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PO Box 3300, South Brisbane 4101, Australia
Phone 06 7 3840 7555
Fax 06 7 3846 1226
Email qmlib@qm.qld.gov.au
Website www.qmuseum.qld.gov.au

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FIRST RECORD OF A GIANT VARANID (*MEGALANIA*, SQUAMATA) FROM THE PLEISTOCENE OF NARACOORTE, SOUTH AUSTRALIA

ELIZABETH REED AND MARK N. HUTCHINSON

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A humerus attributable to the giant varanid *Megalania prisca* Owen, 1859, from a newly discovered Pleistocene cave site near Naracoorte, South Australia extends the distribution of giant varanids south of any previous record. Unlike the only other known humerus (QM F865 from the eastern Darling Downs), the new specimen represents an immature animal (epiphyses unfused) and allows insight into the pattern of growth of *Megalania*. Both *Megalania* humeri are massively built with the distal width being much broader than the proximal width (proximal is slightly greater than distal in all living varanids). The immature specimen from Naracoorte is within the range of lengths seen in large extant varanids but is far more robust than any living species. Estimates of the size and proportions of *Megalania* have been based on *Varanus komodoensis*, the largest living varanid. However, based on our examination of humeri from 19 living varanid species, the humeri of even large *V. komodoensis* retain the proportions of smaller varanids and do not suggest the remodelling evident in *Megalania*. Rather than being a scaled-up *Varanus*, *Megalania* as represented by the humeri, appears to have been a massively built animal throughout its life, its proportions not matched by those of any living *Varanus*. Size estimates for *Megalania* based on the length of bones in living varanids may well be in error, and the larger estimates are probably overestimates. ❑ *Pleistocene, Naracoorte, varanid, Megalania, humerus, caves*.

E.H. Reed, c/- School of Biological Sciences, Flinders University of South Australia, c/- Naracoorte Caves National Park, PO Box 134, Naracoorte, SA 5271 Australia. ; M.N. Hutchinson, South Australian Museum, North Terrace, Adelaide SA, 5000, Australia; 1 August 2004.

Fossil remains of giant Pliocene to Pleistocene varanids, currently attributed for convenience to *Megalania prisca* Owen, 1859, are known from widely scattered localities in northern and eastern Australia (Fig. 1) (Longman, 1924; Hecht, 1975; McNamara, 1990; Mackness & Hutchinson, 2000). The earliest record of Australian giant varanids comes from the Miocene of the Northern Territory (Murray & Megirian, 1992). Many parts of the skeleton of *Megalania* are represented by fossils, but these stem from only one or two fragmentary skeletons together with numerous isolated bones, mostly vertebrae (Rich & Hall, 1979). Remains have been considered too scanty, with few elements known from multiple examples, to determine whether the remains are attributable to one species or several. Several workers have questioned whether the genus *Megalania* is distinct from *Varanus* (Estes, 1983; Lee, 1996; Hutchinson & Mackness, 2002), given that the differences between the two genera are mostly thought to be due to expansion and robustness associated with large body size. Hecht (1975), Rich & Hall (1979) and Wroe (2002) have discussed the overall size and proportions of *Megalania*, and Erickson et al., (2003) made estimates of growth rates and time to maturity. In the absence of adequate associated remains, reconstructions of *Megalania*'s appearance depend heavily on extrapolations from living varanid lizards. Similarly, reconstructions of its palaeoecology are limited by knowledge of its distribution.

The caves of Naracoorte, South Australia contain some of the richest Pleistocene fossil deposits in Australia and have yielded a diverse array of vertebrate species (Reed & Bourne, 2000), yet fossils attributable to *Megalania* have never been found there. This paper describes a specimen from a Naracoorte cave site that is recognisable as belonging to a giant varanid such as *Megalania*. The Naracoorte specimen is a humerus of an immature individual and allows some insight into the pattern of growth. Comparison between humeral proportions for the fossil varanids and extant species is also presented in this paper.

METHODS

The site of the discovery of the new specimen is Crawford's Cornucopia Cave, located 11km

FIG. 1. Map showing the location of Naracoorte (indicated by arrow) and other localities where remains of *Megalania* have been found.

south of the township of Naracoorte in the SE of South Australia (Fig. 1). The cave was discovered during vineyard preparation in 1999, and contains bone-rich sediment cone deposits. Preliminary excavations have been conducted by one of the authors (ER) and S. Bourne. Dating samples are yet to be processed; however associated fauna indicate a Pleistocene age (Reed & Bourne, 2000). The Naracoorte specimen is registered in the palaeontology collection of the South Australian Museum, and has been assigned the registration number SAMP40102. To assess the proportions of the Naracoorte fossil the following measurements were taken (see Fig. 2): length, proximal width, distal width, maximum and minimum diameter of the diaphysis. Comparative data were taken from a cast of the sole humerus attributed to *Megalania prisca* (QMF865), housed in the Queensland Museum and first described by De Vis (1885); see also Anderson (1930) and Hecht (1972, 1975). Anatomical terms used in this paper for describing lizard humeri follow Lécuru (1969).

To make comparisons between the fossils and living varanids, we obtained a series of measurements for humeral proportions from 19 extant species. These measurements were taken in the same manner as for the fossils (Fig. 2). Data for modern varanid species were obtained from skeletons in the collection of several major institutions. Table 1 provides a full list of specimens used in this study, the measurements obtained and details regarding the institutions in which they are housed.

To compare the relative robustness of the two ‘giant’ varanid humeri with extant species, we used the method of Lécuru (1969) to calculate the ratio of robustness (length / maximum diaphysis diameter) and the ratio of the extremities (proximal width / distal width). The proportions of humeri are presented as bivariate scatter plots, showing humerus length plotted against snout-vent length, humerus proximal and distal width against humerus length, and distal width against proximal width. The snout-vent length of the specimens supplying the humeri was obtained from the museum or, where lacking, was estimated from the skeletal specimens. We estimate that such approximated SVL measurements of larger varanids are likely to be within 10cm of the true value.

RESULTS

DESCRIPTION. SAMP40102 (Fig. 3A-B, Fig 4A-B) is a left humerus with a preserved length of 105.3 mm. It is short, stout and robust with pronounced torsion (~40°) of the distal extremity relative to the proximal. Missing epiphysial caps are unfused indicating an immature individual. Distinct ectepicondylar foramen, prominent ectepicondylar crest, weak entepicondylar crest, deep olecranon fossa and a shallow, oval-shaped muscle scar (for insertion of the *latissimus dorsi)* on the dorsal surface at the base of the proximal head. The proximal head is damaged, with the top of the deltopectoral crest missing.

The proximal width is 47.1mm and distal width is 73.3mm. Maximum and minimum diameter of the diaphysis at its mid-point are 22.4mm and 19.7mm, respectively. Estimating the size and proportions of the epiphyses using the mature humerus attributed to *Megalania* (QMF865) as a model gives values of ~123mm for maximum length, ~48mm for proximal width and ~75mm for distal width (Fig. 4C-D).

REMARKS. The specimen is clearly a lizard. Presence of an ectepicondylar foramen, absence

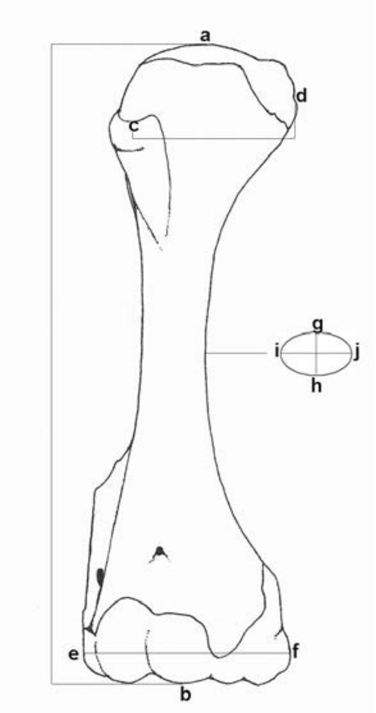

FIG. 2. Measurements taken for varanid humeri. a to b = length, c to d = proximal width, e to f = distal width, g to h = minimum diaphysis diameter, i to j = maximum diaphysis diameter.

of an entepicondylar foramen, and the position of the deltopectoral crest adjacent to the head of the humerus rule out a marsupial. Monotreme humeri (*Tachyglossus* and *Megalibgwilia*) are also eliminated by their extreme modifications to the proximal and distal extremities. Absence of an enlarged medial process opposite the deltopectoral crest eliminates a turtle. The denseness of the bone evident in broken surfaces eliminates a bird as a possibility.

While identification as a lizard is well founded, the general morphology is much more robust than is usual in lizards (see Lécuru, 1969). Relative proportions and general morphology compare favourably with the sole humerus (QMF865) attributed to *Megalania prisca* (see De Vis, 1885 for description of this specimen).

COMPARISON WITH EXTANT VARANIDS. When compared to the humeri of extant varanids, both fossils are more massively built, with particularly short and stout diaphyses (compare Figs 2 and 3). There are clear differences between *Megalania* and extant varanids in the relative proportions of the humerus, and both fossil specimens are far more robust than any living species (Fig. 5, Table 2).

In the extant species studied, there is a general trend for increase in length of the humerus with snout-vent length (Fig. 6). The fossil humeri attributable to *Megalania* are not extraordinary in terms of length when compared to the living varanids (Table 1). The Queensland fossil is only 4% longer than the largest *Varanus komodoensis* specimen studied, and the immature Naracoorte specimen falls within the range of lengths seen in large living varanids (Table 1).

When humeral length is compared with proximal width, all species in this study (including *Megalania*) fall within a similar range (Fig. 5A). However, when distal width is plotted against humeral length (Fig. 5B) and proximal width (Fig. 5C), *Megalania* clearly differs from the pattern displayed by living species in that the distal extremity is much broader than the proximal. In the living species the width of the proximal extremity is equal to or slightly greater than the distal. As the immature fossil shows the same pattern as the adult, it suggests that *Megalania* had a different pattern of growth from any living varanid.

These relationships are further illustrated by the ratios presented in Table 2. The ratio of robustness (ie. the ratio of diaphysis length to maximum diameter) for the *Megalania* humeri indicate they are approximately 1.45 times as robust as the extant species studied. The ratio of the extremities (proximal width to distal width), indicates that the *Megalania* humeri are considerably broader distally.

DISCUSSION

The Naracoorte specimen extends the distribution of giant varanids well south of any previous record indicating a wider geographic range than previously thought. This is important as *Megalania* has previously been described as rare with a limited geographic range, largely restricted to sub-tropical and tropical regions (see Wroe, 2002). The discovery of remains attributable to *Megalania* at Naracoorte shows that giant goannas ranged into temperate as well as tropical latitudes. This is not necessarily surprising as at least one living varanid species, *Varanus gouldii,* has a continent-wide range, while others, notably the relatively large *V. varius*, occur from tropical to temperate latitudes (Cogger, 2000).

TABLE 1. Measurements (mm) of varanid humeri used in study. L = length, PW = proximal width, DW = distal width, D-Min = minimum width of diaphysis, D-Max = maximum width of the diaphysis, est. = estimated to include epiphyses. Unreg. = unregistered specimen. * indicates epiphyses absent. QM = Queensland Museum; SAM P = South Australian Museum palaeontology collection; SAM R = South Australian Museum reptile collection; FU = Flinders University; AMNH = American Museum of Natural History; NHM = Natural History Museum, London ; YPM = Yale Peabody Museum of Natural History; SMF = Senckenberg Museum, Frankfurt; CSIRO R = Commonwealth Scientific and Industrial Research Organisation Canberra, Reptile collection; AZ = Adelaide Zoo; SBLR = comparative collection of the author (ER); LACM = Los Angeles County Museum; NHRM = Naturhistorische Museum, Leiden.

Species	Reg. Number	L (mm)	PW (mm)	DW (mm)	D-Min (mm)	D-Max (mm)
Megalania prisca	QM F865	174.23	73.58	105.28	32.13	35.08
			78.98 est.			
Megalania (Naracoorte)	SAM P40102	*105.25	47.10	73.30	19.70	22.40
		123.5 est.	48.00 est.	75.50 est.		
Varanus sp (fossil)	FU10640	*64.18	25.82	24.63	7.16	7.95
	FU10668	*68.33	28.39	25.16	7.26	8.62
	FU10158	*53.19	20.34	19.51	5.87	6.94
Varanus sp	AMNH139671	67.20	25.90	26.90	6.90	7.80
	AMNH123313	69.80	27.80	26.00	6.40	7.90
Varanus albigularis	NHM RR1961.1760	54.00	24.10	21.10	5.20	6.10
Varanus beccarrii	YPM11899	41.76	9.40	8.50	2.79	2.85
Varanus bengalensis	YPM11028	33.00	11.00	11.50	3.00	3.50
	YPM11202	48.50	16.00	16.00	4.00	5.00
	SMF60428	70.60	33.70	32.60	9.40	10.30
	AMNH29932	64.20	23.80	22.50	5.00	6.60
Varanus dumerilli	YPM11038	37.91	12.21	12.04	3.30	3.79
	YPM11203	44.00	16.00	15.00	4.00	5.50
Varanus exanthematicus	YPM11141	27.00	10.00	9.00	2.00	3.00
	AMNH137238	29.50	11.30	10.60	2.50	3.10
	AMNH137237	32.60	13.10	12.20	3.00	3.80
	AMNH140804	48.60	21.50	19.00	5.40	6.20
	AMNH140803	22.40	8.70	8.10	1.80	2.30
Varanus giganteus	SAM R33352	76.80	34.00	30.40	7.30	9.00
Varanus gouldii	CSIROR01278	61.30	25.50	23.80	6.10	8.40
	CSIROR01278	61.00	25.10	23.60	6.00	7.60
	CSIROR05080	33.70	12.30	12.10	2.70	3.50
	CSIROR05080	33.80	12.20	12.20	2.90	3.50
	CSIROR05085	45.00	15.80	15.00	3.80	5.20
	CSIROR05085	41.50	15.70	15.10	3.90	4.90
	CSIROR - unreg.	46.00	16.40	15.90	3.70	4.90
	CSIROR - unreg.	45.90	16.30	14.10	3.80	4.60
Varanus griseus	YPM14332	62.60	26.64	22.62	5.50	8.08
	YPM 10383	40.00	14.50	12.00	3.50	4.00
Varanus komodoensis	LACM 121971	137.80	69.60	64.30	17.40	18.30
	LACM 121971	138.30	69.10	64.60	17.60	18.40
	YPM10881	132.04	59.64	60.27	17.92	19.95
	NHM 1934.9.2.2	130.30	62.60	57.40	16.20	20.40
	NHRM 19.7.26	160.00	81.10	73.00	21.40	22.00
	NHRM 17497	127.00	63.60	58.40	15.20	18.00
	NHRM 21.11.38	150.00	74.40	66.70	18.00	20.00
	NHRM 17504	143.00	73.30	66.30	19.50	20.20
	SMF37209	140.00	73.80	62.50	18.30	20.30
	SMF57555	140.00	65.70	64.50	18.00	20.90

Species	Reg. Number	L (mm)	PW (mm)	DW (mm)	D-Min (mm)	D-Max (mm)
Varanus komodoensis	SMF68133	102.20	47.80	41.40	14.70	15.50
	AMNH37912	137.30	65.30	62.30	16.10	18.20
	AMNH37909	155.00	77.90	69.90	21.00	21.80
	AMNH37900	112.30	54.00	49.40	11.70	13.90
	AMNH37908	82.30	35.20	33.60	8.10	10.20
	AMNH74606	138.60	67.50	62.70	16.9	18.40
	AMNH37911	132.10	64.60	60.10	15.7	16.60
	AMNH37913	129.10	62.80	58.00	13.9	15.00
Varanus melinus	YPM11202	48.50	16.00	16.00	4.00	5.00
Varanus niloticus	YPM10880	68.00	26.00	24.00	4.00	5.00
	YPM10879	61.00	23.00	20.00	3.00	5.00
	YPM10877	56.00	20.00	19.00	4.00	5.00
	YPM14333	70.32	29.11	25.89	6.90	7.19
	NHM 1975.994	86.50	37.00	31.80	8.20	9.70
	NHM 1970.1983	53.40	19.10	18.40	4.20	5.30
	NHRM - unreg.	75.80	30.50	29.60	7.50	8.40
	AMNH137116	96.30	42.50	43.50	9.80	12.00
	AMNH88635	53.90	20.60	18.30	4.20	5.60
	AMNH140805	34.00	11.40	10.90	2.40	3.30
	AMNH10085	66.30	25.40	24.10	5.70	6.80
Varanus rosenbergi	SBLR002	32.07	10.76	10.69	2.50	3.31
	SBLR002	32.42	10.67	10.59	2.43	3.33
Varanus rudicolis	YPM12234	44.88	15.78	16.03	3.69	4.58
	YPM12235	64.41	25.75	23.82	5.63	7.50
	SMF59216	73.70	28.40	26.70	6.80	7.10
Varanus salvadori	SMF58064	104.70	36.4	32.50	8.90	9.50
Varanus salvator	YPM 10834	92.00	37.00	34.00	8.00	9.00
	YPM 11022	15.00	4.00	4.00	1.00	1.50
	YPM 12723	93.11	39.91	36.55	10.97	11.54
	NHM - unreg.	92.60	40.90	38.90	9.40	11.60
	NHM1961.1761	43.10	15.60	12.80	3.20	3.40
	NHRM 9.5.1906	115.20	45.60	42.50	11.10	12.50
	NHM 1972.2162	77.40	29.20	29.50	6.80	8.40
	SMF40175	86.70	34.70	32.90	7.50	9.50
	AMNH57765	83.10	30.10	30.80	7.40	9.30
	AMNH141148	36.90	12.10	12.00	3.30	4.20
	AMNH141155	36.60	13.00	13.30	3.30	4.20
	AMNH49230	82.40	31.90	32.90	6.70	9.30
Varanus storri	YPM11042	24.04	7.22	6.68	1.89	2.10
Varanus tristis	YPM11175	19.00	6.00	6.00	1.00	2.00
Varanus varius	SAM R33351	55.30	20.20	18.80	4.80	5.20
	SAM R33351	*49.80	18.50	17.10	4.80	5.20
	SAM display	86.10	39.10	37.00	11.70	12.80
	SAM display	86.10	38.60	35.70	10.90	12.80
	CSIROR05081	62.00	25.20	21.60	6.80	7.20
	CSIROR05081	61.90	25.50	21.10	6.60	6.90
	CSIROR05832	72.90	31.00	23.90	6.90	8.00
	CSIROR05832	73.40	31.00	26.80	7.30	8.00
	AZ display	87.50	39.08	38.00	10.30	12.00
	AZ display	87.00	41.09	36.41	10.19	11.81
	SBLR001	61.22	24.68	21.19	5.97	6.75
	SBLR001	61.20	24.89	21.27	5.99	6.76
Varanus yuwonoi	YPM12495	44.30	14.63	14.40	3.40	4.24

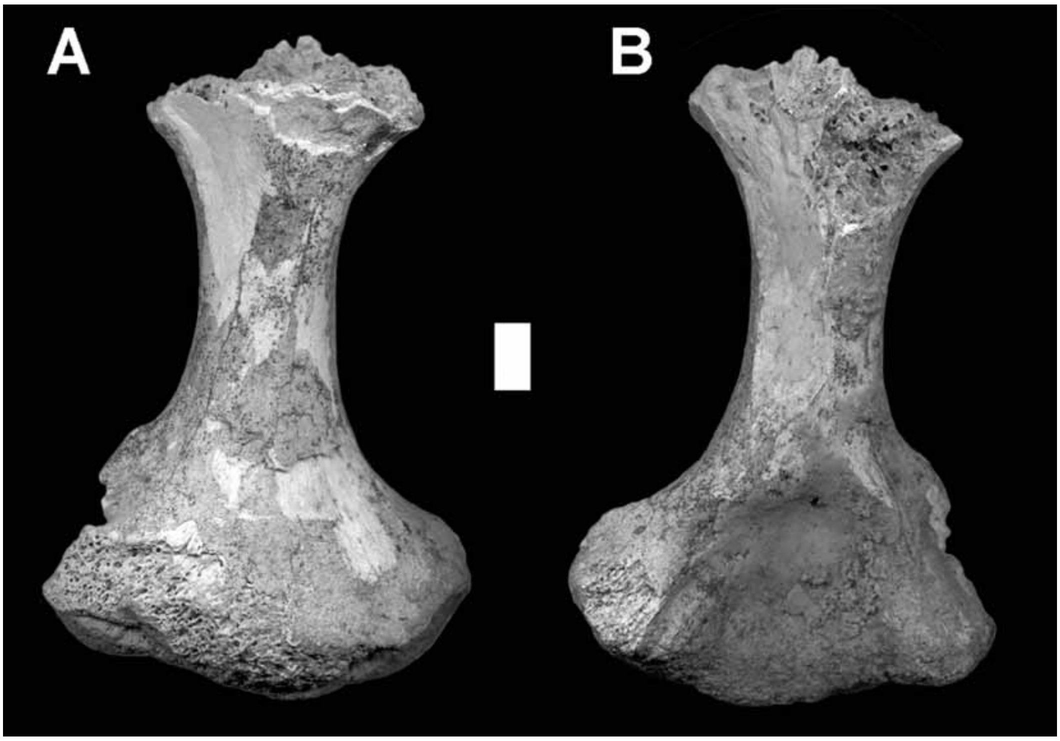

FIG. 3. SAMP40102, left humerus of a giant varanid from Naracoorte. A. Postero-dorsal view. B. Antero-ventral view. Scale = 5cm.

Wroe (2002) favoured the interpretation that the apparent low abundance of *Megalania* in Pliocene to Pleistocene fossil deposits reflected its actual rarity in the palaeofaunas, but acknowledged that some "unkown taphonomic phenomena" may have influenced its representation in fossil deposits. The mode of accumulation would have a strong influence over whether large reptiles would become accumulated in deposits. The site of discovery of the Naracoorte fossil is one of only two sites in the region with evidence of being a carnivore lair, while the majority of other sites are pitfall deposits (Reed & Bourne, 2000). The fact that this is the only site to have yielded evidence of *Megalania* after 30 years of collecting suggests that *Megalania* may not have been vulnerable to pitfall entrapment. Worthy & Holdaway (1996) have made the important point that when attempting palaeoecological reconstructions a range of sites of varying taphonomies should be investigated to eliminate biases produced by single modes of accumulation.

Previous writings on the possible ecological significance of *Megalania* have sometimes been coloured by an apparent lack of knowledge of the growth, distribution and abundance of living large Australian reptile carnivores. Wroe (2002: 18) stated "it is clear for taxa of indeterminate growth in particular, maximum dimensions are likely to represent gross deviations from the mean and do not provide reasonable grounds for predicting ecology". This statement overlooks what is now known of squamate patterns of growth. Estes (1983), Estes et al., (1988) and more recently Maisano (2001, 2002) point out that lizards have determinate growth, with relatively short juvenile periods and adult size rapidly approaching an asymptote following sexual maturity. In the case of the Queensland humerus, the complete epiphysial fusion would indicate an individual within 20% of the maximum size achieved by the species (Maisano, 2002). Thus many populations of extant lizards that live for more than a few years are composed mainly of animals at or near statistically normal adult size.

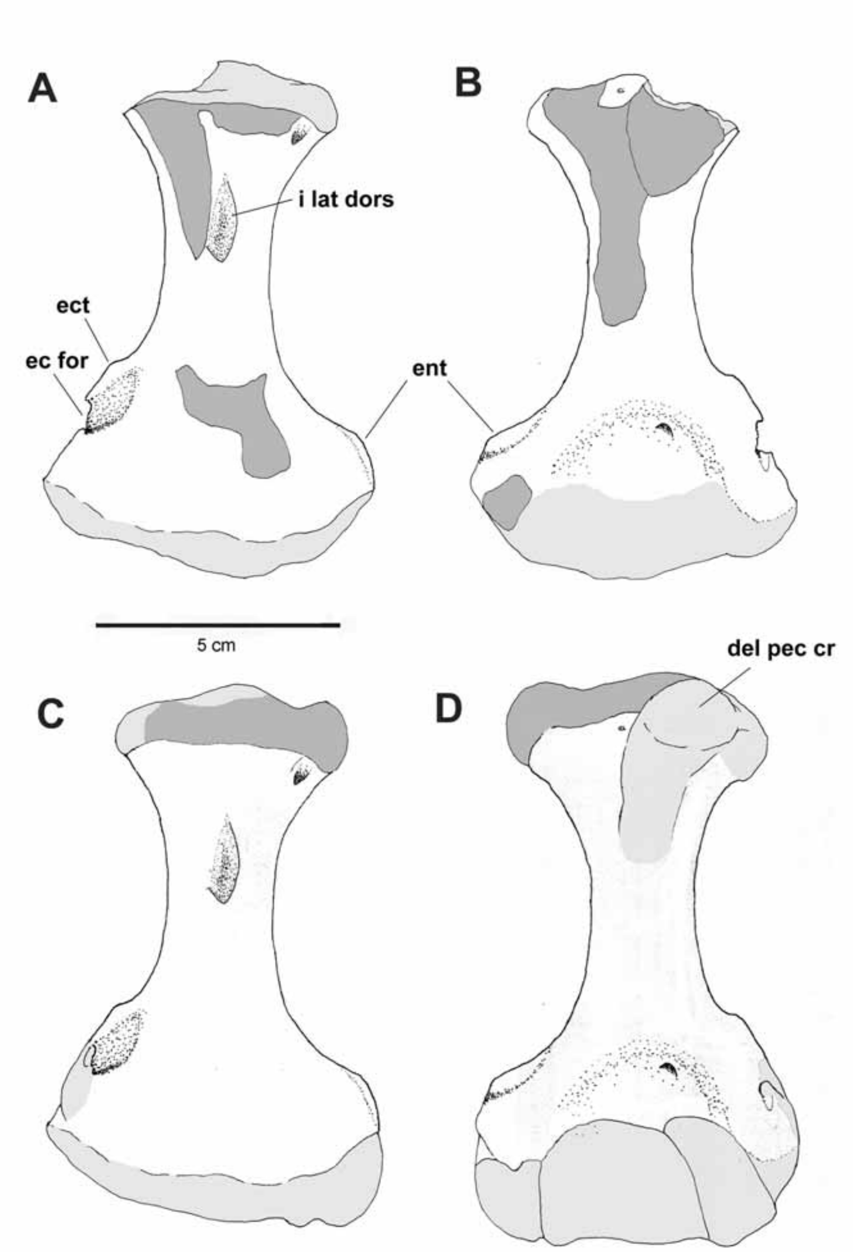

FIG. 4. A , B, diagram of *Megalania* humerus as recovered. Pale grey indicates unfinished bone, dark grey broken bone surface. C, D, restored humerus. Pale grey shading indicates distal joint surfaces and massive pectoral crest restored based on adult humerus (QM F865) and dark grey the surface of the proximal articulation (mostly missing in QMF865) extrapolated from extant varanids. Abbreviations: del pec cr, deltopectoral crest, ect, ectepicondyle, ec for ectepicondylar foramen, ent, entepicondyle, I lat dors, insertion for *m. latissimus dorsi*. Scale bar = 4cm.

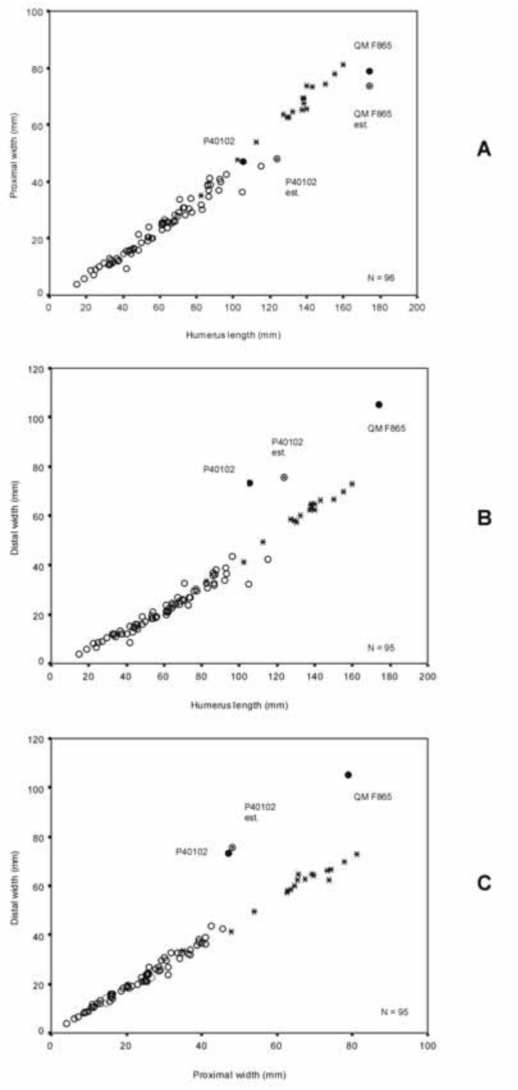

FIG. 5. Scatter plots of measurements taken for humeri of *Megalania* and extant varanids. A, Length vs proximal width. B, Length vs distal width. C, Proximal width vs distal width (see Fig. 2 for measurements taken). All measurements are in millimetres. The fossil specimens are indicated by their registration numbers. * = *Varanus komodoensis*, °= all other species. N = 96 for A. N = 95 individual specimens for B & C.

Erickson et al., (2003) estimated growth rates for *Megalania*, based on an associated femur and dermal bones, and suggested that *Megalania* grew to its large size by maintaining high, juvenile-like growth rates longer than large living varanids. Their data were based on a specimen that had not stopped growing (unfused femoral epiphyses), and they made their sizes estimates based on a published study of living varanids that correlated femur length with snout-vent length. Extrapolating from the living species, Erickson et al., (2003) obtained an estimated snout-vent length for this 'young adult' specimen as about 2m. Most of the recent published mentions of the size of *Megalania* are based on the less explicit review of Hecht (1975), which gave a variety of estimated body sizes, depending on the bone chosen for comparison. Most bones gave an estimate of 2-3 metres for snout-vent length, with one outlying, maximum of 4.5m based on an ungual phalanx and the minimum adult size estimate from the humerus (1.5 m SVL). In all cases, the estimates assume that the overall proportions of *Megalania*, as in *V. komodoensis* (Auffenberg 1981), were simple increments beyond those of living varanids. Few writers (De Vis, 1885; Anderson, 1930) have considered the idea that *Megalania*, throughout its growth, was different in its proportions from any living varanid.

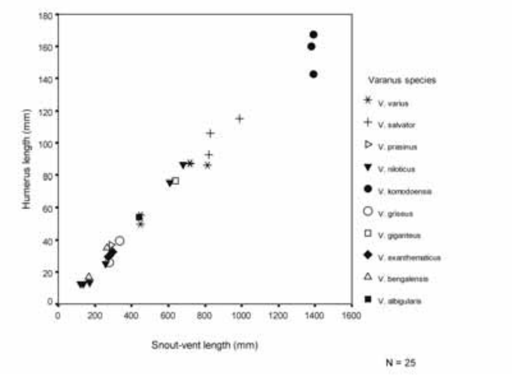

FIG. 6. Scatter plot showing snout-vent length vs humerus length for 10 extant *Varanus* species.

Molnar (1990), in describing the frontal and parietal, also based his conclusions on extrapolation from living large varanids (*V. salvadorii* and *V. varius*), but his data indicate that the frontal region of the skull was thicker than expected from size alone and exaggerated via a sagittal crest. Molnar's conclusion was that these bones showed *Megalania* was qualitatively different from living *Varanus* in frontal thickness and in the bony contacts between the frontal and

TABLE 2. Ratio of robustness (RR) and ratio of the extremities (RE) for the specimens measured for this study. Ratios calculated following the method of Lécuru (1969). Institutional abbreviations follow Table 1.

Species	Reg. Number	RR (L/D-Max)	RE (PW/DW)
Megalania prisca	QM F865	4.97	0.75
Megalania (Naracoorte)	P40102	4.69	0.64
Varanus sp (fossil)	FU10640	8.07	1.05
	FU10668	7.93	1.13
	FU10158	7.66	1.04
Varanus sp	AMNH139671	8.62	0.96
	AMNH123313	8.84	1.07
Varanus albigularis	NHM RR1961.1760	8.85	1.14
Varanus beccarrii	YPM11899	14.65	1.11
Varanus bengalensis	YPM11028	9.43	0.96
	YPM11202	9.70	1.00
	SMF60428	6.85	1.03
	AMNH29932	9.72	1.06
Varanus dumerilli	YPM11038	10.00	1.01
	YPM11203	8.00	1.07
Varanus exanthematicus	YPM11141	9.00	1.11
	AMNH137238	9.52	1.07
	AMNH137237	8.58	1.07
	AMNH140804	7.84	1.13
	AMNH140803	9.74	1.07
Varanus giganteus	SAM R33352	8.53	1.12
Varanus gouldii	CSIROR01278	7.30	1.07
	CSIROR01278	8.02	1.06
	CSIROR05080	9.69	1.02
	CSIROR05080	9.66	1.00
	CSIROR05085	8.65	1.05
	CSIROR05085	8.47	1.04
	CSIROR - unreg.	9.39	1.03
	CSIROR - unreg.	9.99	1.16
Varanus griseus	YPM14332	7.75	0.92
	YPM 10383	10.00	1.18
	Lécuru (1969)	11.73	1.13
Varanus komodoensis	LACM 121971	7.53	1.08
	LACM 121971	7.52	1.07
	YPM10881	6.62	0.99
	NHM 1934.9.2.2	6.39	1.09
	NHRM 19.7.26	7.27	1.11
	NHRM 17497	7.05	1.09
	NHRM 21.11.38	7.50	1.12
	NHRM 17504	7.08	1.11
	SMF37209	6.90	1.18
	SMF57555	6.70	1.02
	SMF68133	6.61	1.15
	AMNH37912	7.54	1.05
	AMNH37909	7.11	1.11
	AMNH37900	8.08	1.09
	AMNH37908	8.07	1.05
	AMNH74606	7.53	1.08
Varanus komodoensis	AMNH37911	7.96	1.07
	AMNH37913	8.61	1.08
Varanus melinus	YPM11202	9.70	1.00
Varanus niloticus	YPM10880	13.60	1.08
	YPM10879	12.20	1.15
	YPM10877	11.20	1.05
	YPM14333	9.78	1.12
	NHM 1975.994	8.92	1.16
	NHM 1970.1983	10.07	1.04
	NHRM - unreg.	9.02	1.03
	AMNH137116	8.03	0.98
	AMNH88635	9.63	1.13
	AMNH140805	10.30	1.05
	AMNH10085	9.75	1.05
	Lécuru (1969)	9.44	0.99
Varanus rosenbergi	SBLR002	9.69	1.01
	SBLR002	9.73	1.01
Varanus rudicolis	YPM12234	9.80	0.98
	YPM12235	8.59	1.08
	SMF59216	10.38	1.06
Varanus salvadori	SMF58064	11.02	1.12
Varanus salvator	YPM 10834	10.22	1.09
	YPM 11022	10.00	1.00
	YPM 12723	8.07	1.09
	NHM - unreg.	7.98	1.05
	NHM1961.1761	12.68	1.22
	NHRM 9.5.1906	9.22	1.07
	NHM 1972.2162	9.21	0.99
	SMF40175	9.13	1.05
	AMNH57765	8.94	0.98
	AMNH141148	8.79	1.01
	AMNH141155	8.71	0.98
	AMNH49230	8.86	0.97
	Lécuru (1969)	10.60	1.02
Varanus storri	YPM11042	11.45	1.08
Varanus tristis	YPM11175	9.50	1.00
Varanus varius	SAM R33351	10.63	1.07
	SAM R33351	9.58	1.08
	SAM display	6.73	1.06
	SAM display	6.73	1.08
	CSIROR05081	8.61	1.17
	CSIROR05081	8.97	1.21
	CSIROR05832	9.11	1.30
	CSIROR05832	9.18	1.16
	AZ display	7.29	1.03
	AZ display	7.37	1.13
	SBLR001	9.06	1.16
	SBLR001	9.05	1.17
Varanus yuwonoi	YPM12495	10.45	1.02

postorbitofrontal. Hecht's (1975) earlier summary pointed out further character states that appeared to be unique to *Megalania*, not just the simple consequence of scaling up a *Varanus*. These include a vertically oriented supraoccipital as well as the unusually short humeral shaft.

Lécuru's (1969) summary of intrafamilial variation in varanid humeri reported little of significance across the small sample of living species. Our larger sample confirms this pattern. As large *Varanus* species reach their maximum size, the proximal and distal regions expand laterally, but distal expansion is only slightly greater than proximal even in *V. komodoensis*. The most obvious proportional difference between humeri of large and small living varanids is expressed by Lécuru's 'Ratio of Robustness' (humerus length to mid-diaphysial diameter; Table 2), with the value of the ratio falling as the bone becomes stouter in larger animals. The humerus of *Megalania*, as represented by the two known specimens, was far more robust (even in immature animals) than is the case for any living varanid, and yet disproportionately short if *Megalania* is reconstructed as an extension of the growth patterns shown by living *Varanus*. The developmental pattern and body proportions do not seem to be merely an extrapolation from living varanid development. *Megalania* appears to have been a very stocky and heavily built animal well before it matured, perhaps with the head, neck and fore-body relatively more robust than living species of *Varanus*. If its proportions did not match those of any living *Varanus*, body size estimates based solely on length of individual bones may well be misleading.

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