EVOLUTION OF BODY SIZE: VARANID LIZARDS AS A MODEL SYSTEM

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Abstract.—Modern comparative methods allow the examination of the probable course of evolution in a lineage of lizards (family Varanidae, genus *Varanus*). Within this genus, body mass varies by nearly a full five orders of magnitude. The fossil record and present geographical distribution suggest that varanids arose over 65 million yr ago in Laurasia and subsequently dispersed to Africa and Australia. Two major lineages have undergone extensive adaptive radiations within Australia: one evolved dwarfism (subgenus *Odatria,* pygmy monitors), whereas the other Australian lineage (subgenus *Varanus*) remained large, and several of its members evolved gigantism. Body sizes of extant varanid species are plotted on a phylogeny, and probable sizes at ancestral nodes are inferred from those of their descendants. Felsenstein's method of phylogenetically independent contrasts, coupled with information on branch lengths, is exploited to identify several likely instances of relatively rapid evolution of body size, both between and within clades. Numerous questions about the evolution of size in this genus within a historical/geographical perspective remain to be answered.

A century ago, Cope (1896) noted that body size frequently increased during the evolutionary history of a phylogenetic lineage, giving rise to "Cope's law of phyletic size increase." More recently, Schmidt-Nielsen (1984) discussed general problems of size and scale, allometry, constraints imposed by body plans, plus the effects of size on a host of physiological processes and animal performances such as locomotion. Calder (1984) stressed how life-historical traits are constrained by and co-vary with body size. For example, generation time is strongly positively correlated with size, whereas rates of increase co-vary negatively with size.

Phylogenetic systematics has revitalized comparative evolutionary biology because this powerful approach allows analyses of the probable course of evolution (Ridley 1983; Felsenstein 1985; McLennan et al. 1988; Brooks and McLennan 1991; Garland et al. 1991; Harvey and Pagel 1991; Garland 1992). Appropriate statistical procedures useful in factoring out phylogenetic effects and estimating ancestral states and rates of evolution were first worked out by Felsenstein (1985) in a now-classic article. These methods have been extended by Felsenstein (1988), Grafen (1989), Maddison (1990), Harvey and Pagel (1991), Harvey and Purvis (1991), Martins and Garland (1991), Garland (1992), Garland et al. (1992), and others.

Here I apply some of these potent comparative techniques to trace the probable course of the evolution of body size within a lineage of lizards. Possible scenarios for the evolution of size in this lizard lineage are discussed, and many questions worthy of further research are raised.

EVOLUTION AND DIVERSITY OF THE VARANIDAE

Varanus are morphologically conservative but vary in mass by nearly five orders of magnitude. To my knowledge, no other terrestrial animal genus exhibits such a range of size variation. There is proportionately almost as much difference in mass among species within the genus *Varanus* as there is between an elephant and a mouse. Mammals vary in size, from 3-g shrews to whales that weigh over 50 tons, but constitute an entire subclass. No mammal genus exhibits size variation anywhere near as extensive as *Varanus*. Varanids are sufficiently conservative morphologically that taxonomic ranking at the generic level seems justified. Even if the genus *Varanus* is eventually broken up into several closely related genera, the comparison with size variation in mammals is still striking. These properties, coupled with the fact that a phylogeny has recently become available, make varanid lizards a nearly ideal model system for examining patterns of size evolution.

All living members of the Varanidae, commonly known as monitor lizards, are placed in a single genus *Varanus,* generally considered to be monophyletic (Pregill et al. 1986; King et al. 1991; Baverstock et al. 1993; Green and King 1993). Many monitor species are large and impressive—they are often the centerpiece of reptile house exhibits. *Varanus,* which are not particularly tractable research subjects, have also received an extraordinary amount of attention from dedicated students. All but one species, the frugivorous *Varanus olivaceus* of the Philippines (Auffenberg 1988), are active predators and eat quite large prey relative to their own body size (Pianka 1982, 1994; but see Losos and Greene 1988 and Auffenberg 1994 for dissenting views). Many monitor lizards are top predators (Losos and Greene 1988; Pianka 1994). Some species are aquatic, others terrestrial, while still others are saxicolous and/or semiarboreal or truly arboreal. Monitor lizards live in a wide variety of habitats that range from mangrove swamps to dense forests, to savannas, to arid deserts.

McDowell and Bogert (1954) recognized the lizard superfamily Varanoidea, which consists of the lineage of lizards that gave rise to the family Varanidae plus several other lineages including North American Helodermatidae (Gila monsters) and Lanthanotidae from Borneo, as well as some extinct taxa such as gigantic marine mosasaurs and the Upper Cretaceous Mongolian *Estesia* known only from fossils (Norell et al. 1992). Pregill et al. (1986) subsequently restricted Varanoidea to Varanidae (Varaninae plus Lanthanotinae) and Helodermatidae. The earliest known varanoid fossils date from the Upper Cretaceous, Paleocene, and Eocene of North America, Europe, and Mongolia (McDowell and Bogert 1954; Norell et al. 1992), which suggests an ancient Laurasian origin for the group. Many of these fossils are very similar to present-day varanids, an indication of the conservativeness and staying power of this basic body plan. Most students of

Varanus believe that the genus arose in Eurasia, where the majority of Mertens's subgenera still occur today (Greer 1989; Baverstock et al. 1993; King and Green 1993). Varanids are usually considered to be a late Tertiary invader of Australia because the earliest Australian fossils are from the middle Miocene of South Australia. Others (Hutchinson and Donnellan 1993; K. Aplin, personal communication) have, however, argued for a Gondwanan origin for varanids, which remains a definite possibility.

The sole surviving varanoids in the New World are the Gila monster, *Heloderma suspectum,* and its Mexican congener, the beaded lizard, *Heloderma horridus* (Bogert and Del Campo 1956). By Nearctic-Neotropical standards, *Heloderma* are large lizards (0.35–0.45 m snout-vent length [SVL]), yet, when compared with an average varanid, they are only moderate-sized lizards.

Currently, 44 extant species of *Varanus* are recognized worldwide, some 27 of which occur in Australia. On the basis of morphological evidence, Mertens (1942, 1958, 1963) erected the first taxonomy. He recognized 10 subgenera (appendix), seven of which contain only a single species. Two subgenera with many species, *Odatria* and *Varanus,* have undergone adaptive radiations in Australia. Almost all 17 members of *Odatria* are small, and all are restricted to Australia, which suggests that this lineage of pygmy monitors arose and diversified within Australia. (Mertens misplaced *prasinus* in Odatria; it and its close relatives belong to an Asian clade; see below.) Most members of the subgenus *Varanus* are also confined to Australia. Only four varanid species occur in all of Africa (*albigularis, exanthematicus, griseus,* and *niloticus*), and these were assigned to three different subgenera by Mertens. Fourteen other species (belonging to eight of Mertens's 10 subgenera) are variously distributed across Asia and southeast Asia: *bengalensis, dumerili, flavescens, indicus* (also found in northern Australia), *jobiensis* (formerly *karlschmidti;* Bohme 1991), *komodoensis, olivaceus, prasinus* (also found in northern Australia), *beccari, bogerti, teleneseotes* (close relatives of *prasinus*), *rudicollis, salvadori,* and *salvator.* One other little-known species (*yemenensis*) is restricted to Arabia. The highest species densities of *Varanus* occur in Australia, where as many as six species occur together in sympatry in the arid desert interior (Pianka 1994) and up to 10 species coexist in Arnhem Land in wet northern tropical Australia (Cogger and Heatwole 1981; S. Sweet, personal communication).

Two distinct evolutionary lineages have undergone extensive adaptive radiations in Australia: the pygmy monitor subgenus *Odatria* and the subgenus *Varanus,* which includes the larger species of Australian monitors plus several species found nearby outside Australia (*indicus, prasinus,* and *teriae* appear to have recently reached Australia from New Guinea). Australian monitors range in size from the diminutive pygmy monitor *Varanus* (*Odatria*) *brevicauda* (0.2 m in total length, 8–10 g) to the largest living lizard in Australia, the perentie, *Varanus giganteus* (total length may exceed 2.0 m, mass = 17 kg). The typical monitor lizard threat posture and behavior have been conserved in the evolution of tiny monitors such as *brevicauda,* which hiss and lunge with their throats inflated as if they were a serious threat. Hatchling *brevicauda* have SVLs of 40–48 mm and weigh only 1.3–1.8 g (G. Thompson, personal communication). Even more

awesome are Komodo monitors (*Varanus komodoensis*) of the Lesser Sunda Islands of Indonesia, which attain total lengths of over 3 m and weights of more than 150 kg (Auffenberg 1981). Komodo monitors, however, are themselves dwarfed by the largest known terrestrial lizard, a closely related gigantic varanid formerly assigned to the genus *Varanus*. *Megalania prisca* is a Pleistocene fossil (19,000–26,000 yr B.P.) from Australia, estimated to have reached 7 m in total length and to have weighed more than 600 kg (Hecht 1975; Auffenberg 1981; Rich 1985). Cladistic systematics will undoubtedly require that the fossil taxon *Megalania* eventually be reassigned to the genus and subgenus *Varanus* (A. Kluge, personal communication). These spectacular creatures must have been even more formidable than modern-day saltwater crocodiles. The major prey of these gigantic monitor lizards is thought to have been large diprotodont marsupials (rhinoceros-sized beasts, now extinct, that were relatives of wombats and koalas). Being contemporaneous with aboriginal humans in Australia, in all probability *Megalania* also ate *Homo sapiens*. *Megalania* teeth were over 2 cm long, curved, with the rear edge serrated for cutting and tearing the skin and flesh of its prey as these powerful predators pulled back on their bite. Many other species of *Varanus* also possess such teeth. Several authors have suggested that *Varanus komodoensis* and *Megalania prisca* are/were ecological equivalents of large saber-toothed cats, using a slashing bite to disembowel large mammals (Auffenberg 1981; Akersten 1985; Losos and Greene 1988). Water buffalo as large as 590 kg have been killed by *Varanus komodoensis,* more than three times their own mass (Auffenberg 1981).

PHYLOGENY

In addition to Mertens (1942, 1958, 1963), several other researchers have attempted to place extant varanids into groups. King and King (1975) and King (1990) studied karyotypes of 27 varanid species and identified six different independent karyomorph groups defined on the basis of chromosome markers such as fixed multiple pericentric inversions and the presence of acrocentric or metacentric microchromosomes. Clusters of species were placed into each of these six karyomorph groups. Other workers have also attempted to place various species of *Varanus* into groups based on hemipeneal morphology (Branch 1982; Bohme 1988) and lung anatomy (Becker et al. 1989). Phylogenetically informative data from chromosomal, hemipeneal, and lung morphology are largely (although not entirely) concordant with microcomplement fixation (MCF) data reported below, on which this article is based.

Using MCF, King et al. (1991) and Baverstock et al. (1993) examined relationships of 30 of the 44 extant species of *Varanus*. Reciprocal testing produced immunological distances and generated a phylogeny for 14 taxa (fig. 1). Less reliable, one-way tests added another 18 taxa to the tree, two of which are subspecies (fig. 2). Despite the methodological weakness of one-way tests, the striking concordance with biogeography (fig. 2) lends some credibility to this phylogeny. Seven of the 14 missing taxa are small Australian monitor species generally considered to belong in the subgenus *Odatria*. Three other missing taxa are the
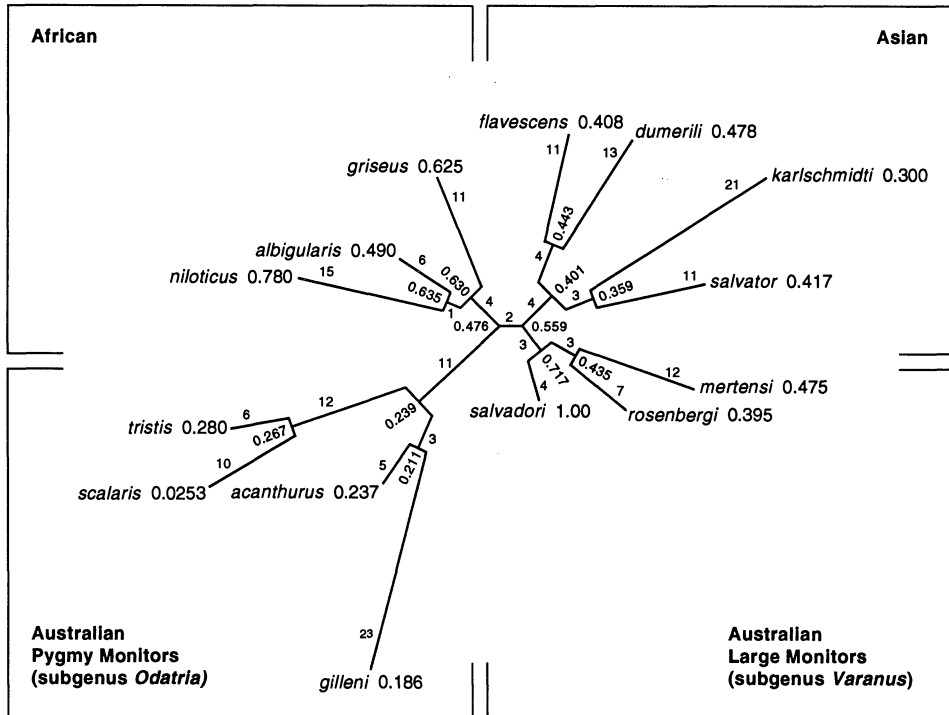
FIG. 1.—Fitch-Margoliash best-fit phylogeny based on immunological distances among 14 species of *Varanus* from reciprocal tests using microcomplement fixation. Jackknifed trees formed after dropping one taxon at a time support all but one node (*karlschmidti* is changed by dropping *salvator;* hence this node remains tentative). Because the tree is unrooted, the apparent basal tetrachotomy is not in fact basal. The numbers above branches are immunological distances (branch lengths); those following the names of terminal taxa are maximum SVLs (in meters); those at nodes are estimates of the size of ancestors. Ancestral sizes were estimated as simple unweighted averages of the states of descendants (see text for discussion). (Adapted from King et al. 1991.)

Philippine *olivaceus,* the African *exanthematicus* (closely allied to *albigularis* [Mertens 1942, 1958], which is included), plus the Arabian *yemenensis* (closely related to *albigularis* [Bohme 1988, 1991]). The remaining four missing species are newly recognized close relatives of *prasinus* (Sprackland 1991*a*), which is included. For obvious reasons, the fossil *Megalania prisca* is also missing from figure 2. Unfortunately, this tree could not be rooted (one outgroup, *Lanthanotus,* is rare and unavailable, whereas the other, *Heloderma,* was too distantly related to cross-react to *Varanus* antiserum). Because the tree is unrooted, the apparent basal tetrachotomy may not in fact be basal. Note, however, that to root this tree so that Australian species could be represented as monophyletic requires either an Asian root or an African root with an exceedingly unlikely transoceanic crossing between Africa and Australia, or rooting the tree at the base of or within either of the Australian groups, which in turn would require highly unlikely separate invasions of Asia and Africa from Australia.
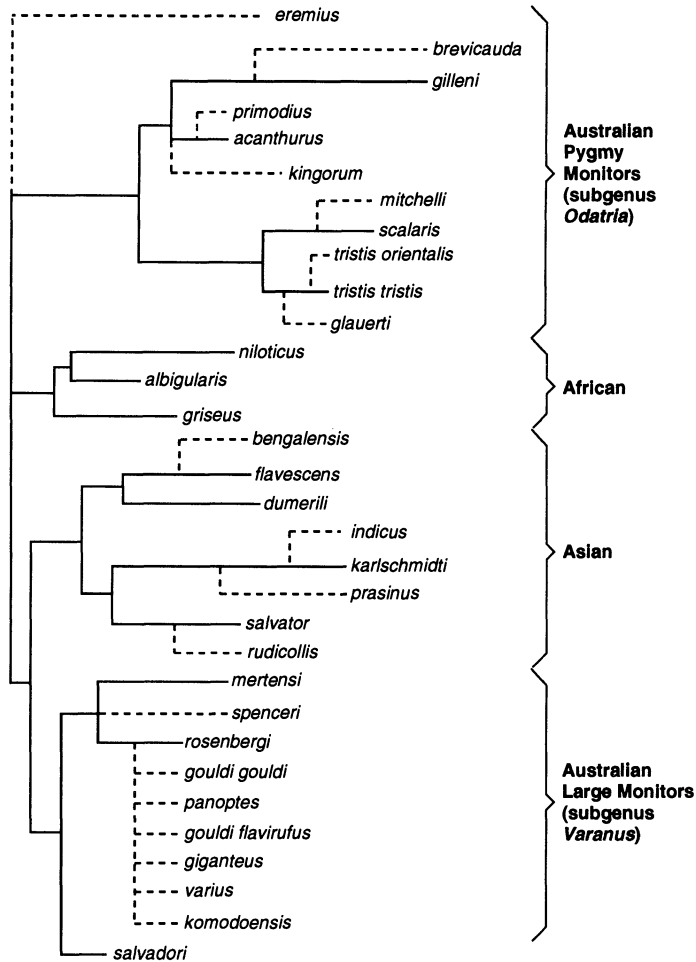
FIG. 2.—Tentative phenogram for 30 species of *Varanus* based on 14 reciprocal plus 18 one-way tests using microcomplement fixation (adapted from King et al. 1991). Two species, *gouldi* and *tristis,* are each represented by two different subspecies. Solid lines represent reciprocal tests, whereas dashed lines represent one-way tests. Most missing taxa are considered to belong to the topmost group (Australian *Odatria*). Again, the apparent basal tetrachotomy is not basal (see text for discussion).

The unlikelihood of such transoceanic movements between Australia and Africa, in either direction, coupled with present-day geographical distributions, justify as a working hypothesis the recognition of four clades: the Australian *Odatria* pygmy monitor clade, an African clade, an Asian clade, and the Australian clade of large monitors (including *komodoensis* and *salvadori*). (The fifth "lineage" leading to *eremius* is only weakly supported, as it relies on one-way tests and is not supported by non-MCF data. The small size of *eremius,* its geographical location in Australia, morphological similarity to other *Odatria,* and hemipeneal

anatomy all suggest that *eremius* will ultimately be found to belong in the subgenus *Odatria*.) Obviously, any of these putative "clades" would be destroyed if the tree were rooted within one of them. However, because these putative clades do make biogeographical sense, I accept them tentatively.

Of course, any phylogeny is no more than a working hypothesis. Much effort has gone into this attempt to reconstruct the phylogeny of this genus; further work remains to be done, but this MCF phylogeny is the only one currently available. The morphological studies alluded to above were taxonomic but not phylogenetic. Thus, this MCF phylogeny offers the first opportunity to undertake a phylogenetic analysis of the evolution of body size in varanid lizards. As is the case in any phylogenetic study of this sort, as soon as a better phylogeny becomes available, data will have to be reanalyzed to confirm that major results are robust (Vitt and Pianka 1994).

Except for *eremius* (positioned with one-way tests), *Odatria* appears to be monophyletic. Relationships of many taxa displayed in King et al.'s (1991) phylogeny do not fit well into Mertens's subgeneric scheme (compare the appendix with fig. 2). For example, Mertens placed three of the four African species (*niloticus, albigularis,* and *griseus*) in three different subgenera. In this phylogeny, these three species represent a single monophyletic group (all positioned with reciprocal tests). Mertens appears to have misplaced *Varanus mitchelli* in the subgenus *Varanus,* and instead it belongs in the subgenus *Odatria* (MCF, chromosomal, hemipeneal, and lung states all support this placement). This conclusion makes sense because *mitchelli* is smaller than other members of its putative former subgenus. Similarly, *indicus* and *jobiensis* (= *karlschmidti*) do not appear to belong in the subgenus *Varanus,* but, along with *prasinus* and its relatives, rather are embedded in a monophyletic Asian clade that includes *bengalensis, flavescens, dumerili, salvator,* and *rudicollis* (fig. 2). (Sprackland [1991a, 1991b] recently revised the *prasinus* group, describing two new species and elevating two subspecies to species status.) This monophyletic group calls several of Mertens's other subgenera into question. After the removal of *indicus, jobiensis* (= *karlschmidti*), and *mitchelli,* what remains in the subgenus *Varanus* appears to be monophyletic. In table 1, the 44 species of *Varanus* are placed into probable clades, and their habits and estimates of maximal SVLs listed. The Philippine *olivaceus* is provisionally listed as being in its own clade on the basis of its highly derived frugivorous dietary habits, but it may in fact ultimately prove to belong to the Asian clade.

The extant sister taxon to *Varanus* is *Lanthanotus* from Borneo (McDowell and Bogert 1954; Pregill et al. 1986; Estes et al. 1988). *Lanthanotus* are smaller than most *Varanus* and still poorly known, but they are aquatic and fossorial, which suggests that the ancestral condition in *Varanus* could have been a small aquatic monitor. If so, large body size, terrestriality, and arboreality would have arisen multiple times. However, *Lanthanotus* could easily be exceedingly specialized, highly derived, and not remotely similar to ancestral varanids. Losos and Greene (1988) argue that the primitive condition in *Varanus* is likely to be a midsized terrestrial savanna dweller; if so, aquatic and arboreal habits would have evolved several times. Moreover, small body size would then be a derived

TABLE 1

Species of *Varanus* Grouped into Probable Clades,
with Habits and Size

Species	Habit	SVL (m)
Australian pygmy monitors (subgenus *Odatria*):		
acanthurus	Saxicolous	.237
baratji	Saxicolous	.170
brevicauda	Terrestrial	.118
caudolineatus	Arboreal	.132
eremius	Terrestrial	.164
gilleni	Arboreal	.186
glauerti	Saxicolous	.227
glebopalma	Saxicolous	.355
kingorum	Saxicolous	.120
mitchelli	Aquatic	.346
pilbarensis	Saxicolous	.169
primordius	Saxicolous	.114
scalaris	Arboreal	.253
semiremex	Semiaquatic	.263
storri	Saxicolous	.132
timorensis	Arboreal	.253
tristis	Arboreal	.280
Australia (subgenus *Varanus*):		
giganteus	Terrestrial	.795
gouldi	Terrestrial	.655
komodoensis	Terrestrial	1.340
mertensi	Aquatic	.475
panoptes	Terrestrial	.500
prisca	Terrestrial	5.000
rosenbergi	Terrestrial	.395
salvadori	Semiarboreal	1.000
spenceri	Terrestrial	.500
varius	Semiarboreal	.765
Africa:		
albigularis	Terrestrial	.490
exanthematicus	Terrestrial	.500
griseus	Terrestrial	.625
niloticus	Semiaquatic	.780
yemenensis	Terrestrial	.600
Asian and Southeast Asia:		
beccari	Arboreal	.340
bengalensis	Terrestrial	.750
bogerti	Arboreal	.335
dumerili	Terrestrial	.478
flavescens	Terrestrial	.408
indicus	Arboreal	.530
jobiensis	Arboreal	.300
prasinus	Arboreal	.335
rudicollis	Arboreal	.450
salvator	Semiaquatic	.417
telenesetes	Arboreal	.217
teriae	Arboreal	.254
Philippines:		
olivaceus	Arboreal	.730

condition. By parsimony criteria, small body size evolved once in the lineage that led to *Odatria* as well as once in the lineage in the Asian clade that led to *jobiensis* (= *karlschmidti*) and the *prasinus* species group. Under this scenario, large body size would appear to have evolved at least three times in *niloticus* and *salvadori* and at least once in the clade containing *giganteus, komodoensis,* and *prisca*.

METHODS

Greer (1989, p. 207) lists maximum SVLs for 24 species of Australian *Varanus*. Snout-vent lengths of other non-Australian species were taken from various sources in the literature or estimated from published total length (SVL plus tail length) using the strong correlation and a linear regression of SVL on total length obtained from other species. Snout-vent lengths of all 44 species were thus collated (table 1). Hecht (1975) estimates a head length of 0.5 m for a *Megalania* with a 3.1-m SVL and puts the maximum SVL of *Megalania* at 5 m.

Comparative methods for explaining phenotypic evolution and interpreting adaptations are reviewed by Harvey and Pagel (1991), Harvey and Purvis (1991), and Losos and Miles (1994). Such techniques usually assume a "Brownian motion" model of evolution, with random changes at each time interval in each branch, such that more change accrues over longer time spans (but see Martins and Garland 1991; Gittleman and Luh 1992). Two basic approaches, both of which require a phylogeny, exist. First, directional methods require knowledge of ancestral character states for comparison of ancestors with their descendants. Second, nondirectional methods, or Felsenstein's method of phylogenetically independent contrasts, make comparisons within evolutionary radiations—descendants of an immediate common ancestor are compared with one another. Ancestral character states need not be known but can be estimated as the average of values of daughter taxa. In this situation, comparisons between ancestors and descendants are not possible because ancestral states are estimated from and therefore dependent on those of daughter taxa. If branch lengths are known, ancestral states can be estimated as weighted means of values of daughter taxa, with greater weight being given to shorter branches.

Given a phylogeny with branch lengths and character state values for terminal taxa, Garland (1992) shows how Felsenstein's method of phylogenetically independent contrasts can be used to compare rates of evolutionary change in phenotypes. Phenotypic data for N tip species of a monophyletic group can be transformed into $N - 1$ independent contrasts or differences. Moreover, because the variance of the difference between any two species is assumed to be proportional to the sum of their branch lengths, branch lengths can be used to standardize independent contrasts, which facilitates their comparison.

RESULTS AND DISCUSSION

Evolution of Size

Ancestral states (sizes) were estimated by two techniques suggested by Harvey and Purvis (1991), both as simple unweighted averages of the states of descen-
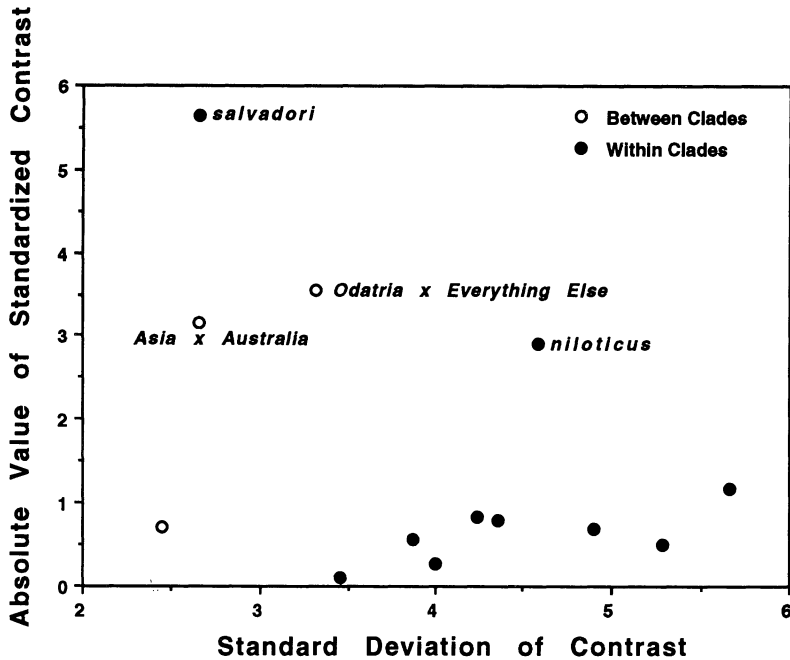
Fig. 3.—Estimated rates of evolution of body size (SVL) based on Felsenstein phylogeneti-cally independent contrasts, standardized as recommended by Garland (1992), plotted against the standard deviation of each contrast. Four (labeled) of the 13 possible contrasts suggest a relatively rapid evolution of body size.

dants and as means weighted by the inverse of branch lengths. For the varanid data, weighted and unweighted estimates are strongly correlated ($r = 0.986$, $P < .001$), an indication that varying branch lengths have little influence on such estimates.

Felsenstein phylogenetically independent contrasts for body size (SVL) were computed and standardized by dividing by the square root of the sums of MCF branch lengths as recommended by Garland (1992). Thirteen standardized inde-pendent contrasts from figure 1 are plotted against their standard deviations in figure 3. Points plotted in figure 3 are weakly inversely correlated ($r = -0.569$, $P < .05$), which indicates that Garland's standardization technique was not effec-tive for this data set (log transformation removes this correlation but scrunches up the data points). Four instances of relatively rapid evolution in size are sug-gested: the lineage leading to salvadori versus that leading to rosenbergi and mertensi, the lineage leading to niloticus versus albigularis, the contrast between the Asian and Australian large monitor clades, and the contrast between Odatria versus everything else. Presumably, with a more complete phylogeny that re-solved the seven species polytomy within the subgenus Varanus (bottom of fig. 2), rapid evolution in body size would also be evident in the lineage leading to giganteus and komodoensis. Another instance of gigantism must have occurred in this clade in the lineage that led to the fossil Megalania, which has not yet been placed in the phylogeny but almost certainly belongs to this clade.
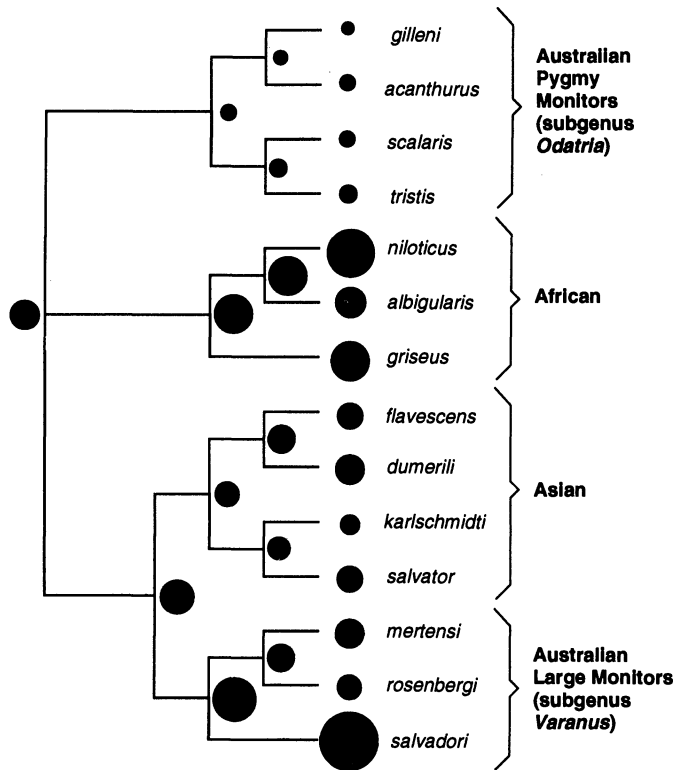
FIG. 4.—Cartoon of the phenogram in fig. 1 depicting the evolution of body size in varanid lizards. Relative sizes of extant species and ancestors are represented by the sizes of dots. Again, the apparent basal trichotomy is only an illusion. The actual phylogeny on which this is based is shown in fig. 1.

Figure 4 summarizes major results from figure 1 in a cartoon depicting putative sizes of lizards at each node by the size of a dot. Thus far, size in varanids cannot be polarized. Consider the two competing historical hypotheses for primitive states: the ancestral monitor was small, like *Lanthanotus*, versus ancestral monitors were already rather large lizards, some lineages of which evolved dwarfism while others tended toward gigantism. Under the first scenario, consistent with Cope's law, it is facile to assert that larger size meant fewer predators and offered more prey. Runaway selection for increased body size led to gigantism in *Megalania prisca* and *Varanus komodoensis*, which lineages subsequently either became extinct or endemic and endangered. Under this scenario, two lineages, *Odatria* plus the *jobiensis-prasinus* group, however, remained small.

Now consider the alternative hypothesis that ancestral varanids were already large. This lizard lineage has been around for more than 65 million yr, since the time of the dinosaurs, and many of the oldest fossils are large (SVLs > 1.0 m). Why has small size evolved only twice? The extensive adaptive radiation of pygmy monitors in Australia (17 described species) suggests still more questions:

why did the Australian *Odatria* clade undergo such an extensive adaptive radiation, and why have varanids in other parts of the world not evolved small body size, too? (This latter scenario seems to have occurred, but only once, and led to several dwarfs—*jobiensis/prasinus* and its relatives—in the Asian lineage.)

Some Questions and Directions for Future Research

In this article, I have stressed that size is exceedingly variable among varanid lizards, and I have identified several lineages in which body size appears to have evolved relatively rapidly.

Is there something innate in the varanid body plan that facilitates the evolution of such extensive variation in size? Why has body size evolved so rapidly among varanid lizards? What unusual ecological circumstances were experienced by populations at the nodes on which strong disruptive selection for size occurred? Were members of one lineage selected to evolve smaller size, whereas members of another sympatric lineage became larger? If so, why? Was character displacement (Brown and Wilson 1956) a factor in the evolution of size in varanids? Could the adaptive radiations of the subgenera *Odatria* and *Varanus* be linked in some way? Did the radiation of large Australian monitors facilitate the radiation of pygmies, and vice versa? What factors allowed the extensive adaptive radiations of *Varanus* in Australia but not elsewhere?

The arrival of varanids on a continent in which other terrestrial vertebrates had not yet completely occupied the carnivore niche may have provided varanids with an opportunity to diversify to fill numerous empty niches (Storr 1964; Pianka 1969; Hecht 1975). Hecht (1975, p. 248) states, "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?" Australian varanids did evolve alongside many predatory marsupials, including the large catlike *Thylacoleo,* the thylacine "wolf," and the Tasmanian devil, plus many other smaller dasyurid "native cats." Flannery (1993) suggests that Australia's low and unpredictable productivity may have favored ectothermic carnivores over endothermic ones. Why have more species of *Varanus* not evolved in Africa, Asia, and southeast Asia? Has the presence of small placental predatory mammals such as viverrids and small foxes precluded African and Asian adaptive radiations of *Varanus?*

Clearly, varanid lizards offer a model system for the study of evolution of size. However, more phylogenetic work on varanids is greatly needed. The tree needs to be rooted. An effort should be made to recover the phylogeny of all varanoids, including *Heloderma* and *Lanthanotus*. Various fossil forms should also be included. Fossil taxa (McDowell and Bogert 1954) include the Cretaceous *Sanivides* and *Telmasaurus* (Mongolia); the well-preserved and large late Cretaceous *Estesia mongoliensis* (Mongolia) (Norell et al. 1992); the Upper Cretaceous *Palaeosaniwa* (North America); the Paleocene → Oligocene *Saniwa* (North America and Europe); the oldest Australian putative varanid remains from the Etadunna Formation of South Australia, considered to be mid-Miocene (Stirton et al. 1961); the Pliocene *Varanus* from the Allingham Formation of north Queensland (Molnar 1985); late Pliocene *Varanus dirus* from Kings Creek, east Darling Downs, Queensland (De Vis 1889); Pleistocene *Varanus bolkayi* of Java (Estes 1983); as

well as the giant Pleistocene *Megalania* from Australia (De Vis 1889; Hecht 1975; Rich 1985).

Rigorous cladistic analyses involving molecular and morphological characters and proper outgroups are needed to corroborate or contradict MCF results. A morphological analysis to infer varanid interrelationships is presently underway (A. Kluge, personal communication). In collaboration with Peter Baverstock, Dennis King, Tod Reeder, and Andrew Gluesenkamp, I have begun collecting mitochondrial DNA sequence data for inferring phylogeny within varanids. Once such a rooted and resolved phylogeny (with fossil forms included) is in place, we will finally be in a position to exploit directional methods to better understand the actual course of evolution of size in this very interesting group of lizards.

APPENDIX

SUBGENERA OF *VARANUS*, SPECIES TENTATIVELY ASSIGNED TO THEM, AND GEOGRAPHICAL LOCATIONS (FROM MERTENS 1942, 1958, 1963; KING ET AL. 1991; AND SPRACKLAND 1991*a*, 1991*b*)

Dendrovaranus	
rudicollis	Asia
Empagusia	
flavescens	Asia
exanthematicus	Africa
albigularis	Africa
yemenensis	Arabia
Indovaranus	
bengalensis	India
Odatria	
acanthurus	Australia
baritji	Australia

beccari	New Guinea
bogerti	New Guinea
brevicauda	Australia
caudolineatus	Australia
eremius	Australia
gilleni	Australia
glauerti	Australia
glebopalma	Australia
kingorum	Australia
pilbarensis	Australia
prasinus	New Guinea, Australia
primordius	Australia
scalaris	Australia
semiremex	Australia
storri	Australia
teriae	Australia
telenesetes	New Guinea
timorensis	Australia, New Guinea
tristis	Australia
Papuasaurus	
salvadori	Southeast Asia, New Guinea
Philippinosaurus	
olivaceus	Philippines
Polydaedalus	
niloticus	Africa
Psammosaurus	
griseus	Africa, Eurasia
Tectovaranus	
dumerili	Southeast Asia
Varanus	
giganteus	Australia
gouldi	Australia
indicus	Southeast Asia, Australia
jobiensis	Southeast Asia
komodoensis	Lesser Sunda Islands, Indonesia
mertensi	Australia
mitchelli	Australia
panoptes	Australia, New Guinea
rosenbergi	Australia
salvator	Asia, Southeast Asia
spenceri	Australia
varius	Australia

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