The Morphology and Relationships of the Largest Known Terrestrial Lizard, *Megalania prisca* Owen, from the Pleistocene of Australia

By Max K. Hecht*

INTRODUCTION

Megalania prisca was originally described by Owen (1860) from the Condamine River deposits of Queensland. It was early recognized as among the largest of known lizards. In general, lizards are relatively small insectivorous vertebrates with the larger forms usually herbivorous or omnivorous. Only members of the Varanidae, Helodermatidae and Teiidae are large and primarily carnivores or scavengers. The preponderance of small forms, less than a half-metre in total length, indicates that there are restrictions, some not completely understood, to the upper size limits of the basic lizard morpholoy. *Megalania* is probably at that limit. The role that this species played in the Pleistocene fauna is of primary interest to biogeographers and paleontologists.

RELATIONSHIP WITH THE VARANIDAE

That *Megalania* is a varanid is indicated by several oestological features listed by McDowell and Bogert (1954), Romer (1956), Fejervary (1935), and Hoffstetter and Grasc (1969), as follow:

1. Vertebrae characterized by oblique condyle-cotylar articulations particularly in the thoracic and lumbar regions.
2. Vertebral centra constricted anterior to the condyles.
3. Caudal vertebrae with pedicles for the haemal arches on the posterior portion of the ventral surface of the centrum.
4. Open Meckelian groove on the dentary.
5. Weakly developed zygosphene but no zygantrum.
6. Proximal bases of the teeth expanded and sculptured with fine vertical fluting.
7. Vagus nerve passing through hypoglossal nerve foramen as indicated by single foramen.
8. Sacrum composed of two vertebrae.
9. Interclavicle anchor-shaped.
10. Phalanges with prominant dorsal arch in lateral view and with well developed ventral process for flexor insertion of muscles.

The Varanidae includes 32 living species, all of which are now allocated to the genus *Varanus* which is in turn divided into ten subgenera. This family contains the largest living species of lizard, *Varanus komodoensis* of the Indonesian islands of Komodo and Flores, which attains a body length of at least 1·5 m with an equally long tail (Mertens 1942).

Megalania differs from all living species of *Varanus* in many features. Many of these attributes are associated with large size, but others are not allometric features and indicate distinct morphological differences. The following differences have been noted:

(a) Adult teeth are large and slightly recurved distally, with the anterior cutting edge rounded and serrated only distally. The posterior cutting edge is thin, blade-like and serrated along its entire length.

(b) Tooth replacement was slow with many teeth showing occlusal wear.

(c) Thoracic and lumbar vertebrae are massive and always have weakly developed zygosphenes and depressed, small neural canals.

(d) The dorsal protuberance of the ilium (attachment of ilio-pubic ligament of Romer 1922) is large, prominent and horizontally oriented (instead of dorsally at an acute angle as in *Varanus*).

(e) The external ridge of the ilium (origin of the the gluteal muscles of Romer 1922) is a thick, prominent ridge; in *Varanus* it forms a thin, blade-like prominence or may be absent altogether.

(f) The humerus has an unusually short shaft.

(g) The supraoccipital bone forms a 90° angle with respect to the occipital condyle, and the processus ascendens is ossified.

* Department of Biology, Queens College of the City University of New York, Flushing, New York, U.S.A. 11369.

(h) The posterior process of the prootic is covered dorsally by the paraoccipital process.

MATERIAL AND LOCALITIES

Material of *Megalania* is widely distributed in museum collections. The best was obtained during the late 19th century from the east Darling Downs and sold by the local inhabitants to various museums. Few complete skeletons were found and if any were known they were disarticulated and distributed among various collections. Little material, however, has come from these deposits during the last 70 years. *Megalania* is now known from the collections of the Queensland Museum (QM), Australian Museum (AM), South Australian Museum (SAM), British Museum (Natural History) (BMNH), University of California Berkeley Museum of Vertebrate Paleontology (UCMP), American Museum of National History (AMNH), Hunterian Museum of University of Glasgow (HM), National Museum of Victoria (NMV), and Western Australian Museum (WAM). The important collections are in the first six institutions listed above. Undoubtedly there is some material from the Darling Downs in the National Museum in Budapest, but this material has not been examined.

On the basis of these collections, it can be stated that *Megalania* is known from the following Pleistocene localities:

Queensland: East Darling Downs (Kings Creek near Pilton, Kings Creek near Clifton, Dalby, Bunya Creek near Bell Line, Warra, Fernless, Dandine Station); Dulacca; Springsure; Lynd Highway at Cape River crossing (Museum of Charters Towers Arch. Soc.).

New South Wales: Cuddie Springs near Brewarrina; Wellington Caves.

South Australia: Lake Kanunka, Coopers Creek (various localities including Katipiri waterhole); Warburton River (various localities); east Lake Eyre Basin (various localities); Diamantina River between Toopoowarka and Kalamurina Government Station.

No material from the Castlereagh River, New South Wales, reported by Etheridge (1917) has been seen. Anderson (1930) reports *Megalania* from Rosella Plains, near Cairns, Queensland. These specimens (AM F25228 and F25227) have been examined and are clearly the teeth of the crocodilian *Pallimnarchus pollens,* an Australian Pleistocene eusuchian crocodilian with a peculiar heterodont dentition. Most of the teeth are typically crocodilian, but several teeth resemble strongly those of the Sebecosuchia (Bartholomai & Hecht, MS in preparation; Anderson 1930, Pl. 1).

Megalania is known from a limited number of skeletal components which are: a complete occipital region (BMNH), a single incomplete large maxilla (AM) and a single incomplete small maxilla (QM), an almost complete large dentary (QM) and fragments of smaller dentaries, numerous dorsal vertebrae, a single cervical vertebra (AM), two incomplete sacra (QM), articulated initial three postsacral vertebrae (QM), other anterior caudal vertebrae (QM, AM (UCMP)), an almost complete humerus (QM), right and left ulna (QM, AM), a complete femur (AM), a complete ilium and pubis (QM), fragments of the radius (QM, AM), a single carpel (AM), several metapodials (AM), terminal phalanges (UCMP, AM, AMNH, SAM) and other phalangeal elements.

Most of the material of *Megalania* is of isolated fragments from many localities. The majority of the complete elements comes from Kings Creek near Pilton in the eastern Darling Downs. The best material in the Queensland and Australian Museums involves either two different skeletons or one nearly complete skeleton. De Vis (1889) records that a Mr. R. W. Frost of Kings Creek had brought to him 'a series of six ribs, an imperfect end of a fibula, and a nearly complete ulna—these together with as many other bones (including a dentigerous jaw) given by Mr. Frost to a local collector, and thereby secluded from examination so far, were discovered lying together in such relative positions, in a common matrix, as to convince the finder, who was then unaware of the value of such evidence, that all were parts of the same individual. Mr. Frost's opinion is strongly corroborated by their obvious identity as to kind and degree of mineralization, as well as to their peculiar subochreous colouration derived from the rather ferruginous sand in which they were buried.' In 1892 a Mr. Herman Lau of Yandilla, Queensland, an immigrant returning to Germany, sent to the Australian Museum complete parts of a skeleton. In a letter of 16 August 1892 he stated, 'Ten years ago I made a tour toward the head of King's Creek, a tributary to the river Condamine in the Darling Downs near the Toowoomba range and a station called Pilton. Here high in the bank I perceived the tip of jawbone with tooth thrusting out about eight feet below the grassy surface. Setting to carefully with pick and knife to work for a whole day I brought successively, what remained from the bony skeleton to light, out of a position, dipping from North (the head) to South. Never broke a single bone, found them as you behold them; the many fractures as you will observe, I believe are due to the small quantity of lime

with which the argillaceous soil was impregnated. Remarkable among the ribs is one, once broken and healed again, from which I imagine the result of a fight. Although I went for several days to the same spot, which I excavated to some extent, I was not fortunate enough in finding more.'

As mentioned above, in the Queensland Museum and Australian Museum there are right and left ulnae, which as will be discussed below are remarkably similar. The proportions of the various other elements are similarly preserved which may indicate that parts of the two collections are from the same individual fossil. In fact De Vis mentioned that Frost may have given part of the skeleton to another collector. A letter from H. Lau clearly indicates that he collected his own material, however. Both collectors indicate the presence of a jaw. There is a fragment of a toothless maxilla in the Australian Museum collections and an almost complete dentary in the Queensland Museum collections. The Australian Museum material was originally catalogued as crocodilian remains, but the broken rib described by Lau is clearly among the materials in the collection. The Lau collection, probably from a single fossil individual, includes a single maxillary fragment, a single cervical vertebra, ten thoracic vertebrae, ribs and rib fragments, a complete ulna, parts of a radius, a single carpal element, metapodials, a phalanx and femur. All bear the Australian Museum numbers F2203-2209 and F2212 (maxilla).

MORPHOLOGICAL DESCRIPTION OF KEY MATERIAL

Skull and Dentition

The skull of *Megalania* is known from only two elements, occipital region and a fragmentary maxillae.

The occiput (BMNH 39965; figured by Owen 1880) is complete except for the paraoccipital process, which is missing from the right side and incomplete on the left. A part of the basisphenoid, bearing the posterior of the sella turcica, is fused to the anterior portion of the basioccipital. General conformation of this specimen is most similar to the varanid occipital region, but there are at least three distinct differences.

In posterior view the supraoccipital abuts the parietal bone at a much more acute angle than in any species of *Varanus* and bears on its dorsal surface a very prominent occipital ridge. In *Varanus* at the dorsoanterior border of the supraoccipital there is a cone-shaped cartilage corresponding to the *processus ascendens tecti synotici*, which fits closely into the deep, funnel-shaped depression (the parietal fossa) in the posterior

border of the median line of the parietal (Bahl 1937). The articulation between the supraoccipital and the parietal bones was called by Bahl (1937) a peg and socket joint. Frazzetta (1962) calls this kinetic area a metakinetic joint and states that it is involved only in a sliding motion. In *Megalania* the supraoccipital bone extends dorsally into a point composed of the processus ascendens completely ossified to the supraoccipital bone. The sliding action of the 'parietal unit' (Frazzetta 1962) of the skull must have been lost.

Furthermore the occiputs differ in another feature. In *Varanus* the posterior process of the prootic (Bahl 1937) and the paraoccipital process abut each other and meet dorsally in a clear linear suture, but in *Megalania* the paraoccipital bone is wrapped around the posterior process of the prootic dorsally. Although sliding action between the two surfaces may have been possible in *Varanus*, it was not in *Megalania*.

In most other respects the occiput of *Megalania* and *Varanus* are similar. An estimate of the size of this piece can best be indicated by the maximum height and diameter of the foramen magnum, 24·4 mm and 21·6 mm respectively. The maximum diameter of the occipital condyle is 41·6 mm. If *Megalania* had the same skull proportions as *V. komodoensis* this occiput would have been derived from a specimen with a body length of almost 2900 mm!

The largest maxilla (AM F2212) is represented by the anterior portion only, bearing one broken tooth and nine sockets. Only about 153 mm of the dentigerous portion of the maxilla is preserved, and the extent of the missing portion is difficult to determine. The width of the larger tooth bases is about 16 mm. This fragment is probably from a specimen of similar size to that producing the femur and ulna.

The other maxilla (QM F14/870) is a much smaller fragment, bearing one complete tooth and four sockets. The single complete tooth has a basal width of 10·5 mm and a maximum height of 17·2 mm. This single tooth is of significance because its anterior dorsal aspect is clearly worn straight and smooth, demonstrating a wear pattern unknown in *Varanus* with this type of dentition although wear patterns are known in lizards with large, molariform, posterior teeth.

The teeth of *Megalania* are quite characteristic and will be discussed in a following section. Among the many isolated teeth available a few show wear facets but none more clearly than AMNH 9015 from the Menindee canal (Pl. 17, fig. 1). This tooth, from a much larger specimen than the maxillae described above, shows a single wear pattern. It has a maximum height of

16·2 mm and a tooth base maximum width of 10·5 mm. The wear surface is 12·9 mm long. It is clear from these two specimens that some of the teeth in *Megalania* did occlude and were also slowly replaced.

The mandible is known from a single, almost complete dentary and several dentary fragments. The most complete dentary (QM F6562, Pl. 17, fig. 3) is broken at the surangular and angular contact. Six teeth are represented by tooth bases, separated by alternate empty tooth sockets. The dentary must have originally borne twelve or thirteen teeth.

The dentigerous portion of the dentary is approximately 180 mm as measured from the posterior border of the area to immediately behind the symphyseal contact. The maximum length of the dentary is 212 mm as measured along a straight line from the coronoid contact to the jaw symphysis. The six teeth are all incomplete, but two have most of the crowns still present. They all bear typical varanid striations or flutings on their bases and are slightly recurved on the anterior distal edges. The anterior edge of the tooth is rounded, and the posterior edge is blade-like bearing fine serrations with about six serrations to the millimetre. The most complete tooth has a maximum basal width of 15 mm and a height of 12·5 mm with about 20-25 per cent of the height missing. At the coronoid contact the dentary must have had a depth of about 78 mm and at the level of the third tooth a depth of 31 mm.

The basic morphology of the dentary is very similar to that of *V. komodoensis* and all other living varanids (Mertens 1942a). The curvature of the dentary, as viewed dorsally, apparently increased in the *Megalania* with greater length. In this respect *Megalania* most closely resembles *V. komodoensis* although it is slightly more curved than the living species. If the dentary occupied the same proportion of the total mandible length as in *V. komodoensis*, then it can be estimated that the head of *Megalania* as measured from the quadrate or ear opening would be about 500 mm. The body length of the specimen extrapolated from this estimate would have been about 3100 mm.

The second smaller incomplete dentary (QM F871) lies within the size range of the larger living varanids, but is clearly identified as a *Megalania* by the teeth which bear an anterior rounded edge and posterior blade-like edge bearing serrations. This specimen bears only one complete tooth, the bases of three teeth, and one empty socket. Its basic morphology is very similar to the previously described specimen. The com-plete tooth has a base of 6 mm and a maximum height of 13 mm.

VERTEBRAL COLUMN

Vertebrae of *Megalania* are very similar to those of *Varanus komodoensis,* but about four times more massive. Many of the differences are primarily due to allometric factors.

The close resemblance of *Megalania* to *Varanus* in general morphology should reveal similar frequencies of the different types of vertebrae. Unfortunately the number and frequency of types of vertebrae is an unreliable index of the number of individuals found because these elements, perhaps from the same locality, have been frequently exchanged with various institutions and are, as a result, widely dispersed. Probably at one time there were as many as a hundred vertebrae known and at least one complete vertebral column. The most commonly preserved vertebrae are those from the dorsal series, which may be divided into the more abundant thoracic vertebrae and the less frequent lumbar vertebrae.

Based on the variation known within the family Varanidae (Hoffstetter & Gasc 1969) there should be 29 presacral vertebrae. Of these, nine should be cervical vertebrae. Of the sixty *Megalania* presacral vertebrae, in various states of preservation, only one is a cervical vertebra. This unexpected low frequency may be explained by the lower probability of preservation of cervical vertebrae because of their less robust morphology. An alternative hypothesis would be the reduction of the number of cervical vertebrae associated with the increased size of the head.

The number of postsacral vertebrae of *Megalania* is also unusually low in frequency. Not more than twelve vertebrae can be definitely allocated to the postsacral position. The few caudal vertebrae known are all from the anterior region of the tail. It may be that the more posterior caudal vertebrae do not bear the classic indications of *Megalania* and have been identified as *Varanus.* In the east Darling Downs no *Varanus* have been identified associated with *Megalania.* There are, however, two isolated varanid vertebrae from the middle or posterior region of the tail, which could be either a large *Varanus* or *Megalania.*

In most fossil deposits throughout the world in which varanids are preserved the caudal vertebrae are most frequently represented. This observation should be expected because of the length of the tail and the number of caudal vertebral elements in most species of the genus. The data from Mertens (1942a, p. 22) indicate an overall species trend in the relationship between body

length and tail length. Longer species have a lower body/tail ratio. As a result total length is not a good indicator of body size. The Komodo Dragon, the largest *Varanus,* has a body/tail ratio of about 1:1 (Mertens 1942b). Other species of almost the same total length have longer tails but shorter bodies. One glaring exception to this rule is the small Australian *Varanus brevicauda.* Therefore the unexpected low frequency of caudal vertebrae in *Megalania* possibly may be explained by this morphological trend. This hypothesis would indicate that the tail length of *Megalania* must be less than the body length.

The largest known *Megalania* vertebrae (QM F2947) is a posterior dorsal, possibly classified as a lumbar, and has a centrum length of 66·5 mm as measured from the ventral lip of the cotyle to the lip of the condyle. If comparison is made directly to the homologous vertebrae in *Varanus komodoensis,* then the approximate body length of this *Megalania* would be 3800 mm. Similar comparisons made with mid-dorsal (mid-thoracics and posterior thoracics) vertebrae from another vertebral column indicate a body length of between 2200 and 2400 mm.

The sacrum of *Megalania* is represented by two specimens in the Queensland Museum and the University of California, Berkeley, Museum of Paleontology. QM F14886, from the east Darling Downs, is only a fragment but enough to determine its varanid affinities and by its size to allocate it to the genus *Megalania.* UCMP 56423, from the Coopers Creek, east Lake Eyre Basin, represents a more complete specimen. The oblique cotyle-condyle relationship clearly establishes its varanid affinities. The condyle is badly abraded and the left transverse process broken. The cotyle has a maximum diameter of 33·2 mm and would have measured at a maximum 118 m across the transverse processes. The specimen, if it belongs to *Megalania,* was of a young adult and within the upper size range of a very large *Varanus komodoensis.*

APPENDICULAR SKELETON

The pectoral girdle is represented by only three nearly complete bones, the humerus, the ulna and a single carpal.

A single humerus, QM F865, is probably from the east Darling Downs and has already been discussed and figured by De Vis (1885, 1889). It is probably from an old individual as all evidence of the epiphyseal plate has been erased by complete ossification. The shape of the humerus is very similar to *Varanus* and the distal end of the humerus has a well-developed trochlea and capitellum. It differs from comparable varanid humeri only in the shortness of the shaft, which De Vis (1889) has already noted indirectly. Maximum length of the humerus measured from head to trochlea is 174 mm and the width across the epicondyles is 102·7 mm.

There are two nearly complete ulnae from the east Darling Downs, a left (QM F867) and a right (AM F2207) (Anderson 1930, Pl. 51). These specimens are both about 256 mm in maximum length. The semilunar notch is complete in the Australian Museum specimen and about 72 mm in maximum length. The coronoid process of the semilunar notch on the Queensland Museum specimen is broken. Both semilunar notches have bony overgrowths which may be old age osteoses. There are no signs of epiphyses or epiphyseal plates, which are usually seen in skeletons of *Varanus.* These ulnae thus appear to be from one or two old individuals. The minimum dorso-ventral diameter of the ulnar shaft is 35 mm. These ulnae are very similar in form to *V. komodoensis* differing primarily in the development of the radial facet and the distinctness of the muscle scars distal to the coronoid process and those at the distal end of the ulna. Direct comparison with ulnae of *V. komodoensis* would give an estimated body length of the individual *Megalania* of 2000 to 2300 mm.

A single carpal element was preserved in the Lau collection of the Australian Museum (F2208). It is a complete radiale and bears strong resemblance with the typical varanid element. Its maximum breadth is 56·1 mm. Comparison with *Varanus komodoensis* carpals indicates its origin to be from an individual of about 2300 to 2400 mm in body length.

The pelvic girdle is represented by two elements, an almost complete ilium and the dorsal portion of the pubis. Both specimens bear the Queensland Museum number F14877 and are from the east Darling Downs. They are not mineralized and clearly fit together.

The almost complete ilium is broken only at the posterior part of the sacral attachment. The acetabular portion of the ilium is perfectly preserved and comprises 40 per cent of the acetabulum, which is shallow and has a maximum diameter (measured across the width of the ilial portion) of 73 mm. The pubic contact of the ilium is 59·8 mm long whereas the ischial contact is 49·4 mm (as measured from the acetabular surface). The ilium of *Megalania* is very similar to *Varanus* but with some noteworthy differences.

The ilium of *Megalania* is characterized by a prominent horizontal, knob-like process to which the iliopubic ligament is attached. It is distinct in conformation from a similar process in

Varanus, which is more vertical in orientation and less prominent. The upper border of the acetabulum bears a prominent scar, probably the origin of the iliofemoralis muscle (Romer 1922). In *V. komodoensis* this is represented by a thin, prominent ridge.

The internal surface of the ilium is very similar to that of *V. komodoensis* with the origin of the gluteal muscles forming a thick, hillock-like prominence separated by a shallow depression from the ridge marking the area of sacral rib attachment.

A fragment of the pubis showing perfect contacts with the ischium and ilium and the entire acetabular region has been preserved. This piece articulates perfectly with the ilium and is undoubtedly from the same individual. It would appear that at one time there was also an ischium available. The pubic contribution to the acetabulum is most similar to that of *V. komodoensis.* The ischial contact is 35 mm long. The obturator foramen is large and prominent and approximately 15·5 mm in its greatest diameter. A part of the border of the thyroid foramen is also preserved. As viewed dorsally the iliac contact is broad and thicker than in *V. komodoensis* and is about 35 mm in width.

The perfectly preserved contacts between the three pelvic bones clearly demonstrate that in this specimen the pelvic ossification had not been completed, thus indicating subadult or young adult status. Most interesting is the fact that these two bones were most unlike all the other material of *Megalania* in not being mineralized. In cross-section at the suture lines both ilium and pubis show a thin compact bony layer on the outside and cancellous bone filling the area between. The entire appearance of both specimens is that of modern bones.

A comparison of this ilium and pubis with similar elements from *Varanus komodoensis* results in an estimate of body length between 1400 and 1600 mm, further supported by the lack of fusion between the various pelvic bones. An individual of this size is clearly a subadult of *Megalania* but would be in the maximum size category of *Varanus komodoensis.*

A single femur of *Megalania* is present in the collections of the Australian Museum and bears the number F2206 (Anderson 1930, Pl. 50). It is complete and is markedly similar to a large *V. komodoensis* but about twice its length. As distinct from those of *Varanus,* the epiphyseal plates are closed and only a weak line indicates their former presence. This femur is obviously from an older animal. Slight differences between the two forms are expressed primarily as more

distinct muscle scars in *Megalania.* The maximum length of the femur is 293 mm and width across the condyles at its distal end is 99 mm. Direct comparison with a *Varanus komodoensis* would give an estimated body length for the *Megalania* as approximately 2200 mm.

In the Lau collection of the Australian Museum there are several elements which may be considered metapodials, but it is difficult to determine whether they are metatarsal or metacarpal elements. Additionally, there are some phalangeal elements which cannot be identified. Unique among the metapodial elements is the classic hooked fifth metatarsal represented by one specimen (AM F2208, Pl. 18, fig. 3). If it is properly associated with the remainder of the *Megalania* skeleton, then it clearly shows some differences with that element of *Varanus.* Unfortunately it is incomplete and has a distal portion missing as well as part of the metatarsal hook. It can be clearly distinguished from the fifth metatarsal of *Varanus* by the expansion of the distal portion of the element, an expansion so great and so different that one might question whether it is part of *Megalania.* Assuming that the association is correct, and the appearance of the bone and the preservation indicate so, then there must have been a remarkable difference in the pes of the fossil probably associated with its large size and its locomotory pattern. The maximum length of the fifth metatarsal was 62·2 mm.

The terminal phalanx of lizards is easily identifiable, and several large complete terminal phalanges are known and allocated to *Megalania.* In the past these elements have been confused with bird phalanges but are distinguishable from these by the prominent development of a rectangular knob on the ventral surface of the phalanx which was probably the point of insertion of the flexor muscle. Furthermore, the varanid phalanx in lateral view bears a highly arched dorsal contour with shallow depressions on each side.

Terminal phalanges are known from the following localities in South Australia: Coopers Creek, east Lake Eyre Basin; Warburton River; Katipirri Sands, Coopers Creek; Lake Kanunka. Another specimen from Bunya Creek, east Darling Downs is present in the Queensland Museum (F2477) collections. The variation in the size of these elements gives data which may be used to estimate body size. SAM P11529 measures 55·5 mm in maximum length and 23·4 in maximum height (from the flexor to the top of the dorsum). This specimen has no definitive data but Mr. N. Pledge suggests it could be the specimen referred to by Zeitz (1899) as a new species,'*Varanus warbur-*

tonensis' (Kuhn 1939). UCMP 47956 measures 41·1 in maximum length and 17·1 in maximum height and is from the Warburton River. QM F2477 is incomplete in maximum length and is 17·5 mm in maximum height. This specimen is 32 mm long but lacks approximately 8 mm of phalanx. It is difficult to compare these phalanges with any of *Varanus* because we do not know from which digit they originated.

UCMP 56420 (Pl. 18, Fig. 1) from Coopers Creek in the eastern Lake Eyre Basin is 84·5 mm in maximum length and 33·4 mm in maximum height. This specimen is over one-third longer than any previously examined material and is distinguished by its greater breadth and marked development of the flexor knob. These distinct features could easily represent either another unknown form or an unusually large *Megalania*. There are no other known remains of *Megalania* which would indicate individuals of this size. There are several possible explanations. Firstly, the terminal phalanx could be misidentified. Secondly, there remains the possibility that some claws have been enlarged in *Megalania*, but the obvious close relationship of the genus to *Varanus* precludes this conclusion, since no varanid is known with this condition. Thirdly, this phalanx is from a large varanid, most probably *Megalania*. If the latter is true, then the type of *Varanus warburtonensis* is certainly a *Megalania*, and the species should be placed in the synonymy of *M. prisca*.

It would appear that the smaller terminal phalanges averaging a maximum length of 40 mm probably belongs to a *Megalania* with a body length of 2·5 m. The larger phalanx represent an individual probably 3 to 3·5 m long. The largest specimen could represent an individual of nearly 4 to 5 m long. At present there is a problem because there are no other osteological elements which indicate a body length of greater than 3 to 3·5 m.

OTHER MATERIAL

In the Australian Museum there are ribs which were associated with other material collected by Lau (AM F2209-2211). Some of the ribs are complete and are more robust and less bowed than the comparable elements in *V. komodoensis*. It is difficult to determine from which area of the rib cage these elements originated.

A single lizard interclavicle, UCMP 47956, from the Warburton River, east Lake Eyre Basin, is most probably a part of *Megalania* as indicated by the characteristic anchor-shaped varanid form and its large size. The median piece of the inter-clavicle has a maximum width of 15·4 mm. If it was derived from a *Megalania* it was within the average size for the species or perhaps a little smaller.

STATUS OF *Varanus dirus* De Vis

De Vis (1889) described *Varanus dirus* from a single isolated tooth from the Pleistocene of Kings Creek, east Darling Downs, Queensland. He did not give a diagnosis but recognized that it was smaller than the usual *Megalania* tooth and much larger than the teeth of the available *Varanus*. Fejervary (1918) concurred with De Vis and figured the isolated tooth. The holotype (QM F873) bears clear resemblance to teeth of *Megalania* in size, structure and general form. The tooth is twice the size of *V. komodoensis*, but two-thirds the size of the average *Megalania*. The tooth has a maximum height of 24·5 mm, which is well within the range of the larger species.

The holotype of *V. dirus* differs from most of the extant Australian varanids by the presence of the posterior serrated cutting edge and the anterior rounded surface. *Varanus* have either anterior and posterior cutting edges with or without serrations on both surfaces or a general rounded surface on both edges. The holotype resembles *Megalania* and *Varanus komodoensis* by its posterior serrated cutting edge and its anterior face rounded at the base with only the slightest serrations on the distal anterior curvature. The tooth is distinctly more recurved than the largest *Megalania* teeth.

The holotype bears resemblances to the teeth of *V. komodoensis* and particularly in the curvature of the distal portion of the tooth. The largest available Komodo lizard skeleton with known body length (1298 mm) has a maximum tooth height of 18 mm. The available teeth of *Megalania* indicate an ontogenetic change in the shape of the teeth as to curvature and thinness, whereby both of these might be reduced as the individual approached maximum size. In the light of the variation within *Megalania* it seems most parsimonious to consider the apparent differences described by De Vis as at best individual variation and thus the name *Varanus dirus* should be treated as a synonym of *Megalania prisca*.

A single maxilla (QM F874) from the Chinchilla rifle range, west Darling Downs which is generally considered late Pliocene has been allocated by Fejervary (1918) to *Varanus dirus* DeVis. This maxilla is almost complete and bears three complete teeth, five tooth bases, one tooth socket. It is complete anteriorly but lacks the

posterior portion of the dentigerous area. The three complete teeth are in a linear series and they become slightly larger posteriorly. The base of the posterior tooth is 6·8 mm and its maximum height is 17·5 mm.

The external face of the maxilla is well preserved (except for the aforementioned area), but the contact with the prefrontal is missing. The slight shelf making contact with the cartilaginous olfactory capsule (Bahl 1937) is complete and well developed. The contact with the premaxilla is complete, and large external nares are indicated at the anterointernal premaxillary contact. The palatal shelf is incomplete.

This bone and its teeth resemble those of *Varanus komodoensis*. It can be compared with a specimen of approximately the same size (AMNH 37913). It differs from this specimen by having a larger external narial opening and a larger more vertical prefrontal process of the maxilla. In general the face must have been broad snouted as in the Komodo lizard, but the orbit may have been further back and the lateral face of the skull more vertical.

In conclusion it seems most reasonable at this time not to assign this specimen to either *Megalania* or *Varanus* because the equivalent material is not available for *Megalania*. It is certain that this form is from an earlier fauna and may indicate the presence of a large varanid in the late Pliocene.

In the older Queensland Museum collections from Chinchilla there are four vertebrae (two caudals and two posterior dorsals) bearing the numbers C20 and C106. The largest vertebra, probably a lumbar, has a centrum length of 32·5 mm as measured from the ventral lip of the cotyle to the posterior end of the condyle. Similarly the caudal vertebra has a centrum length of slightly more than 32 mm. Both of these specimens have the characteristic depressed neural canal of Megalania. The size and form of these vertebrae match closely the general proportions of a Komodo lizard of known body length of 1298 mm. The fossil vertebrae can be distinguished by the more depressed neural canal. The dimensions of the vertebrae and maxilla indicate that they represent a similar sized individual, or individuals.

In the collections of the Queensland Museum there are specimens with no data which appear to be from the same locality based on similarity of preservation. One of these vertebrae appear to be larger than the above. It is probable that the Pliocene species was a smaller species than the Pleistocene form.

DISCUSSION OF *Megalania*

Dimensions and Size

The difficulty in reconstructing the size of *Megalania* is in the lack of complete skeletons. Most of the material in modern collections is fragmentary, of individual bones. Only two collections have associated elements, the Lau collection in the Australian Museum and the Frost collection in the Queensland Museum. As was stated previously, it is quite possible that both of these collections are the remains of a single individual. The most intact collection is in the Australian Museum.

If an assumption is made that *Megalania* had basically the same proportions as *Varanus komodoensis* (except in the length of the tail), then the following comparisons can be made. All the material of the Lau collection (femur, ulna, radiale, thoracic and lumbar vertebrae) yield an estimated body length of between 2200 and 2400 mm. Similarly, the elements in the Frost collection of the Queensland Museum (ulna, thoracic and lumbar vertebrae) yield the same result. Most of this material indicates an average size mature lizard. The humerus in the Queensland Museum may have been part of this series, although it is not clear from De Vis' discussion (1889). As stated previously this specimen is from a mature individual but is characterized by an extremely short shaft as compared with the Komodo lizard and indicates an individual with a body length between 1500 and 1600 mm.

It is most probable that the above-mentioned material was the average for the species as a whole, but in lizards there is continual growth, and undoubtedly there were exceptionally large individuals as indicated by the well-preserved large dentary, the largest lumbar vertebrae and the huge terminal phalanx. The large dentary (QM F6562) indicates a body length of about 3100 mm and a head length of about 500 mm (as measured from the quadrate or the external ear to the snout). The largest known vertebra, a lumbar (QM F2947), has a centrum length of 66·5 mm and would indicate a minimum body length of 3800 mm. The terminal phalanges indicate an average body length of about 2200 to 2300 mm. The second largest phalanx indicates a body length of about 2600 or 2700 mm. The largest phalanx, if it is a *Megalania,* would indicate a body length of 4500 mm.

The discussion of the morphology and frequency of postsacral vertebrae indicates that the tail must have been between one-half to one-third of the body length. Therefore the maximum length attained by this species would be a body length

of 4·5 to 5 m with a tail between 2 and 2·5 m long. The total length must have been close to 7 m.

With an estimate of body and tail length it is possible to extrapolate from data on living lizards and derive an estimate as to the body weight of *Megalania*. Auffenberg (1972) states that an eleven foot (3·3 m) *Varanus komodoensis* would weigh between 150 and 200 lbs (ca 79 kg). With the data provided by Pough (1973) on the relation between body length and body weight in lizards, it is possible to make an estimate of the body weight of *Megalania* as being between 600 kg and 620 kg, at a maximum. It would certainly appear that *Megalania* was a formidable predator.

Systematic Status of the Genus

McDowell and Bogert (1954) placed the genus *Megalania* within *Varanus*. The above morphological analysis reveals significant differences between this fossil and the other forms of *Varanus*, such as: the reduction of kinetism in the skull and its associated morphological changes, the short humerus and peculiar fifth metatarsal indicating a change in locomotory pattern, and the distinct cutting surface of the teeth and associated wear patterns with an associated reduction in tooth replacement. These differences and other changes, possibly allometric, distinguish the fossil from the other subgenera of *Varanus*. They are great enough to justify at least subgeneric status, if not generic. The latter evaluation is preferred.

Ecological Role

The presence of such a large lizard predator in the Pleistocene of Australia further substantiates the uniqueness of the megafauna of the period as demonstrated by Keast (1971) for the mammalian faunas. In his analysis Keast compares the mammalian faunas of Africa, South America and Australia by partitioning the major adaptive zones occupied by mammals. Simple examination of the data reveals an unexpected low percentage of carnivores in Australia, particularly in the large carnivore (large felid zone) and the small carnivore (mustelid) zones. On the basis of this analysis the mammalian fauna of Australia in the late Pleistocene may be considered as unbalanced when compared with that of Africa or South America. This type of analysis of a 'taxocene' (Whittaker 1972) has obvious faults because it implies that a systematic group can, in its adaptive radiation, fill all the available niches. The failure of the mammals to do this in Australia must have some historical basis in the develop-

ment of the stratification of the vertebrate fauna. In the large carnivore adaptive zone Keast (1971) places the bizarre *Thylacoleo*, which must have been the most specialized of carnivores. It certainly could not have filled the big felid niche. Furthermore, in the small carnivore adaptive zone there is a noticeable lack of diurnal predators.

Within the Australian lizard fauna the family Varanidae makes up an unusually large part of the fauna. Of the thirty-two species of Varanidae in the entire world, nineteen are known from Australia. Of the eleven subgenera of the genus *Varanus* only two subgenera occur in Australia and one endemic subgenus occurs in New Guinea. These facts indicate that an adaptive radiation of this family has taken place in the Australasian region. Australia must have been colonized by at least two separate invasions. Within these two subgenera there has been a remarkable adaptive radiation into various niches. For example there are arboreal varanids (*V. prasinus, V. gilleni, V. timorensis*), aquatic varanids (*V. mertensi, V. mitchelli*), mangrove varanids (*V. semiremex*), general predators and scavengers (*V. varius, V. gouldii*), large predators of rabbit-sized prey (*V. giganteus*) and small insectivorous predators (*V. eremias, V. brevicauda*). This remarkable radiation today occupies all the adaptive zones except the large felid predator niche.

All localities for *Megalania* are associated with late Pleistocene mammalian faunas. These localities seem to offer no clear pattern except that they are primarily west of the Eastern Highlands. They indicate more a distribution of known Pleistocene fossil localities than the distribution of any particular organism. Only for the Warburton River area has a tentative radiocarbon date been determined (23,000-25,000 B.P., Stirton et al. 1968, Twidale 1972), and this is the first estimate of the absolute time at which this species lived. The occurrence of a single specimen at Lake Menindee lunette (AMNH 9016) indicates the possibility of another date of 19,000-26,000 B.P. (Stirton et al. 1968, Jones 1968). It is certain that *Megalania* was associated with the large herbivorous mammalian populations of the late Pleistocene, including four giant genera of Diprotodontids, four genera of Macropodids and one giant wombat. It is also evident that except for *Thylacoleo* there is no real carnivore exploiting this trophic level of large herbivore. According to Auffenberg (1972) *Varanus komodoensis* holds such a predator role in the fauna of Flores and Komodo and actively hunts deer, horses and cattle. The larger *Megalania* could easily use the technique of the living *Varanus* and be the miss-

ing carnivore component in the megafauna of Australia, occupying the highest trophic level in the food pyramid based on the late Pleistocene herbivores.

Pough (1973) in a review article on lizard energetics, diet and evolutionary strategy, states that lizards, upon evolving greater size, generally require an herbivorous diet. This observation was based on an analysis of five families which show such a trend. As he pointed out an obvious exception to the rule are the families Helodermatidae, Teiidae, Anguidae and Varanidae. His interpretation is that lizards on attaining the larger size would be unable to obtain large enough packets of food because their physiological efficiency is lower than mammals. It should be pointed out that lizards do have an advantage in that their lower metabolic activity during periods of lower temperature and activity is also a form of efficient utilization of limited resources. A more important difficulty with Pough's analysis is that it is based on his unidimensional interpretation of the present-day fauna. The determinants for any group have an historical background. The arrival of the varanids on a continent (e.g. Australia) in which no terrestrial vertebrates had occupied the carnivore niche completely, allowed for the opportunistic development of the primary consumer. Pough implies that it was the varanid approach to mammalian physiology which was the key factor. Actually the varanid strategy is quite different from the mammal but it was equally effective as Australia moved northwards into warmer climates and developed arid environments during the Mid- to Late-Tertiary. In South America the large Teiid lizards have invaded an analogous adaptive zone for similar reasons. In the Greater Antilles, specifically on Jamaica and Hispaniola, large species of *Celestus* have occupied the crab-eating and small predator niches. In all these environments it was not physiological and behavioural limitations which guided the evolutionary strategy but the opportunity to exploit available adaptive zones, which because of the nature of the fauna, were vacant. The real question is what occupied the varanid adaptive zone before the arrival of the lizards and why did the marsupials not fully occupy the zone?

ORIGIN OF THE AUSTRALIAN VARANIDAE

The living Australasian Varanidae have, as previously demonstrated, undergone an adaptive radiation based on at least two or three separate invasions. The herpetofauna of Australia can be divided into two major elements, the old Gondwana faunal derivatives and the more recent invaders from the north. The Varanidae must be considered a late Tertiary invader of Australasia for the following reasons. Firstly, the earlier fossil varanids are from the Late Cretaceous, Paleocene and Eocene of North America, Europe and Mongolia, certainly a Laurasian distribution. Secondly, the majority of the living subgenera of the family are in Eurasia. Thirdly, had the Varanidae a Gondwana distribution, its closest relatives should have been represented in South America. In place of the Varanidae, the South American lizard fauna have evolved complementary elements in the form of the large Teiid lizards.

The earliest fossils of the Varanidae known from Australia have not as yet been formally described. A single broken varanid vertebra (UCMP 57250) is known from the Etadunna formation (Stirton et al. 1961), now generally considered Middle Miocene. If this identification is correct, then the Varanidae invaded Australia from the north at a time when the continent was further south. The dispersal over the enlarged water gap must have been a formidable feat, thus limiting the number of varanid forms which were capable of making the invasion. Fossil varanid-like vertebrae are known from the Waite Formation in the Northern Territory, which is generally considered late Miocene. Whereas the Varanidae occur in Africa, another Gondwana continent, the invasion must have been very recent as evidenced by the lack there of varanid fossils in the Miocene and Pliocene (Hoffstetter 1962).

CONCLUSIONS

The varanid lizard *Megalania prisca* Owen is known from the Pleistocene of southern Queensland, western New South Wales and north-eastern South Australia. It was the largest terrestrial lizard, attaining a maximum body length of five m and two or three m tail length and an estimated maximum weight of about 600 kilograms. This genus developed various specializations associated with its large size such as reduction of cranial kinesis and changes in limb structure related to locomotory patterns. *Megalania* was probably the important predator of the large diprotodontid herbivores and giant ground birds of the Australian Pleistocene and became extinct along with this associated fauna.

ACKNOWLEDGMENTS

University which made facilities available to complete the study. The illustrations were made by Mr. Matthew Hecht and Mr. John Schweitz.

REFERENCES

ANDERSON, C., 1930. Paleontological Notes No. II: *Meiolania platyceps* Owen and *Varanus* (*Megalania*) *priscus* (Owen). *Rec. Austral. Mus.* 27: 309-316.

AUFFENBERG, W., 1972. Komodo dragons. *Nat. Hist.* 81(4): 52-59.

BAHL, K. N., 1937. Skull of *Varanus monitor* (Linn.). *Rec. Indian Museum* XXXIX (II): 133-174.

COGGER, H. G., 1959. Australian goannas. *Aust. Mus. Mag.* 13: 71-75.

DE VIS, C. W., 1885. On bones and teeth of a large extinct lizard. *Proc. R. Soc. Qd* 2: 25-32.

————, 1889. On *Megalania* and its allies. *Ibid.* 6: 93-99.

ETHERIDGE, R. Jr, 1917. Reptilian notes. *Proc. R. Soc. Vict.* 29: 127-133.

FEJERVARY, G. J. DE, 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. *Ann. Mus. Nat. Hung., Budapest* 16: 341-467. 2 pls, figs.

————, 1935. Further contributions to a monograph of the Megalanidae and fossil Varanidae— with notes on recent Varanians. *Ann. Mus. Nat. Hung. Pars Zool.* 29: 1-128.

FRAZZETTA, T. H., 1962. A functional consideration of cranial kinesis in lizards. *J. Morph.* 111: 287-319.

HOFFSTETTER, R., 1962. Revue des récentes acquisitions concernant l'histoire et la systèmatique des squamates. *Colloques Intern. C.N.R.S.* No. 104: 243-279.

———— & GASC, JEAN-PIERRE, 1969. Vertebrae and Ribs of Modern Reptiles. In: *Biology of the Reptilia*. Academic Press, London. 1: 201-310.

JONES, R., 1968. The geographic background to the arrival of man in Australia and Tasmania. *Archeol. Phys. Anthro. Oceania* 3: 186-214.

KUHN, O., 1939. Squamata: Lacertilia. *Fossilium Catalogus*, Pars 86: 1-83.

KEAST, A., 1971. Continental drift and the evolution of the biota on southern continents. *Quart. Rev. Biol.* 46: 335-378.

McDOWELL, S. B. & BOGERT, C. M., 1954. The systematic position of *Lanthanotus* and the affinities of the anguinimorphan lizards. *Bull. Am. Mus. nat. Hist.* 105: 1-142.

MERTENS, R., 1942a. Die Familie der Warane (Varanidae). *Abhandl. Sencken, Natur. Gesell.* 462: 1-391.

————, 1942b. Die Familie der Warane (Varanidae). Weiter Teil: der Schädel. *Ibid.* 465: 117-234.

NOPSCA, F., 1908. Zur Kenntnis der fossilen Eidechsen. *Beitr. Pal. Geol. Osterr. Ungarn. Orient.* 21: 33-62.

OWEN, R., 1860. Description of some remains of a gigantic land-lizard (*Megalania prisca* Owen) from Australia. *Phil. Trans. R. Soc.* 45-46.

————, 1880. Description of some remains of the gigantic land-lizard (*Megalania prisca* Owen) from Australia. Part II. *Ibid.* 171(3): 1037-1050.

————, 1884. X. Evidence of a large extinct lizard, *Notiosaurus dentatus* Owen from Pleistocene deposits, New South Wales, Australia. *Ibid.* 175: 249-251.

POUGH, F. H., 1973. Lizard energetics and diet. *Ecology* 54(4): 838-844.

ROMER, A. S., 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull. Am. Mus. Nat. Hist.* 46: 517-606.

————, 1956. *Osteology of the Reptiles*. Univ. Chicago Press. 772 p.

STIRTON, R. A., TEDFORD, R. H. & MILLER, A. H., 1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Geog. Rev.* 62: 40-70.

————, ———— & WOODBURNE, M. O., 1968. Australian Tertiary Deposits containing Terrestrial Mammals. *Univ. Calif. Publ. Geol. Sci.* 77. 30 pp.

TWIDALE, C. R., 1972. Landform development in the Lake Eyre basin. *Austral. Geog. Rev.* 62: 40-70.

WHITTAKER, R. H., 1972. Evolution and measurement of species diversity. *Taxon* 21(2/3): 213-251.

ZEITZ, A., 1899. Notes upon some fossil reptilian remains from the Warburton River, near Lake Eyre. *Trans. R. Soc. S.A.* 23: 208-210.

DESCRIPTION OF PLATES

PLATE 17

FIG. 1—Isolated tooth of *Megalania prisca* showing occlusal wear. From the Menindee canal, N.S.W. (AMNH 9015), × 6.

FIG. 2—Isolated, unworn tooth of *Megalania prisca*, × 6.

FIG. 3—Lower jaw of *Megalania prisca* (QM F6562) from the east Darling Downs, Queensland. A. External view, × 1/6th.

PLATE 18

FIG. 1—Terminal phalanx of *Megalania prisca* (UCMVP 56420) from Coopers Creek, east Lake Eyre Basin, × 2.

FIG. 2—Terminal phalanx of the type of *Varanus warburtonensis* Seitz, × 3-1/3.

FIG. 3—Fifth metatarsal of *Megalania prisca* (AN F2208) from Kings Creek, east Darling Downs, Queensland, × 1-1/3.