygomaturus trilobus* and *Palorchestes azael*. Artist Stephen Hayter made the robotic models in consultation with Rod Wells and they were constructed at Flinders University. The models were revealed to the public when the centre opened in 1998. The robot moves its head from side to side and growls. The second model, located in the foyer near the mounted cast, is a more recent addition, again made by Stephen Hayter and installed around 2005.

The cast and life models are popular with tourists, but lack the visual impact of the cast mounted in the Fossil Chamber. The location, pose and atmosphere of the reconstruction at the Fossil Chamber provide a depth and dimension to the science of palaeontology that it is not possible to recreate in a standard museum. The guide's talk, in front of the fossil bed, dwarfed by the shadow of the *Thylacoleo* skeleton on the cave walls, creates a powerful impression. The skeletons at the fossil bed also provide important props to assist the guides in conveying the process of palaeontology and how scientists work from bones to reconstruct extinct animals.

In 1994, Naracoorte Caves, along with the Riversleigh Fossil Sites in North West Queensland, received international recognition and protection under the UNESCO World Heritage program. UNESCO ranks the fossil sites as being "among the world's 10 greatest fossil sites" and singles out Victoria Fossil Cave (5U1) Naracoorte as being "... in terms of both volume and diversity, Australia's largest and best preserved and one of the richest deposits in the world" (UNESCO 2014).

Above. Figure 8 - Thylacoleo and a sthenurine kangaroo skeleton cast shadows on the wall in Victoria Fossil Cave
Below left. Figure 9a - Guide interacting with visitors using Thylacoleo skeleton. Cover of regional visitor guide
Photo: Steve Bourne; Below right. Figure 9b - 2005 park brochure featuring a Thylacoleo skull. Photo: Steve Bourne



The fossil record of *Thylacoleo* at Naracoorte Caves

Victoria Fossil Cave is spectacular not just for the number and size of fossil deposits in its numerous chambers, but also for the excellent preservation of the specimens that have been recovered. The left and right manus of *Thylacoleo*, along with some of the forelimb bones, were recovered fully articulated and preserved in calcite (R. Wells pers. comm. 2014). These specimens finally provided the reference material needed to fully describe these aspects of the animal (Wells and Nichol, 1977). Analysis of the articulated manus showed *Thylacoleo* was capable of a wide range of motion of the first phalanx (tipped with a large recurved claw), including gripping by opposing the pisiform. The other phalanges were each tipped with ungual crests, homologous to those found in felids, which allow the animal to retract its claws. *Thylacoleo* also had a wide range of motion of its forearms, and was capable of using its hands for powerful grasping. Unfortunately, the pes was incomplete, preventing a deep understanding of *Thylacoleo's* locomotion and stance.

In 1969, at a quarry owned by the Henschke family, a cave was opened up during limestone quarrying. The cave, later named Henschke's Fossil Cave (5U91, 5U97) was a substantial cave, first surveyed at about 50m long with later extensions discovered adding an additional 60m of passages at two levels. Henschke Industries kindly changed their quarrying plans and left the cave in an accessible state until 1981, allowing palaeontologists from the SAM to excavate and document the fossils. Neville Pledge (Curator of Fossils), calculated there were at least 46 individuals of *Thylacoleo* from the deposit, making it more far more common that other carnivores such as *Thylacinus cynocephalus* (12 individuals) and *Sarcophilus* (6), and similar to the number of *Sthenurine* kangaroos (52) (Pledge, 1990). The large mammal component of the deposit was dominated by macropodine kangaroos; with *Macropus rufogriseus* and *Macropus giganteus* comprising 482 individuals. Pledge noted that most of the *Thylacoleo* material recovered from the cave system was from juveniles, mostly very young individuals with un-erupted, or recently erupted teeth. He attributed this to the pitfall nature of the cave entrance and the inexperience of younger animals, presumably hunting around the vicinity. The faunal composition of the deposit was similar to that of Victoria Fossil Cave; however, the stratigraphy and taphonomic properties of the Henschke's deposit were unclear. Given the salvage nature of the excavation; the site did not lend itself to a more thorough interpretation.

Table 1 – Fossil sites that have yielded remains of *Thylacoleo carnifex* - Naracoorte Caves World Heritage Area.

Site	Description	Reference
Victoria Fossil Cave 5U1		
Main Fossil Chamber	Excavation by R. Wells, E. Reed and others	Wells *et al.* (1984); Reed and Bourne (2000, 2009).
Grant Hall	Excavation by R. Fraser and later A. Macken.	Fraser and Wells (2006); Macken *et al.* (2012); Reed and Bourne (2000, 2009).
Upper and Lower Ossuaries	Material collected from cave floor and documented *in situ*.	Reed (2006); Reed and Bourne (2000).
Butch and Lake Chamber	Material collected from cave floor and documented *in situ*.	Reed and Bourne (2000).
Bat Cave 5U2	Material collected from the entrance chamber	Tideman (1967); Maddock (1971); Reed and Bourne (2009).
Alexandra Cave 5U3	Material collected by caves caretaker W. Reddan.	Pledge (1977); Reed and Bourne (2000).
Blanche Cave 5U4,5,6	Incidental finds in cave tunnels; later formal excavation by T. Laslett and expanded by E. Reed.	Reed and Bourne (2000, 2009, 2013).
Stick-Tomato Cave (Wet Cave) 5U10, 11	Excavation in the entrance chamber of the cave.	Reed and Bourne (2000, 2009).
Cathedral Cave 5U12, 13	Incidental finds in cave tunnels; subsequent organized excavation in fossil chamber by S. Brown and G. Prideaux.	Daily (1960); Brown and Wells (2000); Prideaux *et al.* (2007).
Robertson Cave 5U17, 18, 19	Excavation in inner chamber of cave by M. McDowell and later S. Brown.	Reed & Bourne (2009).

Table 2 – Cave sites within the Naracoorte District* that have yielded *Thylacoleo* material.

Site	Description	Reference
James' Quarry Cave 5U29	Small cave uncovered during quarrying; fossils collected by N. Tindale and P. Lawson (SAM).	Daily (1960); Pledge (1977); Reed and Bourne (2000).
Henchke's Fossil Cave 5U91, 5U97	Cave uncovered during quarry activity. Excavated by SAM palaeontologists and later J. Barrie.	Pledge (1990); Barrie (1997); Reed and Bourne (2000).
Komatsu cave 5U240	Cave uncovered during quarry activity. Excavated by S. Bourne, E. Reed and others.	Reed and Bourne (2009).
Komatsu Cave 2	Cave uncovered during quarry activity. Excavated by S. Bourne, E. Reed and others.	Reed and Bourne (2009).
S102 Cave 5U47	Isolated pes elements found in cave tunnel by S. Bourne	Reed and Bourne (2009).
Haystall Cave 5U23	Fossil material collected from the sediment of a large cone.	Reed and Bourne (2000).
Specimen Cave 5U35 (also known as Zietz Cave)	Fossil material collected from sediments and cave tunnels by W. Reddan and E. Stirling.	Stirling (1908, 1912); Reed and Bourne (2000).
Cable Cave 5U125	Fossil material collected from cave floor.	Reed and Bourne (2000).
Buckridge Cave 5U169	Small cave uncovered and subsequently destroyed during vineyard preparation. Excavated by S. Bourne, E. Reed and M. McDowell.	Reed and Bourne (2000).
Crawford's Cornucopia Cave 5U171	Small cave uncovered during vineyard preparation. Excavated by S. Bourne and E. Reed	Reed and Bourne (2000).
Whale Bone Cave 5U250	Cave uncovered during vineyard preparation; sediment floored chamber with fossil material evident.	Reed and Bourne (2009).

*Other sites with *Thylacoleo* carnifex in South East Region - Comaum Forest Cave 5U118, Green Waterhole Cave 5L181, Wandilo Forest Cave 5L365, Gouldens Hole 5L8, Un-named Cave 5L441, Moorak, Kilsby's Hole 5L46, Un-named cave in Mount Gambier (site 45 in Reed & Bourne 2000).

In just a few years since these major discoveries, Naracoorte had provided enough *Thylacoleo* material to address some long standing taxonomic questions. Using material contributed from Naracoorte and Wellington Caves, Archer and Dawson (1982) began to revise the taxonomy of the Thylacoleonidae. They found that skulls varied greatly between individuals in the same geographic region and previous taxonomic distinctions actually fell within the normal range. Owen's *Thylacopardus australis* was also found to fall within the normal size range of *Thylacoleo carnifex*, as was Krefft's *Thylacoleo robustus* (Krefft 1872) and McCoy's *Thylacoleo oweni* (McCoy 1876). Krefft's *Mylodon australis* ungual (Krefft 1870) was also found to belong to *Thylacoleo*, as was Krefft's proposed genus *Plectodon* (Krefft 1870). The controversial nature of the taxonomy of the genus *Thylacoleo* had been neatly resolved to just one Pleistocene species, *Thylacoleo carnifex*; and the question of *Thylacoleo's* dietary and locomotory habits could now be addressed. Important biomechanical investigations of the post-cranial skeleton were made during the 1980s (Finch and Freedman, 1986 and 1988), setting the stage for later discoveries at Naracoorte and elsewhere. Wroe *et al.* (1999) used material from Naracoorte and elsewhere to determine body weight of *Thylacoleo.*

Wells et al. (1982) used material from Victoria Fossil Cave to resolve the century old question of *Thylacoleo's* dietary habits. Functional analysis of the jaw and tooth dynamics of *Thylacoleo* showed the animal's dentition was capable of exhibiting forces and shearing required to process large prey. Modelling of feeding behaviour also showed that micro-wear patterns on the teeth matched those generated by feeding on meat, rather than an herbivorous diet. Further supporting evidence came from another Naracoorte specimen from the Henschke's Quarry, where chemical analysis using Strontium (Sr) and Zinc (Zn) ratios was used to show that *Thylacoleo* was carnivorous (Nedin, 1991). The results of these studies have not been challenged and more recent work using finite element analysis techniques (Wroe *et al.*, 2005, 2008) have supported this finding, revealing that comparatively, *Thylacoleo* had a higher bite force than its eutherian namesake. Multivariate analysis of both cranial and post cranial features of *Thylacoleo* show that it clusters closely with other Pleistocene felid predators, such as *Smilodon* (Wroe, 2008). Owen's original hypothesis, that *Thylacoleo* was a well-adapted carnivore despite its ancestors being of a more herbivorous diet and "of good conscience", is now accepted theory.

In 2005 another cave was unearthed in the Henschke's quarry system, this time with a front-end loader, which gave the new cave its name. Komatsu Cave (U240) was opened around 11 metres below surface level and contained sediment cones with numerous fossils; again the Henschke family offered to change their plans to allow palaeontologists to collect and document the material. Two of the authors (LR and SB), assisted by Friends of Naracoorte Caves volunteers and students from Flinders University, conducted a salvage operation to excavate the site. The cave contained the remains of

both juvenile and adult *Thylacoleo* (Figure 10). For the first time, an articulated pes (complete with hind limb attached), was recovered (Figure 11). Using this fossil, Wells *et al.* (2009) were able to reconstruct the morphology of the pes, completing the story of *Thylacoleo's* limb morphology. *Thylacoleo* had morphological elements of both a scansorial quadruped, and adaptations consistent with a climber.

Based on their interpretation, *Thylacoleo* would have been able to grasp branches with its foot, and thrust its body weight upward in a manner of climbing similar to modern possums (Wells *et al.*, 2009). *Thylacoleo* has been found across Pleistocene fossil cave deposits in both the Naracoorte World Heritage Area (see Table 1) and the greater Naracoorte district (Table 2), spanning a time period of at least 300,000 years. It has now been found across fossil deposits in all states of Australia, and in many bioregions and environments (Prideaux, 2006). The regularity of its inclusion in these deposits is interesting, as large carnivores are usually underrepresented in fossil deposits when compared with other animals such as kangaroos. *Thylacoleo* may have been attracted to the caves to feed on trapped or injured animals, creating a similar accumulation bias to that seen in deposits such as the Le Brea Tar Pits in Northern America (eg. Spencer and Van Valkenburgh, 2003).

Megafauna icon

Large, carnivorous animals tend to capture the imagination and a 'marsupial lion' is unique and intriguing to scientists and the general public alike. Reconstructions of the animal have changed over time in light of new scientific evidence. Many of these discoveries have inspired popular articles, documentaries and memorabilia. In 2008, Australia Post published a series of stamps depicting Australian megafauna species. The stamps were designed by Peter Trusler, an accomplished palaeoartist, and featured *Thylacoleo carnifex* on the 55c stamp. In 2014, Perth mint released a 1oz silver coin depicting an adult *Thylacoleo* with a young on its back. This coin, part of a limited release, was also designed by Trusler. In 2011, for the Perth Mint coin release "Australian Fossil Mammal Sites" "World Heritage Area", *Thylacoleo* was chosen to represent Naracoorte Caves.

In recent years, *Thylacoleo* has been prominent in media appearances and scientific interpretation at the Naracoorte Caves. Many of these are filmed at the fossil pit under the shadow of *Thylacoleo*. In 2009, the cast skeleton at the fossil bed was used to discuss the habits of *Thylacoleo* for the Discovery Channel production *"Monsters Resurrected, Episode 6 – Megalania, Giant Ripper"* which aired in October 2009 and included one of the authors (LR). This is just one example from many. A photograph (taken by one of the authors SB) of a young girl posing with the *Thylacoleo* skeleton at the fossil bed, quickly became the 'face' of Geo-tourism in South Australia and was used in multiple tourism promotions,

Figure 10 - Cath Sellars excavating a Thylacoleo skull in Komatsu Cave 2, Naracoorte. Photo: Steve Bourne

Figure 11 - A reconstructed hind limb and pes of Thylacoleo from Komatsu Cave, Naracoorte. Photo: Steve Bourne

advertisements and tourism award nomination documents (Figure 12).

In 2010, an article in National Geographic Magazine ("Australia's Lost Giants"), included a life-like reconstruction of *Thylacoleo carnifex* created by the Kennis brothers. This was based on a skull from Komatsu Cave in Henschke's Quarry at Naracoorte. Many visiting palaeontologists have been photographed with the *Thylacoleo* skeleton at the fossil bed, including Dr Phil Currie and Dr Jackson Njau (Figure 13).

The End of the Tail

Naracoorte has played a pivotal role in both the scientific understanding and public profile of the extinct marsupial lion. *Thylacoleo* fossils have now been recovered from every state in Australia and from various biogeographic

regions and climates. In 2002 on the Nullarbor Plain, a team of cavers from the Victorian Speleological Association (VSA) were systematically surveying the Nullarbor Plain in Western Australia when they discovered a number of previously unknown cave entrances. During surveying of the new caves, they found the almost complete, articulated skeleton of Thylacoleo, exquisitely preserved, lying on the sediment in a chamber as if it had recently expired. The find was reported to the Western Australia Museum (WAM) and collected soon after by palaeontologists including Gavin Prideaux and John Long from Flinders University. The skeleton provided something that had eluded palaeontologists for 150 years – a tail.

Tails play an important part in the locomotion of marsupials; not just in climbers such as possums. Macropods use the tail as a 'fifth leg' in pentapedal locomotion. Tasmanian devils and other dasyurids use the tail to facilitate a 'tripod' stance, allowing these carnivores to stand on their hind legs. Current work by Professor Rod Wells and colleagues involves biomechanical analyses of the vertebral column of *Thylacoleo* skeletons from the Nullarbor Caves and Naracoorte. This will allow insight into the gait and stance of this enigmatic marsupial, putting in place the final pieces of the *Thylacoleo* puzzle.

Figure 12 - Young girl posing with the Thylacoleo skeleton in Victoria Fossil Cave. Photo: Steve Bourne

Figure 13 - Dr Phil Currie (above) and Dr Jackson Njau (below). Photo: Steve Bourne

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