A SKULL of the MARSUPIAL 'RHINO' *ZYGOMATURUS:* MEGAFAUNA from JENOLAN CAVES, NEW SOUTH WALES

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Introduction

Caves are prime sites for discoveries of the bones of extinct animals, particularly those that are not of great geological age (e.g., animals from the Pleistocene or later). Preservation of these sub-fossil remains can be excellent and, since caves act as natural traps, bone accumulations can be substantial.

The animals most often associated with the Pleistocene Epoch are the extinct megafauna, defined as those animals with body weights greater than 44kg. Northern hemisphere Pleistocene mammals like mammoths, giant sloths and sabre-tooth cats are well known. In Australia, extinct megafauna include the megaherbivore *Diprotodon*, its smaller relative *Zygomaturus*, the fearsome predator *Thylacoleo* (the marsupial 'lion'), *Procoptodon* (the Giant Short-faced Kangaroo), and the giant goanna *Megalania*.

Aboriginal people have been in Australia for perhaps 50,000 years or more, and interacted with the last surviving megafauna. What caused the megafauna to become extinct has long been a matter of great debate, with the chief contenders being human causation, climate change or a combination of both.

Many species of megafauna are known from caves. In Australia, megafauna known from cave deposits include *Thylacoleo*, *Procoptodon*, *Megalania* and *Zygomaturus*. The massive Diprotodon, the largest marsupial known, was first discovered at Wellington Caves in New South Wales, and was the first Australian megafaunal species to be scientifically described. Australian caves noted for Pleistocene megafauna include Wellington Caves, Naracoorte Caves in South Australia, Nullarbor Plain caves, and the Western Australian Margaret River caves.

Holotype skull of Zygomaturus
Photo: Anne Musser

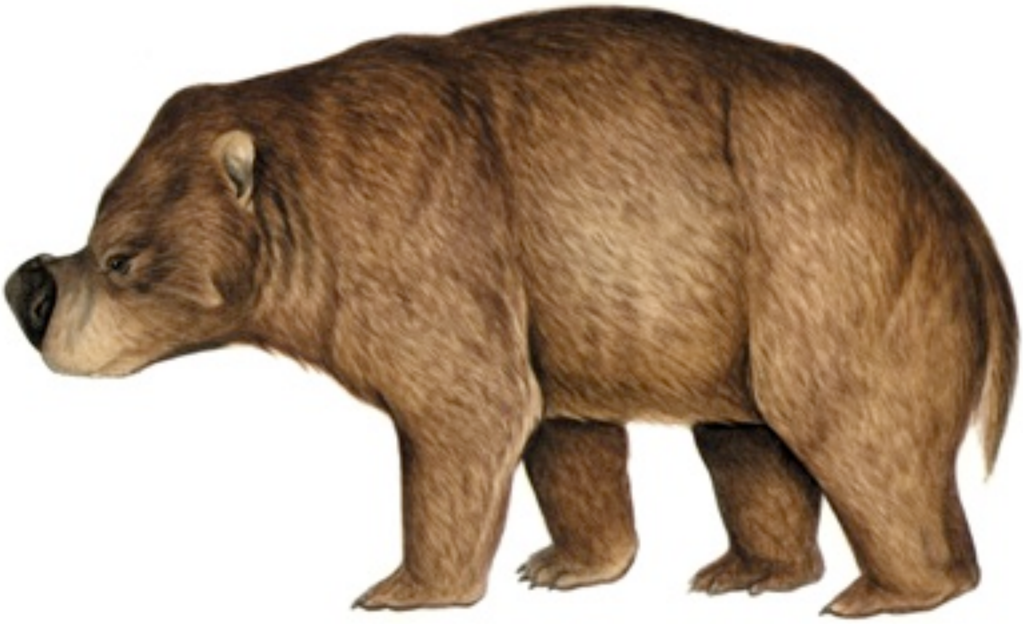
In this paper, we report megafaunal remains from Jenolan Caves in south-eastern New South Wales, a partail skull of the megaherbivore *Zygomaturus* (almost certainly *Z. trilobus*). The following account provides a brief description of the *Zygomaturus* skull from Jenolan, lodged in a rockpile in Wilkinson's Branch of the Chifley Cave in the north side of the Jenolan cave system, along with a history of *Zygomaturus* elsewhere in Australia. This account revises the identification of a skull found in the late 1800s first described as that of *Diprotodon* rather than *Zygomaturus*, and subsequently identified again as *Diprotodon* in an informal assessment in 2007 (for an account of its re-discovery, see Sasa Kennedy's article page 24).

***Zygomaturus*: the Marsupial 'Rhino' or 'Hippo'**

Zygomaturus was a diprotodontid, a member of the extinct herbivorous marsupial family Diprotodontidae, which also includes the larger *Diprotodon* along with several other species of diprotodontids. There are two subfamilies in Diprotodontidae - Zygomaturinae and Diprotodontidae. Zygomaturinae includes several very old genera and species in addition to *Zygomaturus*, including the sheep-sized *Silvabestius* from the late Oligocene of north Queensland, around 25 million years old; the mid-sized *Kolopsis*, from the late Miocene of central Australia, about eight million years old; and dwarf zygomaturines from the Late Pleistocene of New Guinea (Hulitherium and Maokapia). Early zygomaturines were much smaller and less specialised than *Zygomaturus*, with the lineage increasing in size over time. Diprotodontinae, a smaller subfamily, includes the massive *Diprotodon*.

The oldest fossils attributed to the genus *Zygomaturus* date from the late Miocene and are around six million years of age. There are several named species of Zygomaturus, and quite a degree of variability between specimens assigned to *Z. trilobus*, so whether or not these are separate species is still a question. Named *Zygomaturus* species include *Z. gilli* (late Miocene, Victoria, known from just a single premolar); *Z. keanei* (early Pliocene, South Australia); *Z. macleayi* (Pleistocene, Queensland); and *'Z.' nimborensia* from New Guinea (also called '*Kolopsis*' *watutense* or *'Nototherium' watutense*; although all New Guinea diprotodontids are probably Zygomaturinae, it now appears that *Zygomaturus* did not live this far north).

Zygomaturus was first discovered in the Darling Downs area of southeast Queensland. A well-preserved skull, now held by the Australian Museum, was named and described by William Macleay in 1857. The same skull



A reconstruction of Zygomaturus *by Anne Musser*

was later described by the famed Victorian era anatomist and palaeontologist Sir Richard Owen, who thought it should probably belong to the genus Diprotodon rather than to the new genus *Zygomaturus*, or perhaps a third Pleistocene diprotodontid, *Nototherium*. A complete *Zygomaturus* skeleton (now held by the Tasmanian Museum) was discovered by E. C. Lovell in Tasmania in 1920, at Mowbray Swamp.

Zygomaturus was a stout, quadrupedal marsupial – amongst marsupials, second in size only to the hippo-sized *Diprotodon* – with a body form roughly similar to that of a pygmy hippo (*Choeropsis liberiensis*) but slightly larger in size. *Zygomaturus* weighed 500kg or more, was about 2m long, and around 1m at the shoulder. The name '*Zygomaturus*' refers to its unusually broad cheekbones (zygoma), and 'trilobus' refers to the three prominent bumps on its snout. *Zygomaturus* has been dubbed the 'marsupial rhino' because some palaeontologists believe it may have had facial horns like those of a rhinoceros. Other nicknames include 'Swamp Cow', since its bones are often found associated with swamp deposits, and 'marsupial hippo' for its possible semi-aquatic lifestyle. Living as it did near rivers, lakes and swamps, *Zygomaturus* might have fallen prey to large crocodiles like the inland *Pallimnarchus*.

The skull of *Zygomaturus* is outsized (disproportionately large for its body size, as in many marsupials), but made up of surprisingly thin skull bones that helped to lighten its weight. Numerous air sinuses in the skull would have also reduced the weight of its skull (one reason that diprotodontid skulls are seldom preserved). The skull is unusually wide and 'boxy', but with a short, narrow snout. The snout is distinctly upturned and flared on each side, with rounded protuberances that may or may not have supported horns in life. There are large areas for muscle attachment at the back of the skull, which would have given *Zygomaturus* a 'bull neck.'

Zygomaturus had two large divergent, tusk-like first incisors on both upper and lower jaws. It might have used these 'tools' to rip plants up by their roots. Its five-cusped third upper premolar, like those of many diprotodontoids, is highly distinctive, and identification of P3 is the easiest way to confirm an identification. The molar teeth of *Zygomaturus* are broad and low-crowned and were probably used to grind coarse, woody vegetation. *Zygomaturus* had well-developed lips for manipulating vegetation, perhaps stripping leaves from trees and digging up tubers and roots with its tusk-like incisors. Like many marsupials, *Zygomaturus* had syndactylous (joined) toes. Its posture was low and sprawling, so it would have been somewhat lumbering, although it had mobile forelimbs, unlike large placental herbivores like bison.

The Jenolan *Zygomaturus*: A case of mistaken identity

The Jenolan *Zygomaturus* skull was initially found by the first Keeper of the Caves, Jeremiah Wilson, in Wilkinson's Branch off what is now the Chifley Cave (originally called the Left Imperial Cave). An account of the discovery, written by the surveyor Oliver Trickett, reads as follows: 'In October [1899] he [Jeremiah Wilson] found portions of the jaw and molar teeth of the *Diprotodon australis* in the Left Imperial Cave.' Signatures of both Jeremiah and Fred Wilson can be found further into this section of Wilkinson's Branch, not far from the skull.

The discovery of the skull was forgotten, and nothing was known of it for over a hundred years. It was re-discovered in 2007 by Jenolan staff during an after-hours caving trip. Puzzled by the large bones embedded in calcite and sediment, one of the authors along on the trip that night (SK) photographed them and brought them to the attention of Ted Matthews, a long-time Jenolan guide with extensive knowledge of cave science. Ted identified the bones as the teeth and jaws of a very large animal, and the Australian Museum was called in to help with the identification. Another of the authors (Robert Jones, Collection Manager, Australian Museum Palaeontology) confirmed Ted's initial identification, believing it to be the teeth and skull of the massive *Diprotodon*, although the obscuring matrix of calcified sediment made proper identification difficult.

Global media interest followed, with reports from as far away as China. The discovery of *Diprotodon* so close to Sydney, found in the famed Jenolan Caves, was of great interest. Likewise, the assumption that *Diprotodon* fossils were not usually found in a hilly, mountainous environment like that of Jenolan made waves in scientific circles. Jeremiah's original reports were later found, as was surveyor Oliver Trickett's report naming the species as *Diprotodon australis.*

Subsequently, one of us (AM) conducted a more complete investigation, removing as much of the matrix as needed to identify specific dental features that would help with identification. The skull is now confirmed as that of *Zygomaturus*, probably *Z. trilobus,* given its location and the size and shape of its teeth, almost identical in size and form to the dentition of *Z. trilobus* specimens at the Australian Museum used for comparison.

Description of the site

The skull is lodged between limestone rocks in the left hand section of Wilkinson's Branch off the Madonna Chamber, Chifley Cave, in the north side cave system. This partial skull is in an upright position, with the muzzle facing into the wall and the preserved parts of the back of the skull facing outwards. The fragile, lightweight skull has been fragmented, with much of it most likely further embedded in calcified sediments, and it's difficult to determine how much of the skull might actually be preserved. What remains of the left side of the skull is partially exposed, including dentition (the roots of the second and third upper left incisors and the left upper cheek tooth row) and sections of the sides and back of the skull.

Three survey trips were made between 2011 and 2014 to assess the site and skull, prepare and clean the specimen and identify the skull. The survey team included Jenolan staffers Stephen Kennedy and Richard Kennedy as well as the three of authors.

We had a look at the area to determine how the skull might have reached its present position, minus its body, wedged between rocks and encased in calcified sediments (intriguingly, a report by Wilson dated 1891 mentions the long bones of a very large animal from Wilkinson's Branch; were these removed, and were they the bones of our *Zygomaturus*?). The skull might have reached its present position as part of a slump deposit resulting from a collapse at a higher level. There is a mound of sediment chock-full of the bones of several species, to the side of the embedded skull, although the relationship of this deposit to the skull isn't yet known. Both the skull and sediment mound might represent an old pond that has slumped from above. *Zygomaturus* may have fallen into the pond, and the head may have become disarticulated from the body as it decomposed. Acidic water from rotting vegetation might have helped cause the collapse as carbonic and organic acid ate into the soluble limestone. The cave directly above Wilkinson's Branch, Michelmas Cave, is accessible from the surface, and the deposit may have originated in or passed through this cave before ending up below in Wilkinson's Branch.

Dr Anne Musser brushing away calcite that has been scraped from the tooth row of the Wilkinson Zygomaturus *(using a toothbrush on the teeth, of course!).*
Photo: Sasa Kennedy

Description of the skull and dentition

Anatomical information is limited because of the condition and position of the skull, and because preparation was carried out only as far as needed for identification. Matrix was carefully removed from around the dentition using dental tools and small brushes. Cleaning proceeded just to the point where the all-important premolar could be positively identified; further cleaning – with the possibility of damage to the specimen – was deemed unnecessary.

The lower left side of the skull is partly visible (the skull is missing above the tooth row). The partial skull is clearly crushed, and some elements have been displaced. Preserved skull material includes a section of the posterior zygomatic arch and part of the back of the skull. Some parts of this section may have fallen to the floor of the cave before, during or after its arrival in its present position. The posterior of the skull measures around 20cm across; however, as described, it has been broken and displaced, so this is not a useful measurement of the skull. The cortical bone is very thin, as in all diprotodontoids. Part of the inner ear region is exposed at the posterior of the skull. There are two rather chunky, ventrally located bones behind the tooth row, but their identities have been obscured by sediment.

The dentition includes the displaced and broken roots of the second and third upper incisors, the third upper left premolar (broken through the centre), and the complete upper left molar row minus part of the fourth molar (which is broken posteriorly). The animal appears to have been a mature adult at time of death judging from the moderate degree of dental wear. The teeth have been partially covered in calcite, some of which is moderately thick flowstone and some of which was able to removed.

The bases of the two incisor teeth are quite close together, anterior to the cheek tooth row, and displaced posteriorly from their original position in the skull. The anterior incisor root is roughly triangular in outline, while the posterior incisor base has a more oblong outline (its exact shape can't be determined because of breakage), resembling the incisor outlines of other *Zygomaturus*.

In *Zygomaturus* the third premolars are highly distinctive, with five cusps: two cusps on both the inner (lingual) and outer (labial) side, and an anterior cusp in the centre of the tooth (in contrast to the third upper premolar of *Diprotodon*, which has a 'horseshoe-like' circular crest). The premolar has retained the anterior cusp and remnants of the two innermost cusps, although because it is broken along the midline - probably an old break – the outermost cusps have been lost. The two inner cusps are partially visible: the second cusp appears to have been higher than the first, and it meets the first cusp via a slight crest.

The crowns of the second and third upper molars are obscured by calcite and sediment. However, the third upper molar could be cleaned, exposing its lateral side. This third upper molar has a notch or crest linking the anterior and posterior halves of the tooth, differing from the crest in the same tooth of a Queensland specimen (AMF.109960) in that it does not curve dorsally as it does in the Queensland *Zygomaturus*. The last molar (fourth upper molar) has been broken, and doesn't provide much in the way of information.

Measurements of the dentition are almost identical to those taken from an Australian Museum specimen with a complete cheektooth row (AMF.109960, which is a cast of *Z. trilobus*, Queensland Museum specimen QMF6560). In addition, the plaster cast of the Queensland *Zygomaturus* was taken into Wilkinson's Branch for a direct comparison with the Jenolan skull, which proved to be similar in length, measurements and other general features.

If this species is indeed *Z. trilobus*, as is almost certainly the case, the Jenolan skull would likely be Pleistocene in age since this species hasn't been recorded from either the Pliocene or Holocene. Dating of the skull or dentition hasn't yet been attempted, although it would be possible to remove very small samples of enamel from the *in situ* specimen for dating.

Palaeoecology and distribution of *Zygomaturus*

Zygomaturus is usually found in deposits interpreted as lakes, rivers or swamps, deposited during periods when the regions were well-watered and the climate temperate. Habitats are most often interpreted as areas of open woodland or forest, with rich vegetation, except for some drier areas in Western Australia, Kangaroo Island and Queensland. *Zygomaturus* has controversially been interpreted as possibly being semi-aquatic, wallowing in swampy areas close to waterways. As a megaherbivore, it may have feasted on roots and tubers, using its wide, splayed incisors to dig up buried vegetation. *Zygomaturus* fossils are rare, and it may have been a relatively solitary animal or an animal living in small herds.

Zygomaturus has been found in all Australian states, including Queensland, New South Wales, Victoria, South Australia, Western Australia and Tasmania, as well as from the Kimberley region in Western Australia. The geographical distribution of *Zygomaturus* appears to have been through coastal and montane Australia, with inland records along watercourses (for instance, the Lake Eyre region, where large herbivores like *Zygomaturus* and *Diprotodon* followed waterways through otherwise arid or semi-arid areas). Interestingly, the Kangaroo Island *Zygomaturus*, like many island forms, is dwarfed, and is much smaller than its mainland relatives.

In New South Wales, *Zygomaturus* has been recorded exclusively west of the Great Dividing Range until its appearance at Jenolan. Sites west of the Divide include Lake Mungo (where a single specimen has been found), Lake Victoria, Willandra Lakes, Bingara, and Cuddie Springs in the central west. Some evidence suggests that *Zygomaturus* co-existed with Aboriginal people at Willandra Lakes.

Extinction of *Zygomaturus*

Extinction dates for many species of Australian megafauna are hard to pin down, in part because many sites are poorly dated. Some megafaunal species seem to have disappeared well before the arrival of indigenous Australians (who may have entered Australia at least 50,000 years ago); some species disappeared soon after the arrival of people, at around 45,000 years ago; and some species survived until perhaps around 30,000 years ago, overlapping for a substantial amount of time with indigenous people (evidence from Cuddie Springs in New South Wales indicates at least 10,000 years of overlap between humans and megafauna).



Above Left. 'Original' discovery 2007.
Photo: Sasa Kennedy
Above middle.Close-up of the lingual (inside) half of the third upper premolar, with an old break running anteroposteriorly (fore and aft) through the centre of the tooth.
Above right. Dentition in situ.
Below left. Ventral view (underside) of the holotype Zygomaturus skull from Kings Creek, Darling Downs, Queensland (Australian Museum specimen F.49671).
Below right. A small hand mirror was held up to the third upper molar to determine the degree of tooth wear on this individual. Its partially worn teeth suggest that it was a mature (but not aged) adult at the time of its death.
Photos: Anne Musser


Megafaunal extinctions therefore appear to have been staggered across both time and space. Desertification during colder periods of the Pleistocene may have driven some species from now-arid habitats, isolating them in areas too small to sustain viable populations. Mounting evidence suggests that climate change was extensive during the 'extinction window' between 50,000 to 40,000 years ago, when large numbers of megafauna were lost. The role of early Australians in the extinction of the megafauna has been hotly debated; however, a consensus is building that megafaunal extinctions were caused by a combination of factors, including climate and human activity such as hunting and firestick farming.

Zygomaturus seems to have been one of the species that disappeared at around 45,000 years ago, soon after human arrival. At Tight Entrance Cave in southwest Western Australia, Zygomaturus is recorded in sediment layers dated between 143,000 - 48,000 years, after which it seems to have disappeared from the area. Over twenty *Zygomaturus* individuals were found in Mammoth Cave, also in southwest WA, dated between 55,200 and 44,400 years ago. *Zygomaturus* may therefore have become extinct in WA somewhere around 45,000 years ago. Because these Western Australian extinctions preceded a marked period of aridity, it is believed that human activity must have played a part in their extinction. Mammoth Caves and Tight Entrance caves both show evidence of human use of caves and possible interactions with megafauna.

Zygomaturus has been found in several sites in South Australia, including the Lake Eyre region, Naracoorte Caves and Kangaroo Island (a very young date of 20,000 years for the Kangaroo Island *Zygomaturus* has been questioned, and is probably no longer considered valid). Evidence from Lake Eyre suggests that animals migrated to more habitable areas during glacials (in Australia, 'glacials' were periods of cold, dry climate rather than ice, snow or glaciated landscapes although small areas of the mainland and more of Tasmania had ture glacial conditions), returning to the area when conditions improved. Large mammals, including *Zygomaturus* and *Diprotodon* – both known from Lake Eyre - would have used riverine corridors where water and food were available. When climate change caused these corridors to close, animals would have been vulnerable to local extinction, and populations would have gradually been reduced past the point of viability. One study shows that Lake Eyre was a deep lake at around 80,000 years ago, with well-vegetated habitat, before beginning a decline from which it has never recovered. All megafauna from Lake Eyre were gone by 30-35,000 years ago, in a staggered extinction of megafauna caused principally by climate.

The fossil record to date suggests that megafauna were most abundant and diverse in southeastern Australia (Victoria and New South Wales), followed by Lake Eyre. The latest dates for southeastern *Zygomaturus* are hard to come by. In Victoria, *Zygomaturus* has been found at Spring Creek, but dates are uncertain ('at least 35,000 years old'). Bingara deposits are thought to be Middle Pleistocene (780,000-126,000 years ago) rather than Late Pleistocene (126,000-10,000 years ago) and therefore can tell us little about the local extinction of *Zygomaturus*. At Cuddie Springs in the central west, *Zygomaturus* was found in the pre-archaeological sediments (although Diprotodon has been found in the higher archaeological layers, co-existing with humans). Getting a date for the Jenolan *Zygomaturus* would be quite a useful addition to the discussion.

Significance of *Zygomaturus* at Jenolan

The occurrence of *Zygomaturus* at Jenolan, just east of the Great Dividing Range in New South Wales and around three hours west of Sydney, is of interest for several reasons. First, the Jenolan *Zygomaturus* is the easternmost record for this species in the state, and the closest megafauna species to either Sydney or the Blue Mountains. *Zygomaturus* is otherwise known only from west of the Dividing Range in more central-western parts of New South Wales (Lake Mungo, Lake Victoria, Willandra Lakes, Bingara and Cuddie Springs). At Bingara, *Zygomaturus* co-existed with its larger relative *Diprotodon*, along with the true giant wombat, *Phascolonus gigas, Thylacoleo carnifex* (the marsupial 'lion'), and several species of kangaroos, including *Procoptodon goliah.*

Of the Pleistocene diprotodontoids, *Zygomaturus* would have probably been the most 'at home' at Jenolan, based on studies from other sites where *Zygomaturus* has been found. At Jenolan, *Zygomaturus* would have lived in protected river valleys between wooded hillsides, with swamps, pools and waterfalls, still seen at Jenolan today. *Zygomaturus* was not a climber or hopper, and probably left the limestone bluffs to the rock-wallabies. Perhaps Jenolan acted as a cool, well-watered refuge from the vagaries of the Pleistocene climate, as it does today.

The discovery of *Zygomaturus* at Jenolan, rather than its larger relative Diprotodon, is of interest: significant ecological differences between *Zygomaturus* and *Diprotodon* include choice of food (browsing for *Zygomaturus*, and a combination of browsing/grazing for *Diprotodon*); possible adaptations to semi-arid or arid conditions (some palaeontologists think *Diprotodon* may have had arid-zone anatomical adaptations), and niches as either specialists (*Zygomaturus*) or generalists (*Diprotodon*). *Diprotodon* was a more adaptable animal, found in many areas that would have excluded *Zygomaturus*, and it's not surprising that *Diprotodon* lasted far longer than it appears *Zygomaturus* did (possibly surviving until around 27,000 years ago).

Note: This report on the Jenolan *Zygomaturus* is not being published in a peer-reviewed scientific journal because the specimen, lodged between rock and cemented in by calcite, cannot be removed from its present position within Wilkinson's Branch. It is a condition of scientific research papers that specimens described in the literature must be made available to subsequent researchers, housed in a public institutional such as the Australian Museum, which in the current situation is not possible.

Acknowledgements

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