Earliest Example of a Giant Monitor Lizard (Varanus, Varanidae, Squamata)

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Abstract

Background: Varanidae is a clade of tiny (<20 mm pre-caudal length [PCL]) to giant (>600 mm PCL) lizards first appearing in the Cretaceous. True monitor lizards (Varanus) are known from diagnostic remains beginning in the early Miocene (Varanus rusingensis), although extremely fragmentary remains have been suggested as indicating earlier Varanus. The paleobiogeographic history of Varanus and timing for origin of its gigantism remain uncertain.

Methodology/Principal Findings: A new Varanus from the Mytilini Formation (Turolian, Miocene) of Samos, Greece is described. The holotype consists of a partial skull roof, right side of a braincase, partial posterior mandible, fragment of clavicle, and parts of six vertebrae. A cladistic analysis including 83 taxa coded for 5733 molecular and 489 morphological characters (71 previously unincluded) demonstrates that the new fossil is a nested member of an otherwise exclusively East Asian Varanus clade. The new species is the earliest-known giant (>600 mm PCL) terrestrial lizard. Importantly, this species co-existed with a diverse continental mammalian fauna.

Conclusions/Significance: The new monitor is larger (longer) than 99% of known fossil and living lizards. Varanus includes, by far, the largest limbed squamates today. The only extant non-snake squamates that approach monitors in maximum size are the glass-snake Pseudopus and the worm-lizard Amphisbaena. Mosasauroids were larger, but exclusively marine, and occurred only during the Late Cretaceous. Large, extant, non-Varanus, lizards are limbless and/or largely isolated from mammalian competitors. By contrast, our new Varanus achieved gigantism in a continental environment populated by diverse eutherian mammal competitors.

Introduction

Monitor lizards (Varanidae) are known to have originated by the Late Cretaceous [1–4]. Although varanids are best popularly known by the Komodo Dragon (Varanus komodoensis), and are famous for reaching large body sizes, the earliest monitors were small- to medium-sized lizards (e.g., the Late Cretaceous forms Ovoo gurvel, Aiolosaurus oriens, and Telmasaurus grangeri) [4–6]. Large varanids are noticeably absent from Cretaceous deposits, despite (or, possibly, because of) the apparent ability of montorsaurs to grow to large sizes during those times (e.g., Estesia mongoliensis and Palaeosaniwa canadensis) [1,7–9]. Indeed, large varanids do not appear in the fossil record until the Eocene taxon Saniwa ensidens [10–12], and the earliest example of a described giant monitor lizard is from the Pleistocene (Varanus priscus) [13–16].

More than 70 extant true monitor lizard (Varanus) species are known from across Africa, Eurasia, and Australia [17–20], ranging in size from tiny (approximately 100 mm in pre-caudal length [PCL]) to giant (multiple species exceeding 600 mm in PCL) [21,22] (Tables 1, 2), encompassing more than three orders of magnitude in mass [23], and exploiting a broad diversity of ecological specializations (e.g., arboreal, semi-aquatic, xeric terrestrial) [17,22,23]. However, the Varanus fossil record is sparse and most fossil species are represented only by isolated vertebrae [16,24]. The poor fossil record leaves open many questions about the evolution of the group, including: When and where did monitors originate and diversify? When did they first achieve giant sizes? Can they achieve gigantism in the presence of mammalian competitors [25–27]?

Here, we describe a new, large-bodied, Varanus from the Turolian Miocene of Samos, Greece (Fig. 1). The specimen was collected by Barnum Brown from his locality Q1, in association with fossil mammal remains. It remained undetected in the fossil mammal collections at the American Museum of Natural History until it was brought to the attention of one of us (CMM) by Nikos Solounias who recognized its reptilian affinities in 2009.

In addition to being diagnostic as a new species, the new taxon is a nested member of an otherwise exclusively Asian Varanus radiation. This new species was a giant despite occurring in a time and place (Miocene of Greece) known for its mammalian diversity and its combination of European, Asian, and African faunal influences [28–30].
Table 1. Principal data from the measurement of 28 specimens of *Varanus* for comparison of fossils forms and size predictions.

| specimen # | Varanus sp. | BCL | DVL | PCL |
|-----------|-------------|-----|-----|-----|
| AMNH R-47725 | Albigularis | 37  | 17  | 630 |
| AMNH R 141072 | Beccarii | 18.5 | 8  | 313 |
| AMNH R 29932 | Bengalesis | 25.28 | 14 | 510 |
| AMNH R 118713 | Bengalesis | 30.23 | 17 | 660 |
| AMNH R 140804 | exanthematicus | 28 | 16 | 470 |
| AMNH R 77646 | Flavescens | 21.72 | 10.05 | 339 |
| UF 64743 | Flavescens | 19 | 9.5 | 350 |
| AMNH R 82819 | Gouldii | 28 | 14.5 | 650 |
| AMNH R 74810 | Griseus | 20.5 | 9.81 | 423 |
| AMNH R 142617 | Indicus | 12 | 5.5 | 212 |
| AMNH R 142623 | Indicus | 14.58 | 6.93 | 244.44 |
| AMNH R 37908 | Komodoensis | 44 | 19 | 718 |
| AMNH R 37909 | Komodoensis | 87 | 36 | 1478 |
| AMNH R 7252 | Niloticus | 23 | 9 | 360 |
| AMNH R 137116 | niloticus | 45 | 25 | 832 |
| AMNH R 10499 | Ornatus | 29.5 | 9 | 393 |
| AMNH R 104683 | Prasinus | 16 | 8 | 283 |
| AMNH R 141071 | Rudicollis | 13.5 | 6 | 196 |
| AMNH R 49230 | salvator? | 36.5 | 17 | 660 |
| UF 99317 | Timorensis | 10.5 | 4.5 | 174 |
| UF 45363 | Timorensis | 10 | 4.5 | 180 |

Abbreviations: BCL, linear length of the braincase from the anterior tip of the basioccipital; DVL, length of a posterior dorsal vertebra; PCL, precondylar length of the animal (an osteological skeletal length similar to the snout-vent length often used for extant taxa. All measurements in millimeters [mm]).

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Institutional Abbreviations

AMNH, American Museum of Natural History (New York, NY.); BMNH PR, Natural History Museum, London (London, Great Britain); GM, Gesellschaft Museum of the Martin-Luther Universität in Halle/Saale (Germany); UF, University of Florida, Florida State Museum (Gainesville, Fl.; ZPAL, Zoological Institute of Paleobiology, Polish Academy of Sciences, Warsaw (Poland).

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Clade names follow recent phylogenetic definitions [2,3].

Systematic Paleontology

Squamata Oppel 1811
Anguimorpha Fürbringer 1900
Varanidae Gray 1827

*Varanus* (Varaneades) amnhophilis, gen. et sp. nov. (Varaneades) subgen. nov.

ZooBank LSID urn:lsid:zoobank.org:act:FCD0FAC3-D8C5-4308-912D-7BD8A0C03937

*Varanus* (Varaneades) amnhophilis sp. nov.

ZooBank LSID urn:lsid:zoobank.org:act:65B2D84B-B7FB-48A0-80F2-5E269C6E1E5D

Figures 2–3.

Holotype. AMNH FR 30630; right side of braincase (prootic, parabasisphenoid, otooccipital, basiocipital), right quadrate, partial right coronoid, partial palate, skull roof fragments, glenoid region of right mandible, a small fragment of the right clavicle, and five-and-a-half presacral vertebrae (Figs. 2, 3).

Etymology. *Varanenades* (subgenus) from “Varanus” modern true monitor lizards, and “Neades” a group of mythical beasts from Samos, Greece. *Amnhophilis* from Greek “amnos” (“sheep”) or “amnios,” archaic Greek for “lamb;” and “-philis” (“lover of”), meaning “a lover of.” The name alludes to the propensity of large-bodied *Varanus* to take mammalian prey. Note, also, that the American Museum of Natural History (AMNH) is the repository for the specimen.

Locality and age. Mytilini Formation (Turolian, Miocene) of Samos, Greece; dated at 6.9-7.6 million years old [28] (Fig. 1).

Diagnosis. *Varanus* (*Varanenades*) *amnhophilis* is diagnosed by the presence of the following combination of apomorphies: Ptyerygoid teeth absent (Fig. 2F); Vidian canal without prootic contribution (Fig. 2G, J, M); entocarotid fossa absent (Fig. 2G, J); anterostapedial process of prootic crest distinct; undivided external facial foramen (Fig. 2I); absence of tuberous flanges of parabasisphenoid (Fig. 2G, J); crista interfenestralis extends posterolaterally, partly hiding the occipital recess in lateral view (Fig. 2G, I, J); accessory ventromedial lip on the paroccipital process present (Fig. 2G–J); dorsal and ventral tips of the paroccipital process terminate at the same mediolateral level (Fig. 2G, H, J, M); large quadrate tympanic crest (Fig. 2C); vertebrae with strong precondylar constriction (Fig. 3C).

Description

Skull morphology. Only the supratemporal arch part of the right postorbitofrontal and squamosal are represented in the dorsal skull roof (Fig. 2A, B). The preserved part of each element is elongate. The squamosal bears a broadly concave postorbitofacial facet. The postorbital is sub-ovate in cross section.

The right quadrate is well preserved and lacks only the ventral half of the tympanic crest (Fig. 2C). The straight quadrate possesses a strongly developed posterior process that quickly tapers ventrally. This process is slightly longer than the lateral development of the tympanic crest. This condition, wherein the tympanic and posterior crests are of subequal lengths, differs from...
### Table 2. SIZES OF EXTANT VARANIDAE.

| Genus             | species/subspecies | SVL (mm) | TL (mm) | sex  | comment                        |
|-------------------|--------------------|----------|---------|------|--------------------------------|
| Lanthanotus       | borneensis         | 400      | max     |      |                                |
| Varanus           | albigularis        | 460      | 1200    | F    |                                |
| Varanus           | bengalensis        | 460      | 1200    | F    |                                |
| Varanus           | eremius            | 59       | 150     | approx |                                |
| Varanus           | flavescens         | 118      | 230     |      |                                |
| Varanus           | gouldii            | 113      | 235     |      |                                |
| Varanus           | indicus            | 118      | F       |      |                                |
| Varanus           | komodoensis        | 120      |         |      |                                |
| Varanus           | kordensis          | 125      |         | M    |                                |
| Varanus           | primordius         | 120      |         |      |                                |
| Varanus           | caudolineatus      | 118      |         |      | F                               |
| Varanus           | steari             | 132      | 300     | approx |                                |
| Varanus           | eremius            | 160      | 400     | approx |                                |
| Varanus           | pilborensis        | 169      | max     |      |                                |
| Varanus           | bariti             | 171      | 468     | mean |                                |
| Varanus           | glauerti           | 180      | 324     | F    | approx                          |
| Varanus           | gilleni            | 186      |         |      |                                |
| Varanus           | glauerti           | 215      | 387     | M    | approx                          |
| Varanus           | globopalmna        | 245      | 409.2   | F    | approx                          |
| Varanus           | scalaris           | 250      | 600     | max  |                                |
| Varanus           | semiremex          | 250      | 600     |      |                                |
| Varanus           | griseus koniecznyi | 255      | 620     |      |                                |
| Varanus           | keithhornemi       | 260      | 650     |      |                                |
| Varanus           | kordensis          | 270      | 580     | max field |                                |
| Varanus           | globopalmna        | 290      | 484.3   | M    | approx                          |
| Varanus           | dumerilii          | 292      | 900     |      |                                |
| Varanus           | prasinus           | 295      | 845     | max  |                                |
| Varanus           | tristis            | 305      | 800     | large |                                |
| Varanus           | macrei             | 313      | 912     | F    |                                |
| Varanus           | flavescens         | 315      | 699     |      |                                |
| Varanus           | exanthematicus     | 320      | 640     | M    | mean                            |
| Varanus           | exanthematicus     | 320      | 640     | F    | mean                            |
| Varanus           | mertensi           | 320      | max     |      |                                |
| Varanus           | radicollus         | 336      |         | mean |                                |
| Varanus           | mabiensis          | 340      | 1000    | M    |                                |
| Varanus           | griseus griseus    | 341      | 830     |      |                                |
| Varanus           | ferox              | 342      |         | F    |                                |
| Varanus           | salvadorii         | 350      | 1160    |      |                                |
| Varanus           | macrei             | 360      | 1110    | M    |                                |
| Varanus           | salvadorii         | 360      | 1110    | M    |                                |
| Varanus           | gouldii            | 361      | 931     | F    |                                |
| Varanus           | caerulivirensis    | 375      | 985     | F    | max                             |
| Varanus           | marmoratus         | 391      |         | M    |                                |
| Varanus           | salvadorii         | 397      | 982     |      |                                |
| Varanus           | caerulivirensis    | 400      | 1040    | M    | max                             |
| Varanus           | melinus            | 420      | 1150    | M    |                                |
| Varanus           | cumining           | 431      | 1142    | mean |                                |
| Varanus           | griseus caspius    | 432      | 1050    |      |                                |
| Varanus           | jobiensis          | 445      | 1195    | M    |                                |
| Varanus           | jobiensis          | 450      | 1185    | F    |                                |
| Varanus           | salvator           | 453      | 1198    |      |                                |

### Table 2. Cont.

| Genus             | species/subspecies | SVL (mm) | TL (mm) | sex  | comment                        |
|-------------------|--------------------|----------|---------|------|--------------------------------|
| Varanus           | yemenensis         | 458      | 999     |      |                                |
| Varanus           | bengalensis        | 460      | 1200    | F    |                                |
| Varanus           | doreanus           | 460      | 1255    | voucher |                                |
| Varanus           | rosenbergi         | 470      |         | max  |                                |
| Varanus           | salvadorii         | 478      | 1486    |      |                                |
| Varanus           | mertensi           | 480      | 1300    | max  |                                |
| Varanus           | albogularis        | 500      | 1111    | F    |                                |
| Varanus           | albogularis        | 500      | 1111    | M    |                                |
| Varanus           | olivaceus          | 509      |         | F    |                                |
| Varanus           | niloticus          | 523      | 1308    | F    |                                |
| Varanus           | mabitang           | 527      | 1268    | F    | type                           |
| Varanus           | yuwonoi            | 532      | 1877    | F    | holotype                        |
| Varanus           | spenceri           | 550      | 1250    |      | large                          |
| Varanus           | bengalensis        | 580      | 1500    | M    |                                |
| Varanus           | indicus            | 580      |         | max  |                                |
| Varanus           | gouldii            | 590      | 1410    | M    |                                |
| Varanus           | radicollis         | 590      | 1460    | max  |                                |
| Varanus           | mabitang           | 640      | 1750    |      |                                |
| Varanus           | niloticus          | 644      | 1610    | M    |                                |
| Varanus           | giganteus          | 645      | 1494    | mean |                                |
| Varanus           | olivaceus          | 650      |         | M    |                                |
| Varanus           | giganteus          | 736      | 1690    | M    |                                |
| Varanus           | panoptes           | 740      |         | max  |                                |
| Varanus           | salvadorii         | 745      | 2240    |      |                                |
| Varanus           | ornatus            | 760      | 1900    | max  |                                |
| Varanus           | varius             | 765      | 1920    | large |                                |
| Varanus           | komodoensis        | 775      | 1550    | Auffenberg approx |                                |
| Varanus           | komodoensis        | 840      | 1680    | Auffenberg approx |                                |
| Varanus           | komodoensis        | 850      | 1700    | mean |                                |
| Varanus           | salvadorii         | 850      | 2550    |      |                                |
| Varanus           | salvadorii         | 863      | 2650    |      |                                |
| Varanus           | giganteus          | 880      | 1940    | approx |                                |
| Varanus           | komodoensis        | 1540     | 3020    | max field |                                |
| Varanus           | beccarii           | 950      |         |      |                                |
| Varanus           | melinus            | 950      |         | F    |                                |

Lengths of 52 species of Varanidae (51 species of Varanus and Lanthanotus borneensis) based on published data [21,79]. These data were used to reconstruct the lineage sizes in Figure 5. Note that not all measurements and/or data are available for all included species. Abbreviations: SVL, snout-to-vent length of the animal; TL, total length of the animal (snout to tail tip); approx, approximate length based on published data [21]; Auffenberg approx, approximate dimensions based on data presented for wild-caught specimens in Auffenberg's study on Komodo Dragons [79]; F, female; holotype/type/voucher, measurements based on the type specimen—the data are usually reported in the case of species wherein there are few available specimens; M, male; max, reported maximum measurement; max field, reported maximum measurement of wild-caught specimens—the data are usually included when the species in question is popular in the pet trade. doi:10.1371/journal.pone.0041767.t002

the condition seen in Varanus albogularis, Varanus bengalensis, Varanus eremius, Varanus flavescens, Varanus gouldii, observed Varanus indicus, Varanus komodoensis, Varanus kordensis, Varanus salvadorii, Varanus tristis,
and *Varanus varius* among observed taxa. Those mentioned taxa possess a relatively short tympanic crest.

The saddle-shaped articular condyle is well preserved, but the epiphysis is missing from the dorsal quadrate head. There is no development of a pterygoid lappet like those seen in helodermatids and many non-anguimorph squamates. A large posterior opening of the quadrate canal is located about one-third of the way from the dorsal tip of the quadrate.

Only a small part of the right palatine (Fig. 2D) is preserved and it comes from the maxilla-palatine contact. The fragment includes most of the maxillary process, but lacks the posterior part. It preserves the short choanal groove, but not the posterior margin of the infraorbital canal, the vomerine process, or the pterygoid process.

The main body and the proximal parts of the transverse and quadrate processes of the right pterygoid are preserved. These parts confirm the presence of a columellar fossa, and a well-developed and anterolaterally oriented transverse process (Fig. 2E, F). Importantly, this element confirms the absence of pterygoid teeth (Fig. 2F). Absence of pterygoid teeth is a derived condition of *Varanus* within Varanidae.

The lateral margin of the pterygoid transverse process describes a lateral curve. The anterior margin is concave. The transverse process is thickest posterolaterally. Distally, it bears posterolaterally attenuated ectopterygoid facets on the dorsal and ventral surfaces. Postero medial to the confluence of the palatine and transverse processes is a distinct basipterygoid buttress (Fig. 2F). The quadrate process is medially concave (Fig. 2E).

Most of the right prootic is preserved, but the auditory bulla and the alar crest are missing (Fig. 2G, H, J). The specimen preserves the contacts with the parabasisphenoid, basioccipital, and otocipital. It also preserves the single (undivided) facial foramen (Fig. 2I) and the dorsal margin of the fenestra ovalis. The prootic inferior process dorsolaterally overlies the inferior process of the parabasisphenoid. The prootic-parabasisphenoid suture extends anteroventrally along the lateral surface of the inferior process. From that point, the prootic-parabasisphenoid suture extends posteriorly to the prootic-basioccipital contact, just anterior to the spheno-occipital process from which point it extends posteriorly to a point just anterior to the ventral margin of the crista interfrenestralis (interfenestral crest; separating the fenestra ovalis from the occipital recess). The crista interfrenestralis is developed posteroventrally rather than extending mediolaterally. The posteroventral extension of this crest partly overlaps the occipital recess, hiding its deeper parts in lateral view.

Absence of a division of the facial foramen is unusual in *Varanus* [31]. Among the 18 species for which we were able to see the facial foramen, only *Varanus acanthurus*, some *Varanus dumerilii*, *Varanus prasinus*, *Varanus rudicollis*, and *Varanus salvadori* possess an undivided facial foramen. Noteworthy is the presence of a divided facial foramen in *Lanthanotus borneensis* [32,33] and some *Shinisaurus crocodilurus* [34]. This character was recently discussed at some length in a description of the braincase of *Varanus priscus* [35].

The prootic crest (crista prootica) is relatively well developed anteriorly and posteriorly, but is very weakly developed at the level of the trigeminal notch. More posteriorly, near the level of the posterior margin of the sphen-o-occipital tubercle and extending to a level near the posterior margin of the fenestra ovalis, the prootic crest possesses a pronounced ventrolateral flange. This process, here termed the anterostapedial process, is absent in some *Varanus* (e.g., *Varanus acanthurus*, *Varanus dumerilii*, *Varanus griseus*, and *Varanus komodoensis* [Fig. 4A], among others). When it is present, it may be expressed as a hook-like flange defining a narrow posterior concavity (e.g., in *Varanus bengalensis* [Fig. 4B]), or as an anteroposteriorly elongate tab that is laterally/ventrolaterally directed (e.g., in *Varanus albigularis* [Fig. 4C]). Because it is broken near its base, the shape of the flange is uncertain in *Varanus ammonophilis*, but the broken base attests to its original presence (Fig. 2G, I, J).

Near the posterior base of anterostapedial process, the prootic is developed into a robust paroccipital process that is strongly sutured to, but not fused with, the paroccipital process of the otocipital (Fig. 2G, I, J). The prootic paroccipital process covers more than one-half of otocipital paroccipital process.

Some features of the otic capsule and surrounding anatomical structures are visible on the medial view of the prootic (Fig. 2H). The medial view of the occipital recess does not preserve the medial opening to the brain cavity (the recessus scala tympani). However, much of the division between the occipital recess and the lagenar recess and vestibule is preserved, as is the lateral and much of the ventral wall of the lagenar recess. The narrow posterior connection between the lagenar recess and the preserved (lateral) part of the vestibule is preserved; the lagenar recess and the vestibule describe a “figure 8,” as preserved (Fig. 2H).

We refer to the compound structure formed by fusion of the dermal parabasiophenoid and the endochondral basioccipital as the parabasisphenoid, following some recent usage [9], but differing from others in which this structure has been called the sphenoid [36,37]. The anguimorph parabasisphenoid is often pentaradiate in ventral view, rather than being dorsally concave. The anterior openings of the abducens, carotid, and Vidian canals are typical of those in *Varanus* (e.g., *Varanus bengalensis*, *Varanus dumerilii*, *Varanus griseus*, and *Varanus komodoensis* [Fig. 4A], among others). When it is present, it may be expressed as a hook-like flange defining a narrow posterior concavity (e.g., in *Varanus bengalensis* [Fig. 4B]), or as an anteroposteriorly elongate tab that is laterally/ventrolaterally directed (e.g., in *Varanus albigularis* [Fig. 4C]). Because it is broken near its base, the shape of the flange is uncertain in *Varanus ammonophilis*, but the broken base attests to its original presence (Fig. 2G, I, J).

A robust crista sellaris extends directly mediolaterally in anterior view, rather than being dorsally concave. The anterior openings of the abducens, carotid, and Vidian canals are typical of those in other *Varanus* [31,32,38,39] and in *Shinisaurus crocodilurus* [32,34,37,40]. Abducens canal pierces the parabasisphenoid at the base of the crista sellaris (Fig. 2H), the carotid canal lies in a deep retractor pit, and the anterior opening of the Vidian canal lies ventral to and slightly medial to the anterior opening of the abducens canal. The anterior opening of the Vidian canal lies just ventral to the level of the anterior opening of the carotid canal at the base of the basipterygoid process. A very weakly developed
ridge partly divides the retractor pit. The posterior opening of the Vidian canal occurs within the body of the parabasisphenoid, just ventromedial to the anterior part of the prootic crest at the posterior base of the inferior process (Fig. 2G, J). There is no development of the entocarotid fossa associated with the recessus vena jugularis.

The inferior process of the parabasisphenoid is largely overlaid by the complementary process of the prootic (Fig. 2G, H, J, M).
The prootic-parabasisphenoid suture extends posterolaterally to the inferior process, and then extends posterolaterally, just dorsal to the level of the posterior opening of the Vidian canal toward the sphenoid occipital tubercle. At the base of the sphenoid-occipital tubercle and at an anteroposterior level lying between the trigeminal notch and the anterior facial nerve opening, the prootic-parabasisphenoid suture turns ventrally and becomes the parabasisphenoid-basioccipital suture. The ventral parabasisphenoid-basioccipital suture is mediolaterally oriented.

The right lateral part of the basioccipital is preserved. Half of the parabasisphenoid contact is preserved, as are the contacts with the right prootic, and the lateral and ventral contacts with the right otooccipital (Fig. 2G, I, J). No remnant of the occipital condyle remains. Presence of an unfinished bone surface on the sphenoid-occipital tubercle suggests the original presence of unfused epiphyses (Fig. 2G, I). The sphenoid-occipital tubercle is anteriorly located. Its posterior margin lies anterior to the anterior margin of the fenestra ovalis (Fig. 2G, J). Medial to the sphenoid-occipital tubercles and near the midline, the basioccipital is very robust and thickly developed. The posterior, basioccipital-otooccipital suture extends anteromedially from the sphenoid-occipital tubercle except where it nears the midline and is posteriorly expanded. However, the state of preservation does not allow further characterization of that suture, or of the bone.

The fused exoccipital-opisthotic unit is here referred to as the otooccipital, following recent usage [34,37,41]. The mostly complete right otooccipital is preserved, lacking only the occipital condyle, the margins of cranial nerves X–XII, and more medially occurring structures (Fig. 2G–J).

The otooccipital constitutes the dorsal part of the postero lateral braincase walls. Anteriorly, it preserves most of the crista interfenestralis, which separates the fenestra ovalis from the occipital recess and demonstrates that this crest possesses the postero lateral expansion described above. The contact between the prootic and the otooccipital is vertical and extends from the sphenoid-occipital tubercle dorsally to the crista interfenestralis. The crista interfenestralis extends posteriorly and slightly posterodorsally from a point dorsal to the posterior margin of the sphenoid-occipital tubercle to the paroccipital process (Fig. 2I).

The crista tuberalis extends posterodorsally from the sphenoid-occipital tubercle as in other Varanus. As in many Varanus (but not Varanus griseus and Varanus acanthurus), the crista tuberalis possesses a distinct, ventrolateral, paroccipital tuberosity (Fig. 2G–J). The paroccipital tuberosity of Varanus amnhophilis is not developed into a finger-like flange as it is in Varanus bengalensis. It is located near the base of the paroccipital process and is directed ventrally/ventrolaterally.

**Mandibular morphology.** Preserved mandibular remains for *Varanus amnhophilis* consist of parts of the right coronoid, surangular, and prearticular-articular complex (Fig. 2K–M). The coronoid has a short and gently ventrally concave coronoid eminence similar to that of other Varanus. Similarly, the preserved part of the surangular and prearticular-articular preserve no autapomorphic characteristics and are similar to those elements in most other Varanus.

**Vertebrae.** Parts of three cervical and three complete dorsal vertebrae are known (Fig. 3). Based on comparisons of form between the synapophyses and hypapophyses of *Varanus amnhophilis* and extant forms, we interpret the preserved cervical vertebrae as cervicals 3, 4, and the anterior part of 5. Comparisons of the shapes of the synapophyses between *Varanus amnhophilis* and extant forms suggest that the preserved dorsal vertebrae are posterior dorsals; the first of the three is probably presacral vertebra 23, 24, or 25.

The cervical vertebrae have relatively tall and anteroposteriorly narrow neural spines and well-developed hypapophyseal pedicles capped by hemispherical hypapophyses (intercentra) (Fig. 3A). The dorsal vertebrae are also of a typical *Varanus* form in the short...
and broad neural spines, absence of zygosphenes-zygantra and pseudozygosphenes (Fig. 3B), and the presence of precondylar constriction (Fig. 3C). The precondylar constriction is noteworthy in that it is pronounced as compared to the more moderately constricted centra of taxa such as members of the Varanus (Polydaedalus) clade and Varanus flavescens (Fig. 4E). The minimum precondylar centrum width is approximately 76.5 percent of the maximum condylar diameter in the second preserved dorsal vertebra and approximately 75 percent of the maximum condylar diameter in the first preserved dorsal vertebra.

Zygosphenes-zygantra or structures similar to them (pseudozygosphenes) are characteristic of some varanids, such as Saniwa ensidens [11,12]. However, pseudozygosphenes also occur in Varanus exanthematicus and Varanus albigularis (Fig. 4F).

Materials and Methods

Phylogenetics

Our phylogenetic analysis includes a subset anguimorph species from a recent combined-evidence of Anguimorpha [3] and includes Shinisaurus crocodilurus as a representative shinisaur outgroup (Dataset S1). Five mosasaurs (Adriosaurus suessi, Aigialosaurus dalmaticus, Coniasaurus crassidens, Dolichosaurus longicollis, and Pontosaurus levisdens) were chosen to represent the basal condition in that clade, based on their position in recent phylogenetic analyses [2,3,42–46]. Other taxa were included because they are more closely related to Varanus than to Shinisaurus crocodilurus. These taxa included Paravaranus angustifrons, Proplatynotia longirostrata, Lanthanotus borneensis, Cherminotus longifrons, Aiolosaurus oriens, Ovoo gurvel, and the necrosaurs ‘Saniva’ festi, Necrosaurus cayluxi, Necrosaurus eucarinatus, Sanicodes mongoliensis, and Telmasaurus grangeri. A full list of comparative material can be found with the (Text S1).

In addition to taxa included in the earlier analysis [3], we added some relevant fossils. These included a partial skull referred to ‘Varanus’ marathonensis [12,16,47] and the original holotype Varanus marathonensis vertebra [12], both from Europe. We have treated the partial skull separate from the presumed holotypic vertebra because there is no clear reason to associate them. We added data from the incompletely known, subfossil Varanus hoojer from Flores. In his review of varanids and ‘megalanids’, de Fejérvary [48] described a fossil he believed to be close to Varanus bengalensis, which appears here as Varanus cf. bengalensis. We also include the recently described Birket Qarun ‘Varanus’ [49], and a putative basal Varanus or Varanus outgroup from the Jebel Qatrani Formation (the Yale Quarry ‘varanid’) [24].
Characters, character states, and character state codings are largely from Conrad et al. [3], with some modifications to *Varanus amnhophilis* (AMNH FR 30630) based on additional preparation of the specimen and further study of the material (see the description above). We provide the morphological codings for the matrix below in the (Dataset S1). The molecular character coding is exactly as it was in the earlier study [3] and is derived largely from the work of Ast [50,51].

In addition to the morphological character matrix used by Conrad et al. [3], we add 71 morphological characters (Text S2; characters 423–493). Note that, as with the Conrad et al. [3] and other earlier iterations of this data matrix [2,4,52], the biogeography character (character 364) was not used in phylogenetic hypothesis reconstruction. Note, also, that as in Conrad et al. [3], characters 413 and 414 replace character 236 (deactivated here) and character 415 replaces character 242 (deactivated here). Thus, of the 493 non-molecular characters in the matrix, only 489 were

Figure 5. Temporally calibrated phylogeny of varanids and their outgroups. Size data are indicated by color included on the known temporal ranges are derived from published accounts [21], ranges in black indicate taxa without reliable size data. Extant *Shinisaurus* was used as an outgroup for tree reconstruction, but the shinisaur clade is homogenous in size and extends into the Cretaceous [3]. Some nodes collapsed for space considerations, but the number of included species is in parentheses next to the taxon name (Dataset S1). Maps present the known distributions of the indicated taxa in red. Mosasaur distribution is based on the five basal taxa included in the analysis. *Varanus amnhophilis* is a nested member of the Indo-Asian A clade and the discordant distribution of that taxon with respect to other Indo-Asian A taxa is illustrated by the map on the lower left. doi:10.1371/journal.pone.0041767.g005
used in the tree searches. We performed a phylogenetic analysis of 83 species scored for 489 morphological and 5733 molecular characters.

We used NEXUS Data Editor (NDE) [53] to assemble and manage the data matrix. We performed an analysis using the New Technology Search in the computer program T.N.V.T.: Tree analysis using new technology [54] (1000 replications) with ‘ratchet’ and ‘drift’ options employed.

Paleobiogeography

After tree construction and consensusing, we mapped biogeographic data in the computer program Mesquite [55] and reconstructed the ancestral distributions in a basic parsimony analysis.

Size estimation/reconstruction

The holotype of Varanus amnhophilis consists of cranial, mandibular, and vertebral elements, along with one pectoral fragment (Figs. 2, 3). Having associated skull and postcranial is unusual among fossil varanids, which are often known from isolated vertebrae or long bone ends [12,16,24,49]. Because the AMNH FR 30630 is known from a relatively complete braincase and from cervical and dorsal vertebrae, we measured those elements in 20 specimens of 15 extant species of Varanus (Table 1) representing all of the major Varanus clades (see Fig. 5). The measured dorsal vertebrae come from just anterior to the lumbar vertebra in each specimen (posterior pelvic dorsal vertebrae of recent usage [56]).

We ran regressions of these data against precaudal lengths in those specimens and calculated standard deviations for these regressions. We assumed that a lower standard deviation implied a better correlation between any principal measurement and the precaudal length.

Precaudal lengths (PCL) was used as a proxy for body size because the tails of monitor lizards make up a variable amount of their total body length; that is, some monitors (e.g., Varanus komodoensis) have relatively short tails compared to their overall length, whereas others (e.g., Varanus salvator) have relatively long tails [21,23]. Precaudal length is similar to snout-vent length (SVL), a measurement often used as a proxy for reptile size.

We also took measurements of lateral braincase length (BCL) and length of posterior dorsal vertebrae (DVL). Lateral braincase length is measured from the anterior tip of the paroccipital process to the posterolateral tip of the paroccipital process. Dorsal vertebra length was measured from the anterior end of the centrum) to the posteromedial condylar lip (not extending onto the articular surface of the condyle).

For estimating sizes based on dorsal vertebrae, we used the data in Table 1 along with measurements DVL and BCL of Varanus amnhophilis and Varanus priscus (designated here as ‘measurement of interest’; measurements in Results, below). The equation is as follows:

\[
\text{measurement of interest} = \text{average PCL for relevant extant taxa/average measurement of interest for relevant extant taxa}
\]

For the purposes of our study, we include only non-snake squamates (‘lizards’) for size comparison. Snakes (Serpentes) are, of course, just one of many radiations of ‘lizards’ that show extreme limb reduction and limblessness. However, snakes are much more speciose and diverse than any other single group of limbless squamates. It is noteworthy that snakes include some of the longest extant reptiles—certainly the longest extant squamates, suggesting that they (or some sub-group of them) may have evolutionary innovations causing them to operate under a slightly different set of biological pressures. Although there is the lingering idea that snakes may be closely related to varaniform squamates [57] and, consequently, may share this same innovation(s) with them, still this connection is tenuous [2,58–61] and the innovation(s) (if any) remain unknown. For these reasons, snakes are excluded, hereafter, from comparisons with ‘lizards’ for the remainder of this paper.

Results

Phylogeny

The shortest tree-length recovered by the analysis had a length of 10,325 steps, consistency index excluding uninformative characters of 0.2614, and a retention index of 0.4530 (Fig. 5). The analysis found 5290 trees of that length and none shorter.

Because we included some very fragmentary taxa, a strict consensus of our analysis recovered little resolution (Text S3). Following some recent studies [2,3,62–64], we report the Adams consensus (Fig. 5) because it shows the relationships that are common to all trees and collapses volatile taxa to the level of their least inclusive node. Although species-level coding was used for all of the included taxa, some clades were collapsed in the interest of brevity in the figure (Fig. 5). Full strict and Adams consensus trees are available with the (Text S3).

Our analysis recovers a Saniwa-Varanus clade exclusive of the Eocene-Oligocene varanids from Egypt (see below and Fig. 5). Of the seven unambiguous Varanus synapomorphies recovered in this analysis, Varanus amnhophilis may be demonstrated to possess absence of pterygoid teeth (Fig. 2F) and absence of accessory zygosphene-like vertebral processes (Fig. 3B). The clade referred to as Indo-Asian A [50] and the Australasian clade are united (Fig. 5) by one morphological (presence of strong precodylar constriction of the presacral vertebrae) and 18 molecular unambiguous character states. Indo-Asian A, including Varanus amnhophilis, is united by a Vidian canal completely housed by the parabasal sphenoid (Fig. 2G) and 28 unambiguous molecular synapomorphies. Members of Indo-Asian A exclusive of the salvator/radicollis group are united by absence of postrolateral parabasal sphenoid flanges and 12 unambiguous molecular synapomorphies. The latter clade, exclusive of Varanus flavescens, is united by presence of separate ossifications on the sphen-occipital epiphyses. Varanus dupreii and Varanus (Indovaranus) spp. are united to the exclusion of Varanus amnhophilis by the presence of a prootic contribution to the posterior Vidian canal opening and a ventrolaterally expanded paroccipital process tubercle.

‘Varanus’ sivalensis is a poorly known taxon represented only by a fragmentary humerus and two vertebrae [65], the latter lacking precodylar constriction. This taxon is usually considered to represent an early monitor lizard [12,27,65]. Although these remains represent a very large squamate, possibly a varaniform, they show no special similarity with Varanus and were not included in the current analysis.
Table 3. FOSSIL BODY SIZE ESTIMATES.

| taxon               | comparisons | meas. | L (mm) | PCL est. (mm) | ± |
|---------------------|-------------|-------|--------|---------------|---|
| Saniwa ensidens     | all Varanus | DVL   | 10.9   | 412           | 17.66 |
| V. amnhophilis      | BCL         | 38.38 | 678.64 | 38.12         |
| V. amnhophilis IA-A | BCL         | 38.38 | 712.6  | 83.96         |
| V. amnhophilis      | BCL         | 18    | 681.1  | 29.19         |
| V. amnhophilis IA-A | DVL         | 16    | 664.5  | 36.89         |
| V. priscus A        | all Varanus | BCL   | 106    | 1874          | 105.3 |
| V. priscus A        | Vko and Vgo| BCL   | 106    | 1897          | 456.1 |
| V. priscus A        | V. komodoensis | BCL | 106    | 1777          | 69.63 |
| V. priscus B        | all Varanus | DVL   | 53     | 2005          | 85.94 |
| V. priscus B        | Vko and Vgo| DVL   | 53     | 2170          | 211.2 |
| V. priscus B V. komodoensis | DVL | 53     | 2116   | 169.6         |

Body size estimates for fossil varanids (Saniwa ensidens, Varanus amnhophilis, and two specimens of Varanus priscus). Estimates derived from comparisons with the data presented in Table 1, as described in the text. Headings/abbreviations: taxon, fossil taxon whose size is predicted; comparisons, taxon group used for making the length estimation; meas., measured element; L, observed length of the measured element in mm; PCL est., estimated precocial length of the fossil taxon; ±, the difference between the estimated PCL length and the maximum or minimum length falling within a 95 percent confidence interval; BCL, lateral braincase length (see text); DVL, dorsal vertebral length (see text); V., Varanus; Vko, Varanus komodoensis; Vgo, Varanus gouldii. Underlined measurements indicate those which were deemed most pertinent based on taxonomic comparisons and phylogenetic placement (Fig. 5) and illustrated in Figure 6.

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Paleobiogeography

An African origin for Varanus has been suggested based, in part and most recently, on some Egyptian Paleogene fossils attributed to Varanus or its 'stem' (i.e. Varaninae) [24,49]. However, these fossils were not previously included in a phylogenetic analysis, and our analysis suggests that there is no compelling evidence supporting their inclusion within the Senticos-Varanus dichotomy (Fig. 5). Earlier studies suggested an Asian origin for Varanus based on known biogeographic distributions of fossils and phylogeny of extant taxa based on karyological data [66–68] and 12S rRNA [69].

Many of the most proximal Varanus-outgroups come from across Eurasia or North America [2,70] (Fig. 5), leaving the biogeographic position of the Varanus outgroup unresolved. Varanus rusingensis and the extant clade Varanus (Polydaedalus) exanthematicus (Vex), and the large represents Varanus komodoensis (Vko)—all to scale. Gray bars indicate predictive size range within 95 percent confidence interval. See text and (Text S1 and Text S3).

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Body size estimation

The average PCL/BCL ratio for all Varanus in which those measurements were available is 17.68 with a standard deviation (SD) of 2.322 (y intercept [yi] = 17.16; x intercept [xi] = 14.11; R2 = 0.956). The PCL/DVL for Varanus komodoensis is 16.76 (SD of 0.474) (note, only two data points; yi = 17.67; xi = 24.20, and for the Indo-Asian A clade is 18.57 (SD of 2.73; yi = 22.08; xi = 24.20, R2 = 0.975).
DVL for *Varanus komodoensis* is 39.93 (SD of 2.309; \( \hat{y} = 44.71; \) \( x_i = 131.4 \)) and for the Indo-Asian A clade it is 36.91 (SD of 2.562; \( \hat{y} = 42.21; \) \( x_i = -64.96; \) \( R^2 = 0.994 \)).

The DVL of *Varanus amnhophilis* is 18 mm; its BCL is 38.38 mm. The DVL of *Varanus priscus* (AMNH FR 1486) is 53 mm. The BCL of *Varanus priscus* (BMNH 39965) is estimated at 106 mm based on an incomplete braincase [35].

Correlations between morphological dimensions and body size within eontant *Varanus* allow us to estimate PCL in our new fossil (Tables 1, 2, 3). We found strong correlations between BCL and PCL, and between DVL and PCL in modern *Varanus* (Table 1). Using these metrics and supposing that *Varanus amnhophilis* scaled similarly to other “Indo-Asian A” clade *Varanus*, we estimate its PCL at approximately 712.6 mm (±83.96 mm with a 95 percent confidence interval) based on braincase length, or approximately 664.5 mm (±36.89 mm) based on dorsal vertebra length (Fig. 6) (Table 3). Based on compiled size data for modern *Varanus* [21], *Varanus amnhophilis* is a giant among monitor lizards, being larger than approximately 85% of known *Varanus* (Table 2) and, therefore, the vast majority of known lizards (below).

Among eontant non-*Varanus* lizards, only *Amphisbaena alba* reaches giant sizes and appears to average over 600 mm PCL or SVL [71]. However, the body size of *Amphisbaena alba* and the large, limbless anguid, *Pseudopus apodus* (which may exceed 500 mm SVL [72,73]) is smaller than a *Varanus* with a similar SVL. Among living, limbed lizards, *Cyclura* (which may exceed 500 mm SVL [74]) includes the largest species after *Varanus*. Iguanidae includes several other large-bodied species belonging to the clades *Amphyblychynclus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Iguana*, and the fossil taxon *Lapitiquanu* that approach or exceed 500 mm SVL [75,76]. Limbed lizards, particularly the partly- to heavily-herbivorous iguanids, are thicker-bodied than the elongate limbless forms, and may, therefore, have greater masses than said limbless forms or the mostly predatory *Varanus*.

Polyglyphanodontidae includes some of the largest fossil lizards (AMNH, USNM, and YPM collections include specimens with PCLs of more than 410 mm [pers obs. of the authors]). However, except for the mosasaurs, which were marine and could reach total lengths of as much as 17 m [77], no other clade of lizards exhibit giant average sizes (>600 mm) common to several species of *Varanus* (Figs. 5, 6; Tables 1, 2).

*Varanus amnhophilis* has a PCL greater than approximately 99% of known, non-snake, squamates ever.

We also estimated the size of *Varanus priscus* (= *Megalanina priscas*; Megalania [35]). Given that Megalania is a nested member of the large-bodied Australasian *Varanus* clade, the largest specimen of *Varanus priscus* available to us (AMNH FR 6304 (east); dorsal vertebra length = 52.97 mm), we estimate its PCL at 2116 mm (±169.6 mm) (Fig. 6A). A recently redescribed braincase [35] comes from an individual whose PCL we estimate at 1777 mm (±69.63 mm) (Fig. 6) (Table 3) (Fig. 6B). By employing the size-reconstruction metrics of a earlier analysis [13], a recent study suggested that *Varanus priscus* would have had an average total length of approximately 3450 mm [25] (presumably suggesting a SVL of 1725 mm or less given the scaling of *Varanus komodoensis* and *Varanus varus*). Our metric and the available *Varanus priscus* data suggest that at least AMNH FR 6304 was much larger than that, but considerably smaller than many historical estimates [13,15,78]. It is, however, noteworthy that the largest-known wild specimens of some species may far exceed the mean or average size. For example, very large *Varanus exanthematicus* may be 151 percent of the mean, large *Varanus rudicollis* may be 175 percent of the mean, *Varanus komodoensis* may be 181 percent of the mean, and the largest *Varanus salvator salvator* measured nearly 225 percent of the mean size for the subspecies [21,79] (Table 2), suggesting that exceptionally large specimens of *Varanus priscus* might have exceeded 3000 mm PCL. This is similar to some of the larger body-size estimates for the species. It is also possible that Megalania is a species-complex, not a species [27], but that little influences our size estimates.

These metrics are also applicable to proximal *Varanus* outgroups. The posterior most 10 dorsal vertebrae of a specimen of *Sanuxa ensidens* with an SVL of 420 mm, average 10.89 mm in length [11]. Assuming *Sanuxa ensidens* scales similarly to *Varanus* generally, our model predicts a PCL of approximately 412.0 mm (±17.66 mm)—within two percent of the reported SVL [11]. Consequently, we believe that our method for estimating varanine sizes from isolated vertebrae has considerable predictive power for varanines generally, at least within the *Varanus-Sanuxa* dichotomy.

**Discussion**

*Varanus rusingensis* (the Rusinga Monitor) and *Varanus amnhophilis* (the Samos Dragon) are the earliest-known demonstrable *Varanus*. *Varanus amnhophilis* offers the first evidence of a Miocene divergence for major *Varanus* clades beyond the basal dichotomy between the African *Polydaedalus* and all other true monitors (Fig. 5). Given the phylogenetic hypothesis recovered here, no fewer than eight major *Varanus* lineages must have been present by the Turolian. These radiations include groups of Indo-Asian A monitors (the *Empagasia*, *Indovaranus*, and *Tectovaranus* clades), the *Dendrovaranus-Sotovaranus* clade, the Australasian clade, the Indo-Asian B clade, the lineage including *Varanus griseus*, and the *Polydaedalus* clade.

In addition to the morphological diversity suggested by the presence of these clades, we hypothesize a broad distribution for *Varanus* across Africa, Arabia, Eastern Europe, and Asia by the late Miocene. This is further supported by fragmentary material of uncertain phylogenetic affinity, such as *Varanus ‘cf. bengalensis’*, *Varanus marathensis*, and others [12,16,24,47–49]. As opposed to the recently favored out-of-Africa hypothesis [24,49], we suggest a Laurasian origin for *Varanus* with subsequent major diversification perhaps occurring in southern Asia.

As with some recent analyses of *Varanus* [3,50,51,80,81], our data support a basal dichotomy, perhaps representing a vicariant split, between the *Polydaedalus* clade and all other *Varanus*. However, our analysis differs from some recent molecular analyses [50,51,80,81] in that *Varanus griseus* is not found to be a part of *Polydaedalus* radiation. Given this hypothesis, the distribution of *Varanus griseus* requires some further attention. One interpretation would be that *Varanus griseus*, like all non-*Polydaedalus* monitors, is of a primarily Asian origin with a later invasion of northern Africa. Aridification during the Miocene, which probably made the Sahara a more significant biogeographic barrier [82,83], led to the eventual isolation of the southern African clade. Occurrence of *Varanus yemenensis* (which was not included in our phylogenetic analysis, but is very similar to *Varanus altigularis* and *Varanus exanthematicus*) on the Arabian Peninsula would represent a dispersal across the Red Sea, perhaps at its southern end where Arabia approaches Africa and the Indian Ocean.

An alternate interpretation would be that the out-of-Africa hypothesis is correct. If *Varanus* is of African origin and subsequently dispersed northward and eastward to its present range, *Varanus griseus* and its lineage might represent an early emigration. However, this would require complete extirpation of non-*Polydaedalus Varanus* from Africa, with no remnant of their presence. Our data more strongly support the Eurasian origin for *Varanus*. 

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Varanidae originated in the Cretaceous and soon exploited small body-size ecomorphs [4], something they still do today with no fewer than nine species averaging below 150 mm in SVL [21], but it is only since the late Miocene that there is any evidence of giant varanids (Fig. 5). Lizard gigantism and dwarfism is thought to be influenced by a complex set of pressures and is often associated with island endemism [26,84,85]. Today, the largest lizards have a variety of ways of dealing with mammalian competitors. The only giant, non-Varanus lizards alive today (Amphisbaena athenae) are limbless and have adopted some degree of fossoriality. Cyclura evolved large (if not giant) sizes on isolated islands. This is similar to some of the larger varanids, including Varanus komodoensis, Varanus salvator, and Varanus niloticus.

Varanus is unique in that it contains giant lizards that co-occur with endemic mammalian competitors. Numerous species of Varanus appear alongside marsupials in Australia [21,23,86] and Varanus flavescens appeared alongside marsupials in Australia [21,23,86]. Today, the largest remaining members of the clade today live on isolated islands and on Australia where eutherians are human-introduced newcomers. It is only in Africa that giant Varanus (Varanus niloticus and Varanus ornatus) co-occur with numerous eutherian mammals similar to the competitors Varanus annuliferus would have encountered [29,30].

Boa species and Pythonidae include the longest and heaviest extant squamate species [22,87,88]. Locomotion, hunting, and feeding in these snakes is different from that of ‘lizards’, even limbless lizards, perhaps offering a different set of parameters for producing giants. Boa species reached their largest known sizes long before varanids, but they seem to have done so in the absence of significant eutherian competitors [87]. Even so, modern boas and pythonids reach great size in the presence of eutherian competitors in the tropics worldwide today [22,88]. Without the benefit of mammalian-style parental protection, young and small members of large-bodied lizard and snake species must use camouflage, water, burrows, and/or trees to escape predators, and/or grow to adulthood relatively quickly [22,79].

Geological data from Samos suggest that Varanus annuliferus lived in an environment including mixed forest and open areas with freshwater streams, and possibly strong seasonality including some flooding [29,30]. Modern members of the larger clade to which Varanus annuliferus belongs (also including Varanus dumerilii, Varanus flavescens, Varanus rudicollis, the Indosaurus-group, and the Saurisaurus-group) are largely terrestrial, but are often strong climbers and swimmers [21].

The Samos Dragon, Varanus annuliferus, shared its environment with mustelids (e.g., Procyon, Pardaxidae, and Procanidae), hyaenoids (e.g., Hyaenidae and Hyaenidae, among others), and suids (Microstenininae) [29,30]. Each of these mammals would have posed significant threats to a monitor lizard and/or would have been predators on Varanus eggs. Despite this, Varanus (Varanus) annuliferus is the earliest-known giant limbed lizard and the first to establish the upper one-percent of lizard sizes on land.

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Supporting Information

DATASET S1 MORPHOLOGICAL CHARACTER-BY-TAXON MATRIX. Here, we include the full morphological data matrix, including the character scorings for those characters described in earlier analyses. Note that some taxa were coded for only molecular characters (see text). Those taxa have a ‘?”’ for each coding but are included here for ease of the reader should she or he desire to reproduce our matrix. (DOC)

TEXT S1 COMPARATIVE MATERIAL. Observations on the following specimens were used for this study. Institutional abbreviations: AMNH, American Museum of Natural History; BSP, Bayerische Staatsammlung für Paläontologie und Geologie; BMNH PR, Natural History Museum, London (Great Britain); GM, Geiseltal Museum of the Martin-Luther Universität in Halle/Saale (Germany); UF, University of Florida, Florida State Museum; ZPAL, Zoological Institute of Paleobiology, Polish Academy of Sciences, Warsaw (Poland). (DOC)

TEXT S2 CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS. Morphological characters and character states used in the phylogenetic analysis. (DOC)

TEXT S3 FULL CONSENSUS TREES FOR THE ANALYSES. Below we include the strict and the Adams consensus results for the results of the TNT [54,89,90] analyses as read out by PAUP* [91]. Note that the strict consensus lacks resolution because of the volatile nature of some taxa (e.g., Jebel Qatrani ‘Varanus’). (DOC)

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Author Contributions
Conceived and designed the experiments: JLC AMB CMM. Performed the experiments: JLC. Analyzed the data: JLC CMM AMB. Contributed reagents/materials/analysis tools: CMM AMB. Wrote the paper: JLC AMB CMM. Prepared the specimen: AMB.
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