

Is *Gopherus agassizii* a Desert-Adapted Tortoise, or an Exaptive Opportunist? Implications for Tortoise Conservation

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ABSTRACT. – The desert tortoise (*Gopherus agassizii*) has traditionally been viewed as an archetypal desert-adapted vertebrate. However, evidence from historical ecology, phylogenetics, anatomy, physiology, and biogeography qualifies this view significantly. Ancestors of *G. agassizii* stabilized as an essentially modern morph some 17–19 million yrs ago, perhaps 12 million yrs before the formation of major regional deserts in North America. Some physiological mechanisms for avoiding or accommodating desert stressors may be symplesiomorphies, primitive character states common to most ectothermic amniotes. Prominent among these are slow metabolic rates and high tolerances for osmotic flux in body fluids. Other functional characteristics for accommodating contemporary aridity are exaptations shared with forest-dwelling batagurid and manourine chelonian antecedents, originally evolved for terrestriality, not aridity. Large brittle-shelled eggs, herbivory, and a generalized and expansive digestive tract may all be among these symplesiomorphies, at least relative to the gopherine clade. Other anatomical and behavioral features are associated with a fossorial life style which may have developed in sandy habitats within grasslands and along forest edges, where microclimates were semi-arid, but at a time North American landforms had not yet experienced desert aridity. Burrow excavation may have evolved in response to the stress of intense insolation in exposed scrub, grasslands, and meadows, only later serving as protection against cold, heat, and predators. Modern climate and vegetation typical for contemporary populations of *G. agassizii* have only developed episodically during perhaps the most recent 1% of its 3–5 million yrs history as a distinct species, and especially during the last 7000 yrs. Biogeographically, neither the testudinids as a group, nor *G. agassizii* as a species, are confined to deserts. Both track more reliably with warm temperate to tropical climates, and appear to be excluded from the extremely arid zones with less than 50–80 mm mean annual precipitation, such as the lowland deserts of the Baja California Peninsula, Sahara, Atacama, the Choco, and most of the Arabian Peninsula. Both extant and fossil *G. agassizii* range well beyond the limits of deserts ecologically into thornscrub, woodland, and grassland habitats. Ecologically, *Gopherus* tortoises generally, and Mojave *G. agassizii* in particular, exploit a wide variety of food resources. Preponderant components of the diet are succulent, herbaceous vegetation ranging from cactus fruit to a variety of grasses and forbs. Even carrion and insects can constitute a small portion of the diet. Sclerophyllous vegetation, so characteristic of extreme desert habitats, is largely absent from the diet. The desert tortoise functions well in some, but not all, undisturbed desert landscapes. Its survival is contingent upon a combination of ancient exaptations and contemporary adaptations which resist drought and locally dry microclimates and soils, but evolved long before their desert habitats themselves. Semi-arid steppe vegetation, such as the mesquite grasslands of the Tamaulipan Plain may combine habitat attributes that are optimal for the *G. agassizii* (“*Xerobates*”) species group, as evidenced by the continuing high densities of group member *G. berlandieri*. Nutritionally, *G. agassizii* is an opportunistic generalist, shuttling through temporally and spatially patchy forage. As a consequence, *G. agassizii* appears to be able to accommodate a wide range of environmental changes. Yet when anthropogenic desertification of a pre-existing desert impoverishes the landscape floristically and depletes forage, the opportunities for continued tortoise survival and recruitment may be significantly compromised.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; exaptation; nutrition; paleoecology; biogeography; evolution; conservation; adaptation; Mojave Desert; USA

The desert tortoise, *Gopherus agassizii*, is a conspicuous and characteristic flagship species of the Mojave and northwestern Sonoran deserts. To the American public this species is a symbol of desert adaptation, much as the greater panda serves as a virtual trademark for endangered species.

It is perceived as a strict herbivore, capable of storing immense water reserves in the face of extremely hot and arid environments (Schmidt-Nielsen and Bentley, 1966; Nagy and Medica, 1986; Peterson, 1996a, 1996b; Henen et al., 1998). In the past several decades, caution has been ex-

pressed about assumptions that functional adaptations evolved directly for their current uses and in their current ecological settings. The critique of the “adaptationist programme” (Gould and Lewontin, 1979) and the concept of exaptation (Gould and Vrba, 1982; Armbruster, 1997) offer alternatives to this perspective. Too often, adaptations attributed to a single species or population and operating in the current geographical setting and epoch actually evolved in an ancestral population living in different ecological and geographical contexts in a prior age. Brooks and McLennan (2002:344) made clear the liability of analyses of function which assume adaptation:

“There is a subtle but crucial difference between ‘the environment changed, so the organism changed’, and ‘the environment changed, and those organisms that *already possessed traits* allowing them to survive in the new environment flourished’.”

Many of these ecologically-interpreted adaptations are better described as exaptations (Gould and Vrba, 1982). They originated either as outcomes of non-Darwinian processes (such as genetic drift) or in response to selective pressures which were different than those to which they now respond. Relative to their current uses, exaptations constitute character states in plesiomorphic forms while taking on derivative functions.

Whether the functional physiology and morphology of desert reptiles constitute adaptations or exaptations (“pre-adaptations”) has been addressed extensively by Bradshaw (1988). His “pre-adaptations” evolved very early in ectothermic amniotes (and even anamniotes), and were both functionally adequate and sufficiently plastic to explain most features by which modern reptiles cope with desert conditions. Relative to their first appearance in ancestral amniotes, these character states could be treated as symplesiomorphies (shared primitive character states) within and among particular lineages of modern reptiles. Therefore the success of desert reptiles was generally attributed to exaptations evolved prior to desert habitation. The Bradshaw arguments were based largely on the comparative physiology of lizards, though he did include tortoises among his examples. Here we focus on the desert tortoise as a test case of the Bradshaw generalizations. This species is particularly well studied, has been assigned its phylogenetic position in gopherine genealogy by means of robust molecular and morphological trees (but see Berry et al., 2002a), and has the best known fossil history of any desert reptile (though admittedly burdened by major gaps, McCord, 2002). The *G. agassizii* lineage lends itself well to morphological and paleontological tests unavailable in Bradshaw’s original examples. Furthermore, this tortoise species includes a threatened population that includes both Mojave and western Sonoran populations (termed “Mojave population”) (U.S. Fish and Wildlife Service, 1994). The resolution of its status as ‘desert tolerant’ versus ‘desert adapted’ has significant implications for its future management.

The hypothetical framework of this paper is evaluated from these alternative perspectives. In this review we ask:

Did *G. agassizii* evolve in direct response to the selective pressures of a desert environment? Or was it a more generalized omnivore in which pre-existing exaptations made survival possible as more arid climates overtook its woodland, savanna, and semi-desert scrub habitats in the Late Tertiary and Quaternary Periods?

The evolutionary and ecogeographical contexts in which the tortoise is placed may profoundly influence how biologists characterize its niche, its functional morphology and its nutritional needs, and how well researchers and resource managers anticipate its adaptive plasticity in response to environmental changes. The desert tortoise has been depicted as a K-strategist, a bet hedger (Germano, 1994; Henen, 1997), a double-bet hedger (Morafka, 1994), a fugitive species (Morafka et al., 1997), a nomadic species (Auffenberg, 1969), and a relict species (Peterson 1996a, 1996b; Van Devender, 2002a; Van Devender et al., 2002). It might also be viewed as a “living fossil” (an example of the “coelacanth” effect), which diverged early from other testudinids and still shares generalized primitive traits with ancestral terrestrial batagurids (Crumly, 1994; Shaffer et al., 1997).

Through the use of phylogenetics, biogeography, evolutionary ecology (in the sense of Brooks, 1985), and contemporary ecology we may establish the original contexts in which functional character states developed for addressing contemporary desert stressors. We will evaluate the two competing alternative propositions, namely (1) that *G. agassizii* exploits resources as a specifically and narrowly adapted desert species, much as heliothermic iguanines (*Dipsosaurus* and *Sauromalus*) and phrynosomatine lizards (*Uma*); or (2) that the desert tortoise is a relict species, much like some desert anurans (*Spea*, *Scaphiopus*), essentially avoiding desert temperature extremes and aridity through a combination of microhabitat modifications (the burrow) and diel and seasonal activity restrictions (Nagy and Medica, 1986; Duda et al., 1999) influenced by temperature (Zimmerman et al., 1994), and coupled with opportunistic, but select feeding and rehydration strategies (Peterson, 1996a, 1996b; Henen et al., 1998; Van Devender, 2002a; Van Devender et al., 2002; Oftedal et al., 2002). In this latter view, *G. agassizii* is considered a relict species, in some cases, restricted to geographically fragmented refugia which recede as inhospitable climatic or crustal changes take place (Peterson, 1996a, 1996b; Van Devender 2002a, Van Devender et al., 2002). In other cases, the tortoise is portrayed as exploiting temporal refugia, dew-laden early mornings, and ephemeral spring forbs and grasses within a more hostile desert landscape (Nagy and Medica, 1986; Henen et al., 1998). We will attempt to establish the proper position of *G. agassizii*, somewhere in the continuum between these two polar extremes.

Here, we propose five tests which will help resolve the status of *G. agassizii* as a desert species:

The Phylogenetic and Evolutionary Ecology (= Paleoecology) Test. — Did the desert tortoise evolve in response to selective pressures unique to deserts? The question requires the examination of concordance between defining

Table 1. Testudinid time scale. The sequence of vicariance events and paleo-climatic shifts through which modern *Gopherus agassizii* became differentiated. mya = million yrs ago.

Faunal Age Geological Time	Taxa	Climate	Ecosystem (Southwest NA)	Vicariance Event	References
Cretaceous 145.6-65 mya	early testudinid (<i>Hesperotestudo</i>) from terr. batagurids	tropical to temperate	forests, Arcto-Tertiary to Neotropical Geoflora	Laurasia separates	1,2,3,4,5,6,7
Eocene 56.5-35.4 mya	<i>Manouria</i> (= <i>Hadrianus</i>)	subtropical	woodland thornscrub	Turgai Sea separates Europe/Asia	2,3,5,8,9,10
Oligocene 35.4-23.5 mya	<i>Stylomys</i> <i>Gopherus</i>	warm temperate 13°C drop at 33 mya; arid pockets expanded and pockets	edaphic sandy grasslands limited sclerophyllous vegetation edaphic/rain shadow scrub, grassland, oak, chaparral; also palms, riparian as above; forest clearings semidesert	Madrean-Tethyan Geoflora	2,8,9,11,12,13,14
Miocene 23.5-5.2 mya	<i>Gopherus</i> genus (<i>sensu lato</i>)	as above	desert scrub develops further	Mid-Continent Orogenies	2,3,8,9,13,15,16
18-17 mya	<i>G. polyphemus</i> - <i>G. agassizii</i> ; groups diverge	first deserts	scrub, steppe from thornscrub	Texas Embayment and its recession ("Cannon Ball Sea") (Oligocene to Miocene) Continental Divide Orogeny; Late Miocene initiates separation of Sonoran-Chihuahuan deserts	5,8,11
6-10 mya	<i>G. agassizii</i> - <i>G. berlandieri</i> diverge	aridity cont.	desert scrub develops further	Bouse Embayment separates Mojave- eastern Sonoran Deserts	3,7,8,9,11,12,16
5.7-5.3 mya	<i>G. agassizii</i> Sonoran-Mojave diverge	increasing aridity Sierra Nevada Rainshadow Glaciopluvial 94% of Epoch	semi-desert patches steppe, arid woodlands	Orogeny/cooling complete Sonoran-Chihuahuan division pluvial lakes	7,9,11
Pliocene 5.3-1.6 mya	<i>G. agassizii</i> - Mojave metapop. Sonoran-Sinaloan divergence (4 mya)	13 cycles interspaced by interglacials	Pinyon-Juniper superimposed on scrub & Great Basin steppe; thornscrub displaced; oak, Joshua tree in Sonoran Desert; equable climate		7,11
Pleistocene 1.64 mya-12,000 y	<i>G. agassizii</i>	interglacial?	First creosote, <i>Larrea tridentata</i> , enters North America Glaciopluvial recession of pinyon- juniper; Joshua trees in central Mojave	lakes	8,13,17,19,21,22, 23,24,25
22,000 + y ?	(oldest N. American fossil)	as above	grassland expansion	-	11,17, 19,20,26
12.5-10,000 y	megafauna extinctions in N. America include <i>Geochelone</i> sp. <i>Terrapene c. putnami</i> <i>Gopherus laticauda</i>	glaciopluvial transition	juniper-oak-grass savannas mixed with Joshua tree woodland blackbush scrub; and saltbush scrub scrub and grasses expand in Sonoran Desert	-	4,11,19,28
10,000 y ?	<i>G. agassizii</i> extirpated from San Joaquin Valley; Orange Co., CA; East to Texas	transitional warming still more mesic	arid scrub; Sonoran Desert: tropical elements grasses riparian expand as above	-	11,19,21,22,23,28
Early Holocene (11,000-8900 y)	<i>G. agassizii</i>	Altithermal temp. peak; loss of monsoon in W. Mojave Desert aridity often higher than present	cooler, more mesic	Central Mojave: River and lakes as above	2,11,17,19,20,24
Middle Holocene (8900-4000 y)	<i>G. agassizii</i>	as above	as above		13,18,20
Late Holocene (4000-present)	<i>G. agassizii</i>	as above	as above		18,20,28
Neoglacial 3620 y	<i>G. agassizii</i> local genotypes	as above	as above		20,29
Little Ice Age 390 y	<i>G. agassizii</i>	as above	as above		20,29

References: 1. Harland et al., 1990; 2. Brattstrom, 1961; 3. Crumly, 1994; 4. Gaffney and Meylan, 1988; 5. Hallam, 1994; 6. Hirayama, 1984; 7. Lamb and Lydeard, 1994; 8. Auffenberg, 1969, 1974, 1976; 9. Axelrod, 1950, 1958, 1975, 1979; 10. Estes and Hutchison, 1980; 11. Morafka, 1977, 1988, Morafka et al., 1992; 12. Van Devender and Burgess, 1985; 13. Van Devender et al., 1987, 1990, see also Holman, 1995; 14. Prothero, 1994; 15. Raven and Axelrod, 1978; 16. Bramble, 1982; 17. Betancourt et al., 1990; 18. Davis, 1984; 19. Van Devender et al., 1976; 20. Spaulding, 1990; Spaulding et al., 1994; see also Holman, 1995; 21. McDonald, 1984; 22. Miller, 1942; 23. Miller, 1970; 24. Jefferson, 1991; 25. Wells, 1979; 26. Garcia et al., 1960; 27. Reynolds et al., 1991a, 1991b; 28. Reynolds and Reynolds, 1994; 29. Enzel et al., 1989, 1992.

character state transformations and the paleo-ecological transformations in the direction of modern desertification. Lack of concordance would favor rejection of this hypothesis, especially so when an alleged adaptation evolved prior to its use in desert habitats (as with exaptations).

The Anatomical and Physiological Test. — Are the morphological and physiological features of *G. agassizii* adapted to uniquely desert conditions? This is a test of function and specificity of adaptive character states. For example, does a particular character state enhance fitness only in desert settings, or would it serve equally well in most terrestrial habitats?

The Climatic Region Association Test. — Do testudinids globally, and *G. agassizii* regionally, occur in eremitic bioclimatic zones (< 50mm annual precipitation) or in hyperarid deserts (50–100 mm annual precipitation) as defined by LeHouérou (1996)? This is a test of how well tortoise distributions correlate with desert geography.

The Ecosystem Association Test. — Is *G. agassizii* associated with unambiguous desert vegetation, in both Pleistocene and Recent (Holocene) epochs? In other words, is the desert tortoise an obligatory desert species or a more generalized organism now largely limited to deserts by historical contingency and/or anthropogenic factors?

The Forage Exploitation Test. — Does *G. agassizii* forage upon sclerophyllous desert vegetation primarily, or does it select more mesic types of vegetation? Is the ingestion of succulent forage (ephemeral forbs, annual and perennial bunch grasses, and cacti) merely a function of opportunity or is it highly selective? Are tortoise occurrence, growth, and recruitment contingent on the seasonal formation of these ephemeral patches of forage within the desert?

TESTING HYPOTHESES

The qualifications of *G. agassizii* as a highly adapted desert species are reviewed here in five tests and tables. The first two tests follow an informally cladistic phylogeny of desert tortoises in an attempt to recover the historical sequence and context in which intrinsic (genetic) character states arose. In most cases characterization is for the species as a whole, or for its antecedent lineage. Where it is so stated, some conditions are specific to a geographical metapopulation that is defined by its morphology, mtDNA haplotypes, and behavior. Some metapopulations, especially Sonoran and Sinaloan, may prove to be sibling species by evolutionary species criteria (Simpson, 1961; U.S. Fish and Wildlife Service, 1994; Lamb and Lydeard, 1994; Lamb and McLuckie, 2002; Van Devender, 2002a, 2002b; Berry et al., 2002a).

The Phylogenetic and Paleoecological Test

The chronology presented in Table 1 has more explanatory value when lineages antecedent to *G. agassizii* are described and their contributions to the modern tortoise and its life history (Table 2) are hypothesized. The hypotheses

are based, at least informally, upon the cladistic ordination of shared primitive character states, or symplesiomorphies through the use of outgroup analyses, and subsequent ordering of the remaining shared derived character states, or synapomorphies, which define the descendant gopherine taxa (Table 2).

Mesozoic Antecedents: The Batagurid Heritage. — Numerous lines of evidence affirm the probable derivation of testudinids either directly from one group of Old World batagurid turtles or from a sister group sharing a common ancestor with batagurids (McDowell, 1964; Hirayama, 1984; Sites et al., 1984; Carr and Bickham, 1986; Gaffney and Meylan, 1988; Lamb and Lydeard, 1994; Shaffer et al., 1997; but see McCord, 2002, and Van Devender, 2002b). The batagurid family, recently elevated from subfamilial rank within the emydids (Ernst and Barbour, 1989), may itself be polyphyletic. Among these batagurids are several distinct river and mesic terrestrial groups of genera, and one largely terrestrial group, the *Heosemys* clade, including *Heosemys*, *Cuora*, *Cyclemys*, and *Pyxidea* which may have shared ancestry with the testudinids (Bramble, 1974). Assigning familial rank to testudinids renders their ancestral batagurid clade paraphyletic and thus cannot be defended as cladistically accurate taxonomy. Tortoises are simply a speciose batagurid lineage that has developed a nearly obligatory terrestrialism manifest in both morphology and behavior. Use of related batagurids (the *Heosemys* clade) as an outgroup may serve to root primitive, plesiomorphic states in relation to the testudinid clade.

Manourines: Ubiquitous Tortoises. — Manourines were the ubiquitous Northern Hemisphere tortoises of Arcto-Tertiary forests, riparian woods, and grasslands in the Paleogene Period of the Tertiary (Estes and Hutchinson, 1980; Obst, 1988; Ernst and Barbour, 1989). They either gave rise to gopherine tortoises directly or comprise their sister clade. The two extant manourines (*Manouria emys* and *M. impressa*) share a set of primitive character states with gopherines (Crumly, 1994). Given the presence of the Turgai Sea separating Euramerica from Asiamerica along the modern latitudinal axis of the Ural Mountains (Cox, 1974; Hallam, 1994), manourine distribution leading to modern North American tortoises could have involved tracks from either or both Cretaceous-Paleogene continents. The continuity of terrestrial land masses in Asiamerica has been more robust for a longer period. Continuation of this track in the early Tertiary Period appears to explain the modern distribution of the pit vipers (Crotalinae) (Cullings et al. 1999). However, the presence of an ancient fossil tortoise (originally reported as *Hesperotestudo*, now referred to *Hadrianus* [McCord, 2002]) in Eocene deposits of what is now Arctic Ellesmere Island certainly provokes interest in this first track which established tortoises in the emerging New World (Estes and Hutchinson, 1980). The suggestion that *Hadrianus* is congeneric with extant southeast Asian upland forest tortoises of the genus *Manouria* establishes some basis for an Asiamerica track (McCord, 2002), though it does not *a priori* establish a 'center of origin' or a polarization of

Table 2. Chronological and environmental assignment of anatomical and physiological character states of the *Gopherus agassizii* lineage. Estimating the first appearance of specific character states in relation to geological time and the demands of specific environments. * = symplesiomorphic characters with respect to the testudinds and their outgroup lineages. Data from Bramble, 1982; Crumly, 1994; Auffenberg, 1969; Spotila et al., 1994; Morafka, 1994; Schmidt-Nielsen and Bentley, 1966.

Character state	First Taxon	First Appearance	Habitat	Function
Brittle egg shell*	batagurid	Mesozoic	Asian-warm Arcto-Tertiary temperate forest	reduce dehydration
Large eggs*	batagurid	Mesozoic	terrestrial, as above	yolk reserve nutrition
Mental glands*	batagurid	Cretaceous	as above	sex pheromones?
Class I	(and manourines)			
Omnivory* (herbivorous bias)	batagurids	Mesozoic	as above	terrestrial diet
Fused centrale	<i>Stylemys</i>	Oligocene	sandy grassland	fossorial
Large cavum	<i>Gopherus</i>	Oligocene	sandy grass/scrub	fossorial
labyrinthine and contains saccular otolith				
Small eyes	<i>Gopherus</i>	mid-Miocene	woodland; scrub/steppe	reduce dehydration
Large re-absorptive bladder	<i>Gopherus</i>	as above	as above	as above
Facultative uricotelic	<i>Gopherus</i>	as above	as above	as above;
Hind-gut* fermentation and generalized digestive tract	manourines or gopherines?	unknown	as above	variable fiber digestion (Barboza, 1995)
Thermoregulation*? and high critical thermal maximum (CTM)	gopherines or manourines?	unknown	warm terrestrial	shuttling within thermal mosaic; high CTM: 39-44°C (McGinnis and Voight, 1971)
Thickened epidermis	manourines?	unknown	terrestrial	fossorial (Spearman, 1969)

potential dispersal routes. As an alternative, a Euramerican track binding together early Paleogene gopherine antecedents may not be entirely eliminated from consideration. The occurrence of *Manouria* in early Tertiary beds of central Europe (Obst, 1988), the early distribution of the Oligocene *Euroderma gallicum* in France, possibly as a contemporary with another large venomous helodermatid lizard in Colorado, all provide circumstantial evidence which could be interpreted as supporting a trans-Atlantic corridor or vicariance track. Ambiguous evidence, supporting trans-Pacific, Atlantic, or both connections between mammalian faunas in western Europe, Asia, and North America continued into the earliest Oligocene Period (McKenna, 1983).

In either case, these large ancient tortoises were generalized morphologically and could have existed over a wide range of climates and habitats, and exploited a wide variety of resources. Fossorial proclivities were not evident in the known morphology of these early forms.

Oligocene Gopherine Tortoises. — By the Oligocene Epoch, early gopherine tortoises (*Hesperotestudo*, *Stylemys*, and later *Gopherus*) reveal a progressive localization in warm temperate and subtropical North America. This regional confinement may have been a response, at least in part, to the "Grande Coupure," a global drop in temperature averaging 13°C that occurred 33 million yrs ago (Prothero, 1994). As a result of progressive cooling and polarization of climates, concomitant aridity led to the localized, early development of grasslands, chaparral, and semi-desert scrub. Some of these plant associations may have been edaphic pockets, or were induced by rain shadows, which developed

in response to Oligocene orogenies (Axelrod, 1950, 1958, 1975; Raven and Axelrod, 1995). This scenario has been developed to explain the appearance of Oligocene grazing mammals before grasslands were extensive in North America (Retallack, 1983). Even if Paleogene grasses were archaic in morph (McClaran and Van Devender, 1995), they could have supported localized meadow-based niches long before the expansion of geographical prairies, steppes, and savannas in the drier and more temperate Neogene Period.

Fossil record evidence regarding this hypothesized dramatic climatic deterioration is not unambiguous, however. The Florissant Flora and associated ichthyofauna provide contradictory data. In the Eocene–Oligocene of northeast Utah and southwest Wyoming, floral and faunal changes do not correspond with the elevation and climatic estimations (Wolfe, 1992, 1993) utilized by advocates of the "Grande Coupure." Climatic changes were sometimes inferred from shifts in predominant leaf morphology without regard to the contemporary biophysical associations of the identified plant taxa (Van Devender, 2002b). Nonetheless, less dramatic shifts toward cool and dry and more temperate climates in response to volcanism and other orogenic processes would have favored the development of mid-Tertiary grasslands and grassland diets among North American gopherine tortoises.

The most abundant gopherine genus of this period, *Stylemys*, has generally been depicted as fossorial, as evidenced by fossils preserved within self-excavated burrows (Auffenberg, 1969, 1974, 1976) and was confined to North America. However, one recent account (McCord, 2002)

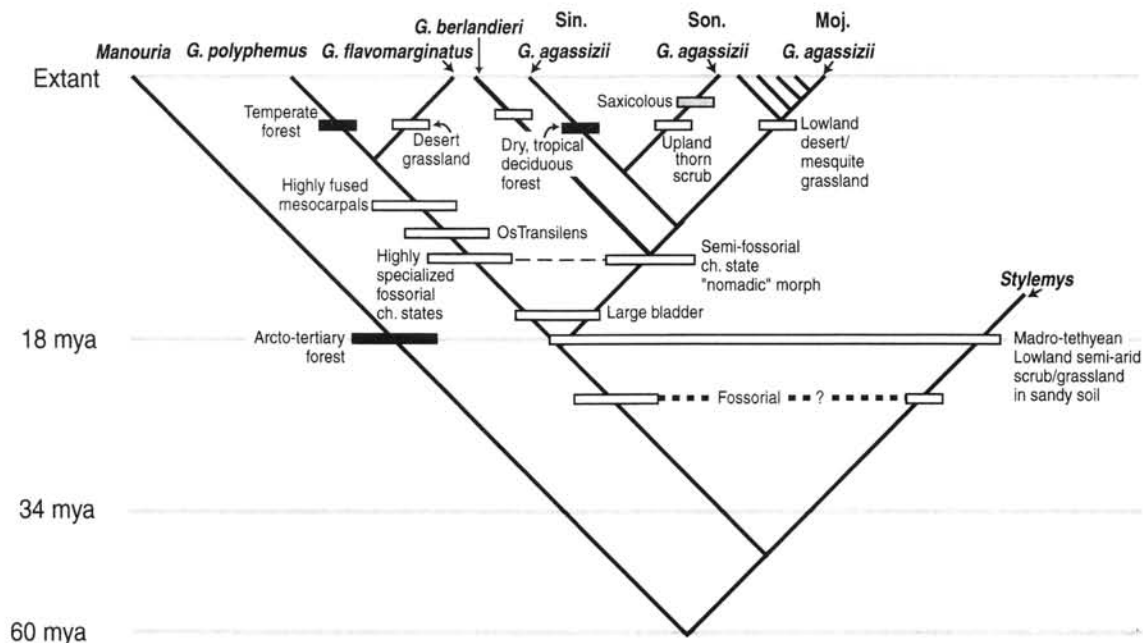


Figure 1. Cladistic ordering of gopherine adaptations and ecological affinities is depicted here. Black bars indicate the independent evolution of forest dwelling association in both manourines and gopherines. It evolved two separate times in the history of living gopherines (as homoplasies). The one shaded bar assigns the saxicolous association as a presumed autoapomorphy to Sonoran *G. agassizii* (though it may be shared with the Sinaloan haplotype as well). Open bars indicate that xeric and fossorial character states and ecological association developed as basal synapomorphies of the entire group. Cladogram modified from osteological and genetic data (Crumly, 1994; Lamb and Lydeard, 1994; Britten et al., 1997; McCord, 2002).

contradicts this view, treating *Stylemys* as non-fossorial generalist. Even if this revised interpretation proves correct, at least one Eocene–Oligocene gopherine, *G. laticuneus* had already manifest considerable morphological features placing it not only in the *Gopherus*, but also interpreted by some to be related to the most fossorial clade within that genus, the *G. polyphemus*–*G. flavomarginatus* species group (Crumly, 1994; Hutchinson, 1996; McCord, 2002). This hypothesis is inconsistent with the molecular clock dates of Lamb and Lydeard (1994) which estimated the divergence of this specialized clade much later, about 18 million yrs ago. Yet the ambiguous suite of characters states are still sufficient to support the evolution of basal *Gopherus* with fossorial proclivities in the early Tertiary Period. Figure 1 illustrates that some fossorial morphology and behavior are synapomorphies shared by virtually all *Gopherus* (*sensu lato*). Therefore, such character states were present in the common ancestor of this clearly monophyletic group. To suggest otherwise would be to invite non-parsimonious explanations invoking two or more homoplastic (independent, convergent) events in which fossorial attributes were evolved independently among most of the lineages within *Gopherus*.

This first major divergence of the *polyphemus* group from an array of other *Gopherus* has been attributed to the isolating effects of the early Tertiary extensions of “Cannonball Sea” across most of the modern North American Great Plains. This landform could have acted as a vicariance event dividing mid-latitudes of the continent into east and west before the orogenic events that built the Rocky Mountains (Auffenberg, 1969). However, widespread occurrence of

the *polyphemus* group across middle latitudes of Miocene North America, and asynchrony with molecular clocks render the hypothesis problematic (Bramble, 1982).

Perhaps burrow excavation was, in part, a response to the climatic extremes produced by greater aridity and loss of sheltering forest canopy. Certainly fossorial morphology seems better correlated with climatic and habitat shifts than with any hypothetical change in predation pressure, the only probable alternative source of selective pressure favoring this behavior. Tortoises exposed in open grassland and meadow may have excavated burrows to avoid maximal soil surface temperatures (and to insulate against potential dehydration), and perhaps the effects of flood and fire in open range. In Oligocene times, tortoises at South Dakota latitudes (Retallack, 1983) may not have been exposed to stressful minima. Shelter from thermal minima might be an exaptive function in later epochs. Predation has always been a background threat, therefore we question that this stressor alone stimulated a particular fossorial response in Oligocene gopherines. Certainly in tropical habitats like the deciduous dry tropical forest at Alamos, Sonora, predation pressure would be expected to be high given the increased diversity of potential predators. However, tortoises typically use superficial shelter, enhanced little or not at all by burrow excavation. Even now, adult *G. agassizii* from southern Nevada may limit their above-ground activities to approximately five percent of a given year (Nagy and Medica, 1986; Duda et al., 1999), probably to mitigate against biophysical stressors. Extant tortoises typically become subterranean during drought and in response to high ambient temperatures approaching their critical thermal maxima (CTMax > 38°C;

McGinnies and Voigt, 1971) and their lower thresholds for voluntary surface activity ($< 15\text{--}17^{\circ}\text{C}$, Hillard, 1995). That tortoise distributions correlate with tropical to subtropical temperatures better than with aridity has been well documented for several decades (Brattstrom, 1961:552):

“Many workers...have generally assumed that the presence of tortoises is indicative of arid environments (cf. “the desert tortoise”, *Gopherus agassizii*...). It will be shown below that most fossil tortoises are, in fact, probably indicators of tropical and subtropical climates.”

Mio-Pliocene Differentiation. — This critical chapter in North American desert development and differentiation, extending over a 15 million-yr time span, is largely without a tortoise fossil record (McCord, 2002). These periods were critical to both the modernization of gopherines and to the habitats that they now occupy in the semi-arid to arid Southwest. Virtually all of the vicariance (fragmenting) events responsible for speciation and the development of the most strongly differentiated Evolutionarily Significant Units, or ESUs, probably occurred during these periods, according to molecular clock evidence (Lamb and Lydeard, 1994; Lamb and McLuckie, 2002). Southwestern North America has been radically transformed topographically, climatically, and botanically since the mid to late Tertiary Period.

Three major processes acted upon the geomorphology of the desert Southwest to modernize landscapes, both generating vicariance events that stimulated speciation, and redirecting fundamental patterns in hydrology, which guided subsequent patterns of dispersal. These three, sometimes overlapping processes likely included the following geological episodes: (1) early (12–17 million yrs ago) extension and fault block formation of Basin and Range topography, including the establishment of the Continental Divide separating a proto-Sonoran Desert from a proto-Chihuahuan Desert; (2) redirection of Basin and Range extension from west to north 8 million yrs ago, and (3) progressive reversal of internal drainage patterns from the Oligocene Colorado Plateau to external drainages 6–10.5 million yrs ago, culminating in the completion of the Colorado River and its discharge into the Gulf of California.

Extension (largely to the north) preceded fault block structures by 20–25 million yrs, starting as long as 40 million yrs ago, and enlarging the region by perhaps 100% (Wernicke, 1992). Furthermore, the development of the Colorado Plateau, another delimiter of future warm deserts, had already taken place by the Oligocene Period (Pierce et al., 1976). This process was augmented by the subduction of the Farallon Plate traveling east under the Pacific and North American plates, about 17 million yrs ago. Volcanism contributed flows to this region for the past 40 million yrs, with the most recent dating less than 40,000 yrs ago (Wernicke 1992).

Development and orientation of Basin and Range topography within the proto-Sonoran Desert landscape, and its derivative the Mojave Desert, was produced by horst-graben faulting (Stewart, 1980). An initially western extension of crustal plates underlaid the faulting process (Wernicke and Snow, 1998). North of the Garlock Fault (just south of

the Inyo-San Bernardino County line in eastern California), the physiographic (but not always biological) Great Basin Ranges reflect a modern shift in the direction of extension about 8 million yrs ago, turning the process to the north (Atwater and Stock, 1998).

The *G. polyphemus* group had already diverged from one of the lineages of the pre-existing *Gopherus* in the Oligocene, presumably from the more generalized grade (Crumly, 1994) or clade Bramble (1982) formerly recognized as “*Xerobates*” by the early Middle Miocene, when the oldest member of the former group, *G. brevisterna*, first appeared (Bramble, 1982). A tortoise with an essentially modern skeleton of the *G. agassizii* complex (= the species group assigned to *Xerobates*) was present by middle Miocene (14–18 million yrs ago) based upon both fossil (Bramble, 1982; *G. mohavetus*, McCord, 2002) and molecular evidence (Lamb and Lydeard, 1994).

Miocene orogeny along the Continental Divide continued from Late Oligocene to middle Miocene Epochs, and involved Rocky Mountain uplifts from 1500 to 2200 m in elevation (Van Devender, 2002b). By 12 million yrs ago, extensive volcanic extrusives coupled with fault block uplifts to establish a modern Continental Divide along the north-south axis of the Sierra Madre Occidental (McDowell and Keizer, 1977). These uplifts and flows may have been the vicariance events responsible for the speciation of *G. berlandieri* from its western sister taxon, *G. agassizii*. Molecular clock estimations place the divergence at about 10.5 million yrs ago, as calculated by McCord (2002) from Lamb et al. (1989) data and rates. Fossil evidence however, does indicate the subsequent distribution of tortoises resembling or conspecific with *G. berlandieri* as far west as Sonora (Lamb et al., 1989), based on an undated fossil, and as far south as the great Altiplano of Mexico in Aguascalientes in Pleistocene times (Mooser, 1972). Likewise, *G. agassizii* extended (secondarily?) east into New Mexico and Texas during Late Pleistocene to Late Holocene episodes (Van Devender et al., 1976).

Recognition of the earliest divergence of *G. berlandieri* is important to our subsequent analyses of the evolution of defining character states within this *G. agassizii*–*berlandieri* species group. Establishing *G. berlandieri* as an outgroup to other members of the *G. agassizii* clade roots (or establishes the priority of) symplesiomorphic character states in phylogenetic analysis. Rooting may be further re-enforced by use of a member of the *G. polyphemus*–*flavomarginatus* clade as a second outgroup. Figure 1 utilizes the stable elements of several robust cladograms for living *Gopherus* species and ESUs to ordinate the first occurrence of key ecological features in tortoise morphology as those of a generalized tortoise with a high-domed carapace, engaging in fossorial shelter excavation in typically sandy lowlands. Indeed, if we were to combine all known localities for living *Gopherus agassizii* complex populations, more than 90% would still occur in open to semi-arid microhabitats on friable soils in lowland localities. A similar correlation could be demonstrated for fossil forms, but here the fossil record itself has a

pre-disposing bias toward the preservation of organisms living in sites of lowland sedimentation (with the exception of wood rat middens, a special circumstance we shall revisit later). Figure 1 establishes the secondary nature of *Gopherus* associations with mesic and upland habitats. Forest dwelling traits, if genetically based, evolved as homoplasies (= independently derived but superficially similar features) in both Sinaloan *G. agassizii* and in *G. polyphemus* of the U.S. Southeast. They are not associated with the basal ancestry of the genus or its species groups. The upland, rock-dwelling proclivity of Sonoran *G. agassizii* (and its more vertically compressed carapace) appear to be an autapomorphy, a unique evolutionary novelty, which is phylogenetically uninformative.

By the end of the Miocene Epoch, another vicariance event was occurring along the current Colorado River bed, either with formation of the Bouse marine embayment (Metzger, 1968) about 5.5 million yrs ago (Shafiqullah et al., 1980), or by formation of a lacustrine spillover from the Colorado Plateau which, in turn, caused deposition of a chain of lakes fed by the Colorado River spillover across the Mogollon Rim (Spencer and Patchett, 1997). As a result and now somewhere east of the current Colorado River bed, the western and northern Mojave *G. agassizii* haplotype (mtDNA) populations give way to Sonoran haplotype populations (McLuckie et al., 1999). The divergence of Sinaloan from Sonoran lineages occurred approximately 4 million yrs ago, and was followed by the separation of haplotypes within the Mojave *G. agassizii* clade (Lamb and McLuckie, 2002).

By the Pliocene Epoch, Sonoran and possibly some lower elevation Chihuahuan (Mapimian Subprovince; Morafka, 1977) desert geomorphology was essentially modern, though most ranges continued to gain elevation throughout the Quaternary Period. The ecological status of the more northern upland Mojave Desert region remains much more problematic. A well-defined modern Mojave Desert biota may have developed much later in the Pleistocene and through a process interrupted repeatedly by glaciopluvial episodes (Enzel et al., 1989, 1992; Reynolds et al., 1991a, 1991b, 1991c; Reynolds and Reynolds, 1994; Van Devender, 2002a, 2002b). Mio-Pliocene tortoises evolved in increasingly temperate and arid paleoclimates, in which modern plant genera, even species, were progressively sorted into edaphic mosaics of semiarid grasslands, chaparral, and semi-desert associations (cited in Table 1, Axelrod, 1950, 1958, 1975, 1979; Raven and Axelrod, 1978; Betancourt et al., 1990). The extreme aridity induced by vigorous Pleistocene mountain building and consequent rain shadows (Spaulding, 1999; Van Devender, 2002b) may not yet have been manifest.

Presumably many of the morphological features associated with each of the subordinate gopherine groups became fixed at the time of divergence, or early thereafter, before phenotypes became narrowly canalized. Morphological variation between both fossil and living gopherine species and their subordinate ESUs is modest, best expressed in absolute size differences, modest chromatic differences, sexual dimorphisms, appendicular skeleton, and jaw kinet-

ics (Bramble, 1982; Germano, 1993). Such conservatism within a single vertebrate tribe parallels that reported for plethodontine salamanders (Wake et al., 1983). These amphibians constitute another group in which most species are bound to a single type of subterranean, or at least subsurface, microhabitat, despite their occurrence in geographically diverse macrohabitats.

The aforementioned plethodontine salamanders are not the only anamniotes that provide model analogues by which to interpret desert tortoise evolution. Simpson (1953), using the lungfish (Order Dipnoi) as a model, illustrated the quantum evolution model of macroevolution. It appears to be a common trend of early modernization and diversification within a clade (later popularized by Eldredge and Gould, 1972, as the "punctational equilibrium" model of macro-evolution). Fossil evidence indicates the same trend in gopherine tortoises with both major anatomical morphs becoming well established in the Miocene, and both lineages manifesting considerable phenotypic stasis over the subsequent 15–17 million yrs. In fact, the origin of the desert tortoise morph preceded the differentiation of North American deserts, a process originating not earlier than middle Miocene and possibly much more recently (Morafka, 1977; Axelrod, 1979; Bramble, 1982; Morafka et al., 1992; McCord, 2002; Van Devender, 2002b). The evolution of a suite of fossorial character states in ancestral *Gopherus* prior to Mio-Pliocene radiations is consistent with the fossil record, cladistic phylogenetics of this group, and the predictions of the punctational equilibrium model.

Glaciopluvial Times (Pleistocene and Holocene). — For as much as 94% of the past 1.6 million yrs, North American deserts and their tortoises may have existed in more equable climates in which pine and pinyon-juniper parklands, grasslands, cold Great Basin (*Artemisia*) desert and chaparral scrub, commingled or interdigitated with Joshua tree (*Yucca brevifolia*) to form localized parklands (Van Devender and Mead, 1978; Wells, 1979; Van Devender and Burgess, 1985; Betancourt et al., 1990). The single most prominent shrub of the warm desert, creosote bush (*Larrea tridentata*), was not a significant participant in these ecosystems, except at the very lowest and most southern locations along the USA–Mexico border (Van Devender, 2002a, 2002b; see also Morafka, 1977, 1988; Morafka et al., 1992). *Larrea* was not documented from the paleobotanical record of North America until 23,000 yrs ago and its history on this continent is unlikely to have predated the Pleistocene Epoch (Van Devender et al., 1987; Betancourt et al., 1990). It is apparently an Argentinean (Chocoan) species, the seeds of which might have been introduced into this continent by plovers or other migratory birds with antitropical migration patterns (Garcia et al., 1960).

As noted in Table 1, even during the most warm and arid last 8900 yrs, significant fluctuations affected the continuity of Mojave Desert climates (La Marche, 1974; Davis, 1984; Douglas et al., 1988). Summer monsoons only ceased to characterize the western Mojave Desert in the middle Holocene Epoch, some 8900 to 4000 yrs ago (Van Devender et

al., 1987, Betancourt et al., 1990). Pliocene desert tortoises might have simply survived *in situ* into the Quaternary Period as the modern Mojave uplands underwent conversion to pinyon juniper woodlands. Glaciopluvial reconstructions of juniper woodland habitats may be somewhat subject to bias, however. Drawn largely from fossil wood rat middens sheltered in upland caves or at localities that were prehistorically more mesic than surrounding lowlands, Midden samples may reverse the general fossil record bias against upland habitats that characterize a fossil record drawn from lowland sediments in general. Midden data thereby serve to oversimplify between-site comparisons since spatial variation in edaphic conditions are held to a minimum in these samples. "In general middens probably underestimate the extent of shrublands and grasslands and overlook the mosaic aspects of vegetation distribution induced land forms" (Webb and Betancourt, 1990). Pleistocene "woodlands" might be better characterized as open coniferous parklands, which much like modern Joshua tree parklands support a varied patchwork of annual and perennial undergrowth. In such settings, shifting in forage items might have been more the manifestation of flexible foraging behavior and a tolerance of diverse diets rather than genetic adaptations by local desert tortoise populations. *Gopherus agassizii* populations now occurring west of the present Colorado River valley were separated perhaps 5.5–7 million yrs ago from those to the east with the Sonoran haplotype. The divergence of Sinaloan from Sonoran lineages occurred approximately 4 million yrs ago, and most recently the separation of haplotypes within the Mojave *G. agassizii* clade (Lamb and McLuckie, 2002).

As an alternative hypothesis, it has been proposed that *G. agassizii* established its modern populations in the upland Mojave Desert later, perhaps within the last 2.4 million yrs, evolving as a behaviorally adapted specialist in response to newly differentiated environments, including climates, substrates, and diets, especially targeting C_3 grasses as forage (Van Devender, 2002b). We will critically evaluate Van Devender's hypotheses about the evolution of a "Mohave" desert tortoise in Pliocene to Holocene times in our closing discussion of this phylogenetic test.

Recent molecular assessments of the differentiation of Mojave desert tortoise populations provide independent tests of some implicit predictions of both models. The genetic homogeneity (allozymes, Rainboth et al., 1989; mtDNA haplotypes, Lamb and Lydeard, 1994) both within and between central and western Mojave Desert tortoise populations, lends itself to ambiguous interpretation. Low levels of local differentiation and low polymorphism may also be viewed as evidence of recent dispersal into the western part of the Mojave Desert, especially when they are contrasted with the several well differentiated local haplotypes and five proposed Management Units (MU) among the northeastern Mojave Desert tortoises (Britten et al., 1997; Lamb, 2002). Recent summaries of paleo-botanical evidence indicate that the Lucerne Valley of the western Mojave Desert may have sustained a cold desert/Great Basin vegetation until about 5500–6000 yrs ago when modern

warm desert creosote-burro bush dominated flora replaced it (Spaulding et al., 1994; Spaulding, 1999).

Molecular evidence, especially the blood allozyme data (Rainboth et al., 1989), may also be interpreted to support a history of continuous gene flow west across much the region throughout the Quaternary Period, glaciopluvial times as well as inter- and post-glacial. Direct fossil evidence from Mojave Desert/southern Great Basin/Grand Canyon caves and wood rat middens (Brattstrom, 1954; Van Devender et al., 1976; Van Devender and Mead, 1978; Jefferson, 1991; Reynolds et al. 1991a, 1991b, 1991c; Reynolds and Reynolds, 1994; McCord, 2002) document the occurrence of the desert tortoise in late Wisconsin glacial times in the Mojave Desert. Its occurrence further west in this desert region during glacial maxima is more problematic, but late Pleistocene fossils of *G. agassizii* from coastal southern California and San Joaquin Valley (in Rancho La Brea times) make such a continuous distribution a credible hypothesis (Miller, 1942, 1970). Recently, new protocols for separating population structure from population history have been developed for another highly philopatric poikilotherm, the tiger salamander, *Ambystoma tigrinum* (Templeton et al., 1995).

In the Late Holocene as recently as 390 yrs ago, in the "little ice age," perennial lakes (filled for 40 continuous years) occurred along the entire length of the Mojave River drainage (Enzel et al., 1989; Enzel et al., 1992). These lakes drew their waters largely from the north faces of the San Bernardino Mountains. Relict populations of the western pond turtle, *Clemmys marmorata*, survive in the Mojave River in association with permanent surface water, apparently with little or no modification of their typical coastal life history and behavioral characteristics (Lovich and Meyer, 2002). If desert tortoises occurred in the western Mojave region at this time, they occupied grasslands, parklands (savannas), and even non-desert scrub to the west in the San Joaquin Valley and south in the Los Angeles Basin of California (Miller, 1942, 1970). Pleistocene *G. agassizii* extended eastward to New Mexico and western Texas, and northward into the Great Basin (Brattstrom, 1961; Van Devender et al., 1976; Holman, 1995; McCord, 2002). A contemporary desert tortoise population still lives in semi-desert grasslands of southern Arizona, foraging on grasses of the genera *Aristida*, *Bouteloua*, and *Erioneuron* during the summer-fall monsoon (Martin, 1995). While "blue Northerners" (southward processions of cold, low pressure fronts moving across the mid-continent from Arctic sources) may have contributed to some interior continental extirpations (Van Devender et al., 1976; Morafka, 1988), Pleistocene desert tortoises have also been extirpated from regions where glaciopluvial and Holocene changes may have actually propagated mild climates and better grassland forage (McDonald, 1984).

Reconstruction of the San Joaquin Valley site indicates that Pleistocene tortoise habitat and vegetation was not dramatically different from current conditions (Miller, 1942). This reconstruction has provoked interest in human predation as a cause of extirpation of San Joaquin Valley tortoises.

Human exploitation of *G. agassizii* for food appears to be tribe-specific among native Americans (Schnieder and Everson, 1989). Coastal southern California and San Joaquin valleys might be examples of an 11,000-yr old anthropogenic extirpation of much of temperate North America's macrofauna, a manifestation of Martin's (1958, 1984) "overkill" or later, "blitzkrieg" hypotheses. Pre-Columbian extirpation of tortoises by human predation may account for their absence from the first two areas while the shorter growing season and/or more severe winters may account for its absence from the modern Great Basin (Schneider and Everson, 1989) and New Mexico (Van Devender et al., 1976). Human-induced extirpation, both pre- and post-Columbian, has been well documented for the Bolson tortoise, *G. flavomarginatus* (Bury and Morafka, 1988; Morafka, 1988).

In conclusion, ancestors of the *G. agassizii*–*berlandieri* group evolved some 15–17 million yrs ago, probably in semi-arid warm temperate steppe grasslands and sclerophyllous (including, but not confined to, thornscrub) plant associations growing on well-drained, sandy soils. Desert tortoises may have lived continuously in a *Larrea*-dominated Mojave Desert scrub for less than 1% of its own 2–5 million-yr history as a distinct species.

As noted previously, an alternative hypothesis has been developed which arrives at a similar conclusion to the one presented here, namely that the *G. agassizii* lineage has not had a long continuous evolution in lowland desert landscapes (Van Devender, 2002b). This alternative scenario implies that *G. agassizii* differentiated by the Late Miocene Epoch, possibly in tandem with an upland Sonoran desert biota which was derived from species which had previously arisen in the thornscrub and tropical deciduous forests of western Mexico. As climates changed these populations became progressively upland forms, often living in rocky substrates. The "Mohave" *G. agassizii* continued to differentiate from this ancestral Sonoran form, gradually (?) establishing many of its specialized attributes only during the last 2.4 million yrs as Mojave Desert communities resolved into modern biotic assemblages. Both models depict *G. agassizii* as a recent component in the typical desert biota of southwestern North America, a peripheral and relictual upland saxicolous organism in the Sonoran Desert, and as an inhabitant of a recently differentiated Mojave Desert community (according to Van Devender, 2002b, the Mojave Desert is North America's most recently differentiated "biotic province").

However, the two models invoke very different paleoecological scenarios by which to derive current conditions. While our model portrays members of the *G. agassizii*–*berlandieri* complex as opportunist generalists, variably fossorial, and typically lowland semiarid forms, the Van Devender model focuses only on a pairwise comparison of two highly specialized and divergent morphs, an older Sonoran–Sinaloan form and a recently evolved "Mohave" counterpart. Several different lines of evidence tend to undermine the hypothesis that the Mojave *G. agassizii* has recently evolved as a single distinct form with a genetically

encoded natural history distinguishing it from the Sonoran *G. agassizii* (Van Devender, 2002a, 2002b). While the two forms include populations with very different natural histories, it is clear that the Mojave populations are composed of three regionally distinct haplotypes indicating sustained survival in several different ecological, climatic, and physiographic settings across California, Nevada, and Utah (Lamb and McLuckie, 2002). Using these criteria rather than the narrowly defined and mtDNA-dependent ESUs, the Mojave Population Desert Tortoise Recovery Plan (U.S. Fish and Wildlife Service, 1994) recognized at least half a dozen regional units, in effect, as distinct populations segments (Berry et al., 2002a). The aforementioned array of locally endemic mtDNA haplotypes, distinctive allozyme frequencies, and morphological distinctions among northeastern Mojave *G. agassizii* populations have been employed to define five separate Management Units in the northeastern Mojave Desert only (Britten et al., 1997; Lamb and McLuckie, 2002). These ESU and MU subdivisions collectively span more than 600 km of diverse habitats from east to west and varying by more than 1000 m in elevation. In the absence of a single stable paleo-ecological environment during the Quaternary Period, it is hard to conceive of a homogeneous unitary "Mohave" tortoise ranging across these various landscapes, ranging from the grasslands of the San Joaquin Valley to the mountains of southwest Utah.

Furthermore, the two models differ conceptually in their evolutionary scenarios as to how these conditions and ecological relationships developed. Our model draws upon molecular and morphological phylogenetics and vicariance biogeography to reconstruct the *in situ* differentiation of an already semi-arid steppe and sclerophyllous *G. agassizii*–*berlandieri* complex. The Van Devender (2002b) model utilizes phenetic pairwise comparisons of Sonoran vs. "Mohave" *G. agassizii* primarily, without the benefit of the ordering of cladistic analyses including the use of outgroup rooting of primitive states. It compares only two forms (three when the peripheral Sinaloan haplotype is distinguished) in this paraphyletic clade which excludes both the sister species *G. berlandieri*, and the subordinate ESU and MU subdivisions among the Mojave *G. agassizii* complex proper. It invokes comparisons of behavioral and reproductive traits that have not been demonstrated empirically as stable attributes of one group of tortoises or another, and fails to establish that these putative states are, in fact, heritable. This alternative model assumes adaptation, instead of demonstrating it. The new Mojave Desert habitat that was to have induced this newly selected form of *G. agassizii* has not been stable in either time or space. As documented in our preceding review of Quaternary paleoecology, most of the Mojave Desert has had its modern climate and vegetation for less than 7000 yrs, only 350 tortoise generations—not the 2.4 million yrs proposed by Van Devender (2002b). Similarly, it presupposes both dispersal from a geographical origin and a gradual orthogenesis as the most likely mode of evolution, concepts difficult to accept as assumptions for this revised shorter time frame.

Both models challenge our traditional views about the evolution of “desert” tortoises. Both are subject to refinement, revision, and empirical testing. As an example of the latter, it would be profitable to test the existence of distinct and heritable dietary preferences of “Mohave” desert tortoises by experimentally testing for the selection in choice trials presenting C_3 and C_4 plants to both experienced adult and naive neonate *G. agassizii* drawn from the one Sonoran and the several “Mohave” haplotypes. In such trials, bite counts targeted toward specialized food items (C_3 for Sonoran tortoises) could be statistically evaluated against the frequency with which those items were encountered. Refutation of the null hypothesis (especially, a demonstrated bias toward a predicted forage item) in adults would affirm that these diet selections are predictable for geographically distinct populations. In experiments using naive neonates, refutation of the null hypothesis would favor recognition of the heritability of such diet preferences. Likewise, results consistent with the null hypothesis in either test would favor our interpretation of Mojave *G. agassizii* as a very flexible generalist and opportunist with respect to diet.

The Anatomical and Physiological Test

Table 2 documents the long history of character states that appear to be desert-adapted. Bradshaw (1988) suggested that desert reptile survival depended on the plasticity of fundamental symplesiomorphies shared with other early amniotes: dry skins with epidermal scales, large eggs, direct development, low metabolic demand (10% of mammals) and high digestive efficiency (10x that of mammals), behavioral thermoregulation, excretion of nitrogenous wastes as relatively insoluble uric acid without utilizing high volumes of water as a solvent, tolerance of perturbations in their internal osmotic and electrolytic environments which prove fatal to mammals, and behavioral avoidance of stressful surface environments through extended subsurface retreat, aestivation/hibernation. All of these attributes were incorporated into the phenotypes of the first Paleozoic amniote, and retained by most vertebrate ectotherms. From cladistic analysis of character state distributions, it may be inferred that the batagurid ancestors of tortoises had produced large, brittle-shelled eggs before the end of the Mesozoic Era. In one extant batagurid, *Rhinoclemmys funerea*, a female with a plastron length of 200 mm deposits one of the largest eggs of any chelonian, 76 x 39 mm (Ernst and Barbour, 1989). Both large and brittle-shelled eggs are clearly shared primitive character states inherited by testudinids from batagurids. Omnivory with a propensity toward herbivory, as well as diurnal activity coupled with color vision and sight-oriented foraging, constitute a suite of character states also inherited by tortoises from their common ancestor within the batagurids, probably the terrestrial *Heosemys* group.

Both extant *Manouria* species consume a higher proportion of animals and other non-plant matter (especially fungi) than more arid land-dwelling tortoises (Obst, 1988; Chan-ard et al., 1996). Members of this ancient testudinid

genus still live in warm moist forests and are omnivorous when local conditions present diet options (Ernst and Barbour, 1989). The aforementioned forests contain both tropical and temperate elements, reminiscent of those reconstructed for subpolar regions in the very early Tertiary Period in Asiamerica (Axelrod, 1958). Omnivory was probably typical of the common ancestors of batagurids and manourines. Such behavior would have broadened the range of feeding opportunities and potentially raised the nutritional (especially protein) quality of their diets (Bjorndal, 1991; Bjorndal and Bolten, 1993). Herbivory-omnivory may well have been an exaptation that facilitated later terrestrialism in batagurids and their testudinid descendants. No obligatory carnivores are known among any extant terrestrial chelonians, a finding consistent with morphological constraints on their mobility, an issue we shall visit in the Forage Exploitation Test.

The functional synapomorphies that define gopherines, *Gopherus*, and *G. agassizii* as taxa are summarized in Table 2. Character states are matched with the hypothetical environmental stresses to which they are responding, and where possible to the geological time frame in which they first evolved. As Crumly (1994) demonstrated so thoroughly through osteology, most *G. agassizii* – *berlandieri* group (“*Xerobates*” or “*Scaptochelys*” of Bramble, 1982) character states are symplesiomorphic. These include digitigrade, non-spatulate claws, less developed inner ear structures (*os transilens* and saccular otolith) and well-developed mesocarpal joints. Because these shared character states appear to be primitive, symplesiomorphies rather than synapomorphies, they leave the legitimacy of the group as a valid separate genus (or even as a clade) unresolved. These character states may better define a grade of gopherines than a well defined clade. Nonetheless, *G. agassizii* and *G. berlandieri* are clearly sister taxa by genetic criteria (Lamb and Lydeard, 1994). Those legitimate synapomorphies possessed by lineages within the gopherines appeared to have evolved early, by the middle Miocene Epoch. Even the most pronounced states evolved to resist dehydration, such as resorptive bladders and relatively small eyes, are not unique to *G. agassizii*, but are shared with the more mesic *G. berlandieri* (and, in the case of the bladder, with *G. polyphemus* as well). Thus, most distinguishing characteristics of *G. agassizii* are symplesiomorphies and exaptations, utilized by a variety of distantly related chelonians in a wide range of ecological and geographical settings.

Desert tortoises may have developed large resorptive bladders and other character states in response to dehydrating stressors. These character states may have evolved as responses to edaphic conditions found within microhabitats/microclimates in pre-desert Miocene landscapes, and in response to seasonal droughts, but probably, not to modern deserts. Bradshaw (1988) argued that squamate reptiles were generally exapted (Bradshaw’s pre-adaptations) for desert environments. These evaluations are relative. When desert tortoises are compared to the aforementioned sympatric desert iguanids (the iguanines *Dipsosaurus* and *Sauromalus* and the

phrynosomatine *Uma*), they appear to be less specialized and less precisely responsive to extreme desert conditions. For example, the iguanines have salt secreting nasal glands absent in the tortoise. Nagy (1988:201), when comparing *Sauromalus obesus* and *G. agassizii* stated:

“...both husband their water and energy budgets remarkably well, but chuckwalla have opted for precise osmotic and body fluid regulation, which restricts them to feeding only on green, moist vegetation in the spring, whereas tortoises tolerate wide swings in their osmotic and fluid balance, and can thereby drink rainwater and eat dry vegetation during summer and autumn.”

The more generalized morphology, physiology, and behavior of *G. agassizii* in varied habitats is nowhere better illustrated than in the digestive anatomy as stated by Barboza (1995):

“The capacious but simple digestive anatomy of the tortoise may provide the greatest flexibility in utilizing a variety of forages in its unreliable habitat. This wide nutritional niche would encompass low fiber spring pasture as well as the more fibrous senescent forages of drier seasons. The large digestive capacity would accommodate bulky forages to provide energy from fermentation in the hindgut... Subsistence in the long dry seasons and droughts when even these quality forages decline in abundance may therefore depend upon the range of digestive function available to support minimal nutrient requirements until pasture growth resumes.”

The Climatic Regional Association Test

This test assesses the association of desert tortoises with the distribution of climatic and physiographic deserts. The first correlation will focus on local *G. agassizii* distributions in the Mojave Desert, then the comparisons will be extended to the total range of the species, and finally to the more general associations between other tortoise species and climatic desert regions globally. The two tests which follow, the ecosystem association test and the forage exploitation test, extend this theme of correlation further by examining the association between desert tortoises and desert ecosystems (essentially plant associations), and finally, by examining the correlation of tortoise diet with desert plant species actually exploited as forage.

Mean annual precipitation is only one of several important climatic factors. The reliability, seasonality, and proportions of precipitation during fall and winter months vs. spring and summer are also important, as are the numbers of freezing days, the length of the growing season and above-ground activity season, and the regular production and availability of forage. The absence of *G. agassizii* from the San Joaquin Valley, southern California chaparral, and the Great Basin remains unexplained. Possible anthropogenic factors have already been discussed. The cold winters, greater numbers of freezing days, and shorter growing seasons are probably the limiting factors impeding successful incubation, much as has been suggested for factors determining the northern limits of desert lizards in western North America (Pianka, 1966). Similarly, cold winter tem-

peratures that affect egg nests have been implicated in setting the northern distributional limits of the aquatic western painted turtle, *Chrysemys picta belli* (St. Clair and Gregory, 1990). Other important physical/abiotic limiting factors include elevation, the absence of natural caves and soils suitable for digging burrows (for the Mojave populations), physiography, and relief (Weinstein et al., 1987). Highly humid conditions conducive to the propagation of pathogenic bacteria and fungi have been suggested as limiting factors for *G. agassizii* along its southern borders (Van Devender, 2002a, 2002b), but documentation of their causal role in natural settings has yet to be established.

Here we concentrate on precipitation measures because of the greater accessibility of reliable information. During the 20th century, the bioclimatic distribution of *G. agassizii* was centered in the warm temperate deserts of North America—the Mojave and Sonoran deserts, and peripherally in the Sinaloan dry tropical deciduous forest. The species has not been present or equally abundant in all the ecosystems of these deserts (Burge, 1979; Berry, 1984; Weinstein et al., 1987; Fritts and Jennings, 1994). While the distribution of extant *G. agassizii* has been molded by both natural and anthropogenic factors (U.S. Fish and Wildlife Service, 1994; Rowlands, 1995a), we will focus on the former in this section. *Gopherus agassizii* is absent or very rare in the lower, drier, and hotter parts of the Mojave, Colorado (= western Sonoran), and Sonoran deserts. In the Mojave Desert it is absent from the Saline and Eureka valleys, and in Death Valley it is rare. Similarly, in the Colorado Desert, the species is rare in Cadiz Valley, southern Ward Valley, and the mouth of the Colorado River. Semi-isolated and small enclaves of tortoises can be found in the relatively mesic and more productive parts of such valleys, i.e., in a north-facing canyon or surrounding rock outcrops with more cover and forage. The absence or rarity of desert tortoises in some of the drier and hotter areas is due in part to amount, timing, and regularity of rainfall. However, none of the sites could be classified as extreme deserts (Rowlands, 1995b), that is:

“...one in which in a given locality at least 12 consecutive months without rainfall have been recorded, and in which there is not a regular rhythm of rainfall.”

In the Mojave and Colorado deserts, the desert tortoise occurs where mean annual precipitation (P) ranges from approximately 80 to 200+ mm (U.S. Fish and Wildlife Service, 1994). In the Sonoran Desert proper, Fritts and Jennings (1994) reported that *G. agassizii* does not occur in areas receiving < 100 mm P and specifically, in northwestern Sonora, the boundary of tortoise distribution coincided closely with the 100 mm P isopleth. The absence of the desert tortoise from modern peninsular Baja California (notwithstanding Ottley and Velasquez, 1989; see Crumly and Grismer, 1994) may be similarly explained.

In Sinaloa, Mexico, tortoises can be found in tropical-subtropical desert vegetation with thornscrub and to the edges of deciduous forests (Fritts and Jennings, 1994; Bury et al., 2002). The Sonoran desert tortoise is almost entirely

Table 3. Recent global distribution of testudinids in deserts (data drawn largely from Swingland and Klemens, 1989, and Perälä, 2001).

Continent and Desert	Vegetation type	Precipitation (mm)	Testudinid
North America			
Great Basin	scrub/grass steppe	>100	none
	sagebrush(<i>Artemisia</i>)/woodland		
Mojave	<i>Larrea</i> , mixed desert scrub	>100	<i>Gopherus agassizii</i>
Colorado	same	<100	<i>G. agassizii</i>
Sonoran	same	>100	<i>G. agassizii</i>
Peninsular, Baja Calif.	same	<100	none ¹
Chihuahuan	same	>250	<i>G. flavomarginatus</i>
Tamaulipan	same	>350	<i>G. berlandieri</i>
South America			
Atacama	largely barren	<50	none
Patagonian (Monte)	<i>Larrea</i> scrub/pampas	150-300 (<200)	<i>Geochelone chilensis</i> species complex
Africa			
Saharan (+ Sinai)	<i>Artemisia monosperma</i> scrub, peripheral (inland only 60 km)	100-200	<i>Testudo kleinmanni</i> , <i>T. graeca</i> , <i>T. wernerii</i>
	steppe/savanna	>200	only in Sahel, south: <i>Geochelone sulcata</i>
Karoo-Namib	succulent karriod vegetation and scrub	</>100	<i>Psammobates tentorius</i> , <i>P. oculifer</i> ; peripheral species are <i>Homopus bergeri</i> , and <i>Chersina angulata</i>
Asia			
Great Indian	scrub	>100	<i>Geochelone elegans</i>
Central Asian deserts: Kara Kum, Kyzyl-Kum	scrub/steppe	>100	<i>Testudo horsfieldi</i> , <i>T. graeca</i>
Arabian: Rub Al Khali	scrub/barren	<100	none
Gobi	barren/steppe	<50	none

¹The putative *Xerobates lepidoccephalus* (Ottley and Velazques, 1989) notwithstanding (see arguments for synonymy in Crumly and Grismer, 1994).

absent from low valleys (Van Devender, 2002a), although tortoises will cross the valleys *en route* to mountainous terrain (Schwalbe et al., 2002), these tortoises are essentially an upper slope dweller (600 to 1200 m elevation). High temperatures in the lowlands may have suppressed desirable forage, restricted foraging time, and limited or eliminated desirable nesting sites for this species with temperature-dependent sex determination (Spotila et al., 1994). An alternative explanation suggests that the Tertiary–Pleistocene presence in Arizona of the larger and extremely fossorial *G. flavomarginatus* might have displaced *G. agassizii* to upland rocky outcrops (Morafka, 1988; McCord, 2002). Given the behavioral plasticity and generalized morphology of the latter form, it might be expected that any displacement would soon be reversed after the competitor was extirpated. Since this has not been the case, we favor the biophysical explanation, pending more rigorous investigation of egg nest microhabitats of the Sonoran Desert haplotype. Thus, the desert tortoise occupies both hyperarid (50–100 mm P) and arid (100–400 mm P) bioclimatic zones as defined by LeHouérou (1996).

Tortoises may also occur in the semi-arid bioclimatic zone (400–600 mm P). In this latter zone, such as the Sinaloan thornscrub and tropical forest, the tortoise becomes an ecotonal species, perhaps limited by competing herbivores, including other chelonians, by shifts in available forage, substrates that curtail burrow excavation or by lowland relief which expose burrows to flooding and by overhead canopy which reduces insolation for basking and nesting. Unlike helodermatid lizards, gopherine tortoises

only enter thornscrub habitats peripherally in northern Mexico, and their distributions do not continue south in tandem with these habitats.

Precipitation and its ecological and physiographic effects may be limiting at both extremes. Our ability to apply LeHouérou's (1996) definitions are confined to P, because data on potential evapo-transpiration (PET) are often lacking, and thus preclude calculation of an Aridity Index (I) where $I = P/PET \times 100$. Likewise, we lack sufficient information to fully apply Morafka's (1991) definition of desert as a landform responding in specific ways to long-term water budget deficits.

Other species of tortoises follow similar precipitation patterns, as listed in Table 3. No testudinids occur in the largely barren Atacama Desert of South America and large parts of the Saharan and Arabian deserts where P values are low (50–80 mm), even though temperatures may be suitable. Such P values alone may render the presence of tortoises problematic and may support only peripheral, low density populations. Extremes in temperatures (T), as well as P/T ratios affect limited cover of vegetation and forage. In the Mongolian Gobi as in the Great Basin Desert, short and cool summer seasons may have precluded successful egg incubation, though *Testudo horsfieldi* sustains populations nearly that far north further west in central Asia (Obst, 1988; Ernst and Barbour, 1989). Perhaps extremes of continentality and exposure to northern storms on the Mongolian plains plays a role in bringing about their exclusion, as well as impenetrable barriers posed by some intervening ranges.

The current concentration of the desert tortoise in specific warm desert landscapes may be as much the result of localized extirpation by some native American tribes in the Holocene Epoch (Schneider and Everson, 1989; Holman, 1995), as it is the product of restrictions imposed by physiological needs or tolerances. Very dense populations of *G. berlandieri*, the sister species of *G. agassizii*, still thrive in Tamaulipan mesquite (*Prosopis*) grassland (Rose and Judd, 1994). *Gopherus agassizii* still occurs in grassland in south-eastern Arizona (Parker, 1988; Martin, 1995; Averill-Murray et al., 2002), as did its glaciopluvial antecedents across the Southwest (see the Phylogenetic and Paleoecological Tests). The apparent exception to this pattern is the mesic forest dweller, *G. polyphemus*, but this species clusters phylogenetically with *G. flavomarginatus* in a clade which has several derived character states not shared with the generalized *G. agassizii* group (Crumly, 1994; Lamb and Lydeard, 1994; Lamb, 2002).

The Ecosystem Association Test

In this test the correlations shift from desert climate and physiography to the desert plant associations which form in response to those factors. As indicated in Fig. 1, the predecessors of *G. agassizii* lived in a variety of relatively more mesic ecosystems including dry tropic forests and savannas, sclerophyllous woodlands, juniper-oak-pinyon woodlands, and scattered grasslands, sage, and scrub or thorn forests (Van Devender et al., 1976; Van Devender and Mead, 1978), though lowland and exposed semiarid habitats seem to predominate. The trend from the Paleocene to present was from a wetter and more equable to a drier and more extreme climate, as well as to more arid vegetation (e.g., Axelrod, 1979; Van Devender, 2002b).

In the latter half of the 20th Century, *G. agassizii* occupied an equally wide variety of vegetation zones, although more arid. The vegetation types were likely present in previous epochs as small or limited open or more arid areas in otherwise forested or grassland habitats. Vegetation types are summarized for the Mojave and Colorado deserts in Table 4.

In the northern part of the geographical range in the Mojave Desert, *G. agassizii* can be found in saltbush (*Atriplex* spp.) scrub and psammophilous vegetation types at the edges of playas to creosote bush (*Larrea*) scrub, tree Yucca (*Yucca brevifolia*, *Y. schidigera*) woodlands, and steppe communities with perennial bunch grasses. In the western or Coloradan subdivision of the Sonoran Desert, desert tortoises occur in the richer and wetter creosote bush scrub and microphyll woodland communities (U.S. Fish and Wildlife Service, 1994). The geographical race of *G. agassizii* in the Sonoran Desert of Arizona (Lamb and McLuckie, 2002) is more common on steep slopes in upland vegetation of Palo Verde-saguaro (*Cercidium-Carnegiea*) than elsewhere (Burge, 1979). The Sonoran Desert tortoises also occur to a limited extent in oak woodlands with perennial grasses (Parker, 1988; Van Devender, 2002a)

Table 4. Vegetation types occupied by *Gopherus agassizii* in the late 20th Century (U.S. Fish and Wildlife Service, 1994; Rowlands, 1995a).

Vegetation Complex and Subcomplex	Deserts	
	Mojave	Colorado
Desert Scrub Complex		
<i>Mojave-Colorado Desert Subcomplex</i>		
Creosote Bush Scrub	X	X
Cheesebush Scrub	X	X
Succulent Scrub	X	X
<i>Saline-Alkali Scrub Subcomplex</i>		
Shadscale Scrub	X	
Mojave Saltbush-Allscale Scrub	X	
<i>Great Basin Scrub Subcomplex</i>		
Blackbush Scrub	X	
Hopsage Scrub	X	
Desert Microphyll Woodland Complex		
<i>Paloverde Microphyll Woodland Subcomplex</i>		
Foothill Paloverde-Saguaro Woodland		X
Blue Paloverde-Ironwood-Smokedtree Woodland		X
Mesquite Microphyll Woodland	X	X
Desert and Semidesert Grassland Complex		
<i>Desert-Semidesert Scrub Steppe Subcomplex</i>		
Indian Ricegrass Scrub-Steppe	X	
Desert Needlegrass Scrub-Steppe	X	
Big Galleta Scrub-Steppe	X	
<i>Desert Alkali Grassland Subcomplex</i>	X	
Desert Psammophyte Complex	X	X

as well as in the desert grassland of southeastern Arizona (Pinal Co.) (Martin, 1995). Further south into Sonora and Sinaloa, Mexico, tortoises occur in thorn scrub and subtropical forests (Fritts and Jennings, 1994; Bury et al., 2002; Van Devender, 2002a).

In summary, the pinyon-juniper, oak, sagebrush, and grassland associations occupied by tortoises more than 10,000 years ago now occur at higher elevations, in relatively cold and steep mountain settings (Van Devender et al., 1976). They include the same dominant plant genera as their Pleistocene counterparts, but often differ in their total floras considerably. *Gopherus agassizii* populations are uncommon in these associations. These plant associations still frequently border on, and interdigitate ecotonally with, other habitats more commonly occupied by tortoises today. These ecotonal expanses are still unstable in their composition, changing significantly in biotic composition and proportions and productivity in response to local weather patterns, and rendering desert borders blurred, even from the perspective of a few decades.

Patterns of Usage of Microhabitats. — The burrow-dwelling *Gopherus* tortoises demonstrate some defining characteristics of frequently migrating, fugitive species (Grimaldi and Jaenike, 1984). That is, they use patches of ephemeral, palatable forage. Gopherines forage in vegetation patches which are often ephemeral by season, decade, or century, and associated with flood plains, washes, or transitory (disclimax) clearings created in forests from fire (*G. polyphemus*). By targeting such patches, the descendants of manourine forest tortoises may satisfy the dietary needs of a body that is only moderately adapted to the current arid and semi-arid ecosystems. These patches generally occur in well-drained sites of moderate humidity supporting

suffrutescent shrubs, ephemeral forbs, and grasses within microphyllous scrub in deserts and semi-deserts.

Although the ecosystems of the extant four gopherine species appear to be quite different from one another (Ernst and Barbour, 1989), similar patterns exist in choice of microhabitats. In general, *Gopherus* tortoises utilize vegetative and edaphic microhabitats focused around a burrow, pallet, or pre-formed shelter in or near sandy/friable soils suitable for digging. Suitable forage accessible in height, nutritional content, succulence, and palatability (including fiber content and quality) must be nearby. The deep burrows of *G. polyphemus* are generally placed in sandy soils within openings or at the edges of forests, or in clearings induced by lightning-caused fires (Mushinsky and McCoy, 1994). Indeed, the extraordinary depth of their burrows (> 6 m) may represent an exaptation to mitigate against the effects of fire and flood, since biophysical stressors are less manifest in these well-canopied warm temperate forests. Forbs and grasses are readily accessible in the immediate vicinity of the burrow mound. *Gopherus flavomarginatus* uses deep burrows, frequently placed within the drip-line of protective shrubs, closely situated to patches of perennial bunch grasses and herbaceous growth (Lieberman and Morafka, 1988). *Gopherus berlandieri* (Rose and Judd, 1994) utilizes pallets sheltered in mesquite grassland, especially in the low sandy hills of the Tamaulipan Plain of south Texas and the Mexican Gulf coastal plains. The pattern for the Mojave haplotypes of *G. agassizii* is similar to that of *G. flavomarginatus*, although burrows and cover sites of the former can be under large boulders (Burge, 1979), within the walls of washes in calcic layers (Woodbury and Hardy, 1948), and under shrubs (Berry and Turner, 1986). Adult desert tortoises in the western Mojave differentially eat and forage more in washes and washlets which are two of the region's more mesic microhabitats (Jennings, 1997). Although washes and washlets composed only 10.3% of the habitat, more than 25% of all plants on which tortoises fed occurred there, more than twice the number that might be expected based on the amounts of habitat alone (Jennings, 1997). Three of the top ten forage plants were primarily found in washes (*Euphorbia albomarginata*, *Astragalus layneae*, and *Camissonia boothii*). In contrast, rocky slopes provide most shelter and foraging habitats for both Sonoran and some Sinaloa *G. agassizii*. Burrows in these areas are poorly excavated, if they are constructed at all.

The Forage Exploitation Test

In this third ecological correlation, we shift focus from abiotic parameters and responding ecosystems to the actual plant species exploited by the tortoise forager, asking the question: are the forage species ingested by tortoises unique to deserts or at least typical of them?

Ecogeographic Origins of Consumed Plant Foods. — The desert tortoise is a facultative herbivore (Woodbury and Hardy, 1948; Burge and Bradley, 1976; Jennings, 1993; Oftedal, 2002; Van Devender et al., 2002; but also see the reviews of carnivorous behavior by Oftedal et al., 2002, and

Okamoto, 2002). The desert tortoise forages on five major groups of plants: annual forbs (winter or summer ephemerals), annual grasses (winter or summer), cacti, native perennial bunch grasses, and herbaceous perennial shrubs. These tortoises rarely forage on woody shrubs. Affinities for succulent vegetation are apparent, even without an established association with mesic microhabitats. When succulent green forbs or grasses are available during the growing season, tortoises select them over 90% of the time (Burge and Bradley, 1976; Jennings, 1993). The species has a large digestive capacity, can accommodate and digest bulky forage, and generally has a "versatile digestive strategy consistent with the persistence of tortoises in many hot arid regions despite drastic changes in these habitats" (Barboza, 1995).

By way of illustrative examples, we compared the diets and origins of food plants for *G. agassizii* from two areas in the Mojave Desert: far-western (Jennings, 1993) and northeastern (Burge and Bradley, 1976). Desert tortoises in these areas have been observed to consume more than 40 species of plants which have their origins from north and warm temperate areas, Madrean-Tethyan elements historically (Axelrod, 1975), and the California Floristic Province spatially (Table 5). In the far-western Mojave, desert tortoises were highly selective foragers, and legumes (*Astragalus*, *Lotus*, *Lupinus*) formed 43% of the diet of adults (Jennings, 1993). Herbaceous perennial forests and suffrutescent shrubs composed 30% (*Astragalus*, *Mirabilis*, *Euphorbia*, *Stephanomeria*) of bites taken (Jennings, 1993). At one site in the northeastern Mojave, 17 species of plants were observed to be eaten, including the winter ephemeral *Plantago* (34% use), the suffrutescent shrub *Sphaeralcea* (27% use), and *Opuntia* (9% use) (Burge and Bradley, 1976). Some genera have annuals that occur not only in the Mojave and Sonoran deserts, but the Chihuahuan as well: e.g., *Astragalus*, *Plantago*, and *Cryptantha*. Such winter-spring ephemeral herbs and grasses, a staple of current diets, have been recorded from packrat middens from 30,000 years old to recent Holocene times (Van Devender, 1990; Nowak et al., 1994).

In the Sonoran Desert, tortoises have been reported to eat 199 species of plants, primarily grasses, desert vines, and mallows (Van Devender et al., 2002). The forage plants are succulent or dried and occur in a wide variety of microhabitats, e.g., on north or south slopes, in the open, or in moist crevices.

The photosynthetic pathways of plants (C_3 , C_4 , and CAM) provide clues to the origins of desert tortoise forage species. Mixes of the three types of plants are present in the North American deserts today. In discussing desert vegetation, MacMahon (1988) stated:

"...although C_4 and CAM appear to be the species best adapted to deserts, many desert species are C_3 , and one needs to look carefully at the specific microhabitat when interpreting relationships between patterns of distribution and photosynthetic pathways. Mesic microsites or times of the year permit C_4 species to flourish in areas that appear, in general, to be very arid."

In general, many desert annuals that germinate after winter rains have C_3 pathways (MacMahon, 1988), whereas

Table 5. Origins and ecogeographical associations of the plant taxa consumed by desert tortoises in the late 20th Century in the Mojave Desert (floral data from Raven and Axelrod, 1978; food plants from Woodbury and Hardy, 1948; Burge, 1978; Jennings, 1993). Nomenclature after Hickman (1993).

North temperate	Warm temperate	California Floristic Province	Madrean-Tethyan Geoflora
<i>Chamaesyce</i> (<i>Euphorbia</i>) ¹	<i>Eremalche</i> ¹	<i>Aniscoma</i> ¹	<i>Astragalus</i> ^{1,3}
<i>Lupinus</i> ¹	<i>Chamaesyce</i> (<i>Euphorbia</i>) ³	<i>Glyptopeura</i> ¹	<i>Erodium</i> ¹
<i>Achnatherum</i> (<i>Oryzopsis</i>) ⁴	<i>Mentzelia</i> ¹	<i>Malacothrix</i> ¹	<i>Lotus</i> ¹
<i>Poa</i> ⁴	<i>Mirabilis</i> ⁵	<i>Rafinesquia</i> ¹	<i>Strylocline</i> ¹
<i>Achnatherum</i> (<i>Stipa</i>) ⁴	<i>Muhlenbergia</i> ⁴	<i>Stephanomeria</i> ^{1,3}	Gilieae ¹
Polemoniaceae	<i>Opuntia</i> ⁵ <i>Plantago</i> ¹	Polemoniaceae, Tribe Gilieae ¹	Onagraceae ¹
	<i>Sphaeralcea</i> ³		
	<i>Bouteloua</i> ^{2,4}		

¹Annual/ephemeral forb; ²Annual/ephemeral grass; ³Herbaceous perennial forb or shrub; ⁴Herbaceous perennial grass; ⁵Stem succulent, cacti.

summer annuals may be a mix of species with C₃ and C₄ or solely C₄ pathways, depending on the location. Perennial grasses (family Poaceae) and herbaceous perennial species and suffrutescent shrubs in such families as Asteraceae, Euphorbiaceae, and Nyctaginaceae have C₄ pathways (MacMahon, 1988), although two important grasses (*Achnatherum speciosum* and *A. hymenoides*) are in the C₃ group (Raven and Axelrod, 1978; Van Devender et al., 1990). Members of the *Cactaceae* typically have CAM pathways (MacMahon, 1988). Tortoises utilize forage plants from all three photosynthetic pathways (Table 5) and from different floral affinities—the Arcto-Tertiary geoflora, Madrean-Tertiary geoflora, warm temperate and desert elements, and other elements (Raven and Axelrod, 1978). The current availability of each plant species, whether characterized by photosynthetic pathway or by geofloral or other fossil floral source group depends on the desert region, season, microhabitats available locally, and amount of annual precipitation falling in a particular year. In the past, it is likely that tortoises foraged on a wide array of plant species with different origins and different photosynthetic pathways depending on local and regional conditions, just as they do today. The complexity and obscurity of these relationships was in dynamic flux throughout the Quaternary Period (Betancourt et al., 1990:438):

“The composition of western grasslands probably has been unstable throughout the late Quaternary, but paleoecological evidence is scant or lacks taxonomic resolution. Though grasslands may have a characteristic pollen spectrum, pollen grains of grasses are too similar to allow identification below the family level. Classes of opal phytoliths may correspond to subfamilies, but even this questionable... Fossil grass cuticles abound in some lake sediments and other deposits, but they are seldom determinable to species.”

Limitations on Foraging and Diet Selection.—Modern *G. agassizii* are confined to eating plants within approximately 15 cm of the substrate (Fig. 2). Neonate and small juvenile tortoises probably cannot reach much above 3 cm and tend to focus within 1–2 cm of the soil surface. Adults also are rarely observed to push plants over, or climb into shrubs to reach a selected forage item. Instead, efforts are focused on lunging forward and down at the drip line or edges of shrub canopies or in the inter-shrub spaces. The

overhead reaching, head-extending movements characteristic of the giant tortoises in the Galapagos Islands (e.g., *Geochelone nigra hoodensis*), have not been observed, at least in Mojave Desert *G. agassizii*.

Foraging on the preferred succulent herbaceous and stem-succulent species is generally limited to a narrow range of months in late-winter and spring for western Mojave Desert tortoises (Figs. 2 and 3; see also Van Devender et al., 2002) and for both spring and summer in central, eastern, and northeastern Mojave and Sonoran tortoises. At these times, the forage is not only the most accessible, but likely to be the most nutritious (protein-rich). Such seasonally available forage may be particularly important to juvenile tortoises, for which epigeal (above ground) activity may peak as early as February (Woodbury and Hardy, 1948; Burge and Bradley, 1976; Jennings, 1993, 2002; Esque, 1994; Wilson et al., 1999; Van Devender et al., 2002). We have provided a hypothetical model for accessibility, nutritional quality, and total biomass of food plants in Fig. 3. We perceive that forage accessibility, quality, and availability to neonates and juveniles may be critical limiting factors for future population recruitment (see also Jones, 1993). Neonates and juveniles are far more limited in movements, head reaching and extending capabilities and biting strengths, than are adults. Neonates move delicately as they consume tender vegetation in contrast to older individuals that are less precise in their movements. At the same time, the qualitative requirements of their nutrition may be more stringent. Forage of young *G. flavomarginatus* consisted of 16% protein (dry weight), or double that of adults (Adest et al., 1989). Experimental studies with the young of one aquatic emydid, *Trachemys scripta*, revealed that a diet greater than 10% protein (dry weight) was required to sustain growth (Avery et al., 1993).

As a group, gopher tortoises may be more prone to omnivory than most field observations suggest. In sub-Saharan hinge-backed tortoises of the genus *Kinixys*, those species occurring in more mesic habitats are also more omnivorous. *Kinixys erosa* regularly preys upon amphibians and fish in ephemeral pools at the end of the rainy season, whereas other *Kinixys* from more arid habitats tend to be herbivorous (Obst, 1988). The pattern reiterates a trend previously noted for *Terrapene coahuila* and, in a broad sense, reinforces the facultative and reversible nature of

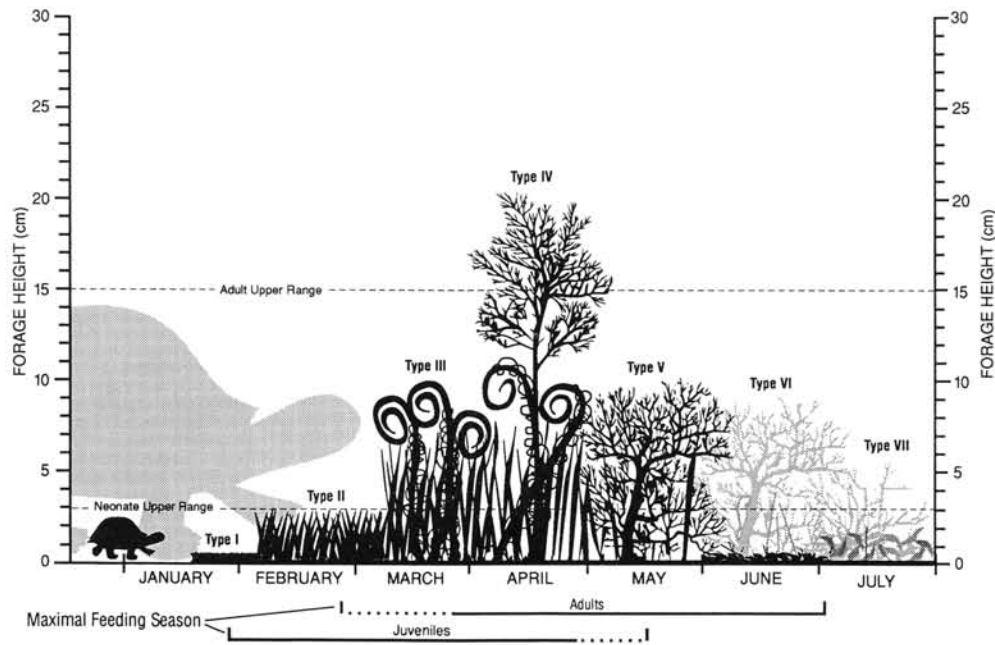


Figure 2. Ephemeral forage availability for *G. agassizii* in the Western Mojave. Silhouette profiles depict both adult (in gray) and neonate (in black) access to forage. Ephemeral forage available to adult and juvenile desert tortoises between January and July in the western Mojave Desert, shown with the maximal foraging seasons for the two size groups. The 7 types of vegetation consist of: Type I, the fresh green and often succulent first leaves and stems of annuals, usually very low vegetation, including rosettes of dicots and short grass stems; Type II, advanced stages of Type I, including some large and tall members of the genera *Phacelia* and *Pholistoma* that grow within shrubs; Type III, an often high diversity of blooming ephemerals, including *Malacothrix*, *Phacelia*, *Mentzelia*, *Amsinckia*, *Cryptantha*, and *Lupinus*; Type IV, similar to Type III, but reaching peaks of height and diversity; Type V, considerable dry ephemeral material, but with *Eriogonum*, *Eriastrum*, *Lotus*, and some *Astragalus* still blooming; Type VI, *Euphorbia* and *Eriogonum* are the most frequent succulent green ephemerals; Type VII, most ephemerals have set seed and are dry.

“herbivory” among terrestrial chelonians (see Ernst and Barbour, 1989; Dodd, 2001). Arid environments might simply deny tortoises access to diurnal and physically accessible arthropod prey, such as lepidopteran larvae, for most of the year. When access is afforded, tortoises may still manifest the omnivorous and scavenging propensities, particularly protein-requiring young tortoises in more mesic seasons (spring and summer monsoon) and settings (Sinaloa scrub and deciduous woodlands). Similarly, more omnivorous behaviors might have been typical of earlier Cenozoic gopherines and manourines which inhabited more mesic and equable climates. Intrinsic insectivory is elicited in captive choice trials with juvenile *G. agassizii* and insects (Okamoto, 2002). Recent field observations of foraging tortoises indicate that tortoises will select for caterpillars (Avery and Neibergs, 1997) and scavenge dead or immobilized lizards (Jennings, 1993; Okamoto, 2002).

Growth, reproduction, and long-term survival in *G. agassizii* are dependent on, and closely related to, the production of fresh, succulent green vegetation which, in turn, is largely a function of precipitation. Ingestion of this succulent vegetation satisfies some of the hydration needs for the tortoise as well as energetic and other nutritional needs. For example, growth of juvenile tortoises is greater in years with average winter-spring precipitation and the more abundant fresh vegetation produced from such rains (Medica et al., 1975; Nagy and Medica, 1986; Berry, 2002). Tortoise egg production is diminished when succulent green plant forage, especially in the form of new spring annuals, is reduced as

a result of repeated below-normal winter-spring rains or summer monsoons (Henen, 1997). Likewise, drought contributes to tortoise mortality (Turner et al., 1984; Peterson, 1994; U.S. Fish and Wildlife Service, 1994; Berry et al., 2002b). Thus, the tortoise depends upon the mesic seasonal patches of forage vegetation within arid and semi-arid environments to optimize, or at least restore its physiological and metabolic needs during and after rainfall events (Henen et al., 1998). This strategy involves both temporal and spatial targeting of foraging behavior and selection of diet items. Limitations may involve complex balances among protein, water content, and potentially toxic potassium (the potassium excretion potential, or PEP hypothesis of Oftedal, 2002; Oftedal et al., 2002). When all of the positive objectives and negative constraints of diet are considered collectively, a hypothetical strategy emerges in which tortoises must forage on a seasonally adjusted basis to optimize water, protein, and caloric uptake, while limiting fiber, depleted food items, and a variety of toxins. These opportunistic and flexible tactics are very reminiscent of the array of behaviors used by heliothermic lizards (Bradshaw, 1988). While seasonal changes in physiological states may be dramatic (Nagy, 1988), these behavioral mechanisms allow tortoises to maintain a net dietary homeostasis over the course of a full year by shuttling across a changing nutritional mosaic of resources. This dietary flexibility is key to the success of *G. agassizii* in both variable and diverse habitats.

Threats to Desert Forage from Drought, Climate Change, and Desertification. — Droughts have been docu-

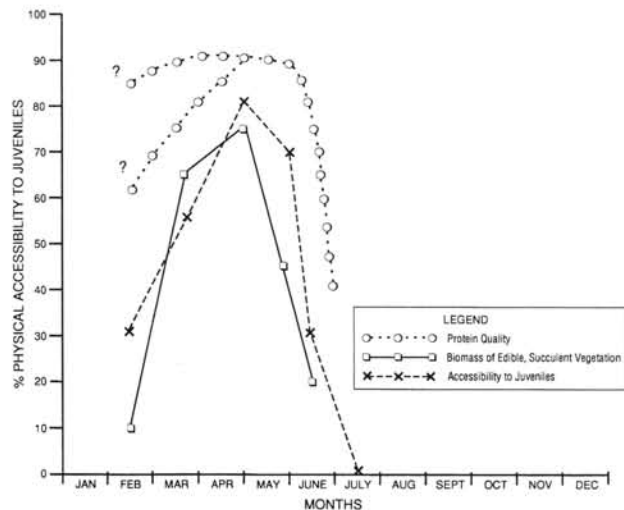


Figure 3. A hypothetical model of the physical accessibility of edible, succulent vegetation available to juvenile desert tortoises in the western Mojave Desert by month and by protein quality.

mented for the past 2000 years through tree ring analysis, lake level fluctuations, and pollen analysis, and are a defining and recurring characteristic of many ecosystems worldwide (Rosenberg, 1978; LeHouérou, 1996). No evidence exists, however, to show that droughts are increasing in frequency or severity in the southwestern United States. In fact, the last 20 years of the 20th Century were the wettest on record (Hereford, 2000).

Climate change may contribute to substantial changes in tortoise habitat in the 21st Century. The National Assessment Synthesis Team (2000), U.S. Global Change Research Program, has projected increased rainfall and temperatures in the West, with increases in grassland, woodland, and forest habitats, and a loss of desert vegetation. Yet, another dry period for the next 25–35 yrs, similar to that occurring between the 1940s and early 1970s, has also been predicted by other sources (Hereford, 2000). Both processes, drought and global warming, have long-term nutritional implications for the survival of the desert tortoise.

Anthropogenic desertification, which is defined as arid and semiarid land degradation (LeHouérou, 1996), has immediate ramifications (Warren et al., 1996) on the quality and amount of forage available. The proposition that deserts are subject to desertification may seem to be an oxymoron. However, the Mojave Desert might be better characterized as a desert steppe in which patchy grasslands are interspersed with perennials (creosote, *Larrea tridentata* in particular) that serve as “nurse plants” and form “nutrient islands” (Fowler and Whitford, 1996). Edaphic soils (MacAuliffe, 1994) form seasonal patches of forbs and perennials which are important sources of forage for small grazers. The predominantly herbivorous *G. agassizii* has survived in drying environments for 12,000 yrs or more and was still locally and regionally abundant in large parts of the Mojave and Colorado deserts until the late 1970s (U.S. Fish and Wildlife Service, 1994; Berry and Medica, 1995). During the 20th Century, the ecosystems and microhabitats on

which *G. agassizii* depend are being degraded by a wide variety of human activities, including habitat fragmentation, urbanization, agricultural development, lowering of the water table, livestock grazing, and off-road vehicle activities (MacMahon, 1988; Sims, 1988; U.S. Fish and Wildlife Service, 1994). These impacts contribute substantially to desertification across the semiarid and arid landscapes of the United States (Humphrey, 1958; Sheridan, 1981; LeHouérou, 1996) and are both widespread and deleterious in desert tortoises habitats (U.S. Fish and Wildlife Service, 1994). Livestock, for example, use the same washes and washlets that are targeted by tortoises as sources of preferred forage plants (Jennings, 1993); differentially consume succulent green forbs (e.g., Webb and Stielstra, 1979; Avery, 1998) and perennial grasses; reduce the biomass of shrubs used by tortoises for cover from the elements and protection from predators; and trample tortoises (Dickinson et al., 1995). Livestock are also implicated in the invasion of alien annual grasses (D’Antonio and Vitousek, 1992).

Coupled with landscape-level patterns of change are the smaller-scale changes to microhabitats from the invasion of alien annual grasses, such as members of the brome and Arab or Mediterranean grass genera, *Bromus* and *Schismus*, respectively (Mack, 1981; D’Antonio and Vitousek, 1992; U.S. Fish and Wildlife Service, 1994). Alien grasses have contributed to both large- and small-scale fires in many desert scrub and stem succulent habitats because they are highly combustible, burn readily, and are prolific, successful invaders (Brooks, 1999a, 199b; Brooks and Esque, 2002).

The fires not only kill tortoises outright (e.g., see Woodbury and Hardy, 1948; Homer et al., 1998; Brooks and Esque, 2002) but may induce serious secondary damage or kill dominant shrubs, such as *Larrea*, thereby reducing the cover of shrubs essential for providing shade. Repeated fires impoverish the flora, and desert shrublands can be converted to alien annual grasslands. Such alien grasslands are inadequate forage for desert tortoises. For example, in experimental trials, desert tortoises fed the alien grass *Schismus*, introduced by humans from the Middle East, were not in nitrogen balance, whereas those fed diets of native plants were in balance (Meienberger et al., 1993; Barboza, 1995; Avery, 1998; Nagy et al., 1998). Alien annual grasses may also be nutritionally deficient compared with the native forbs available to Mojave Desert tortoises (Hazard et al., 2001). Alien annual plants are a significant potential threat as they are displacing native plants in some locations (Brooks, 1999b). All of these anthropogenic processes exacerbate the desertification of desert tortoise habitat, especially in those “grassland steppes” and “meadows” where degradation depletes not only the biomass, but also caloric and protein content of remaining forage, and may render impossible the kinds of shuttling which achieve chemical balance necessary to avoid potassium overload (Ofstedal, 2002; Ofstedal et al., 2002). Successional processes are problematic in the Mojave Desert, slow when they do occur (Vasek, 1983; Lovich and Bainbridge, 1999), and may not respond in predictable ways to the establishment of alien grasslands, if at all.

In contrast, the closely related Texas tortoise, *G. berlandieri*, appears to thrive in habitats both divided by farm-to-market roads and subjected to heavy grazing (Kazmaier et al., 2002). Perhaps the more robust and more reliable summer precipitation of the Tamaulipan Plain provides a more spatially and temporarily continuous carpet of diverse quality forage for that species.

CONCLUSIONS

Our first two tests assessed the selective influence of paleoecological stresses on the evolution of the *G. agassizii* lineage and the morphology of its taxa. Clearly the desert tortoise achieved much of its morphological distinctness as a member of a species group which differentiated some 17–18 million yrs ago. North American desert landscapes may post-date that evolution by 12 million yrs. During the temporal lag time and the subsequent climatic perturbations that disrupted the continuity of desert vegetation, the *G. agassizii* complex of tortoises may have survived in grassland, pinyon-juniper woodlands or parklands, and chaparral, but definitive fossil tortoise evidence is lacking for most of this critical Miocene Epoch. The modern Mojave Desert, its biotic assemblages (typically dominated by creosote), and the climates which have molded both, have a continuous history of only 5000 to 12,000 yrs. Based on our estimated origins of shared primitive and shared derived body features and behavior, we suggest that most desert tortoise differentiation and functional adaptations preceded the appearance of all North American deserts, and occurred instead in response to lowland microhabitats or edaphic patches with sandy or friable soils.

The desert tortoise is neither a chelonian analogue to a spadefoot toad, nor is it equivalent to a heliothermic phrynosomatine lizard. Nor is it a specifically a relict of thornscrub and upland deciduous forests in a sense comparable to that used to accurately characterize the helodermatid lizard, *Heloderma suspectum*. The desert tortoise utilizes desert environments very effectively through a combination of symplesiomorphies, exaptations derived from forest-dwelling terrestrial batagurids, and true adaptations to the challenges of life in dry, well-drained microhabitats within sand hills, grasslands, and scrub vegetation. These functional features involve the excavation of a burrow microhabitat and an array of morphological features that convey resistance to dehydration and long-term drought. The generalized physiological responses and morphological conditions combine with a variable array of behavioral strategies to accommodate or avoid desert stresses, much along the lines described by Bradshaw (1988) for desert reptiles generally. Morphological, physiological, and behavioral plasticity are the functional strengths of this opportunistic generalist. This view does not preclude the evolution of locally adapted populations, but for the most part, these local “adaptations” are modest, and in some cases, hypothetical.

Our last three tests further challenge the assumption that *G. agassizii* is an obligate desert specialist in abiotic, botani-

cal, and nutritional contexts, respectively. Critical to the continued success of this species is its ability to shuttle across temporal and spatial nutritional mosaics, in modes which broadly parallel those of behavioral thermoregulators as they shuttle across a thermal mosaic to achieve physiological stability. In the tortoise net stability is achieved over an annual rather than diel cycle of behaviors and physiological changes. This nutritional mosaic is patchy not only in the physical distribution of forage and in its temporal availability, but in terms of water, calories, protein, potassium, and fiber content. To utilize this shuttling strategy effectively, the tortoise must have an opportunity to exploit a heterogeneous environment. Forbs, annual and perennial grasses, and succulent portions of shrubs and cacti all play a role in providing this mosaic. The complexity and biodiversity of this array of forage species may have been more extensive in its evolutionary past. Tertiary ecosystems in which the tortoise evolved were enriched by plant species derived from non-desert habitats, “preadapted” (= exapted) much like the tortoise itself, as noted by Raven and Axelrod (1978:46):

“Thus the richness of the desert flora owes chiefly not to the antiquity of the desert on a regional scale, but rather to the accumulation of numerous taxa during the Tertiary and the Quaternary, taxa that were preadapted to increasing drought over this region.”

Certainly the innate morphological and behavioral flexibility of the desert tortoise may be viewed as substantial exaptations with which it will be able to withstand changes in climates (National Assessment Synthesis Team, U.S. Global Change Research Program, 2000), habitats, and forage. Nonetheless, the effects of anthropogenic desertification on desert tortoise habitats continue to be a reduction in seasonal, spatial, and nutritional accessibility and availability of tortoise food supplies. The consequences may be manifest not only by the direct effects of starvation but more subtly, through the spread of epidemic diseases like upper respiratory tract disease, especially in tortoises rendered immuno-compromised by malnutrition. Genetic viability may also be degraded in deteriorating environments and the consequentially depleted tortoise populations. Genetically based units, such as the ESU and the MU, may help prioritize and direct conservation actions. These units work most effectively when they both quantify and phylogenetically ordinate genetic (often adaptively neutral) differentiation, and, at the same time, identify the dynamic selection-response processes important to maintaining functional adaptation (Moritz, 2002).

All of the options critical to tortoise survival are being narrowed, in many cases simulating the consequences of natural climatic desiccation. The rapid rates at which these deleterious processes move forward are historically unprecedented. The potential for continued reduction in quantity and quality of tortoise forage plants is high. Mitigating against this reduction, or reversing it, remains a challenge for land-use managers of Southwestern deserts.

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