

A study of the utility of convergent characters for phylogeny reconstruction: Do ecomorphological characters track evolutionary history in *Anolis* lizards?

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Received 13 July 2005; accepted 17 August 2005

Abstract

The reconstruction of phylogeny requires homologous similarities across species. Characters that have been shown to evolve quickly or convergently in some species are often considered to be poor phylogenetic markers. Here I evaluate the phylogenetic utility of a set of morphological characters that are correlated with ecology and have been shown to evolve convergently in *Anolis* lizards in the Greater Antilles. Results of randomization tests suggest that these “ecomorph” characters are adequate phylogenetic markers, both for *Anolis* in general and for the Greater Antillean species for which ecomorphological convergence was originally documented. Explanations for this result include the presence of ecomorphologically similar species within evolutionary radiations within islands, some monophyly of ecomorphs across islands, and the existence of several species that defy ecomorphological characterization but share phylogenetic similarity in some ecomorph characters.

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Keywords: Lizards; Convergence; Ecomorph; Phylogeny

Introduction

Reconstruction of evolutionary history requires homologies, or similarities due to common ancestry, as evidence. Characters used to reconstruct phylogeny are hypotheses of homology, and systematists select characters based on their potential to track phylogeny as consistent homologies over evolutionary time (Wiley, 1981). Characters that are good phylogenetic markers change infrequently so that similarities in such characters between species can be considered homologous similarities. Characters that change or evolve convergently multiple times erase homology and confound

attempts to reconstruct phylogeny. Several studies have evaluated the utility of particular classes of characters for reconstructing phylogeny (e.g., morphology: Scotland et al., 2003; behavior: de Queiroz and Wimberger, 1993; intraspecifically varying characters: Wiens and Servedio, 1997; genes: Graybeal, 1994).

Anolis lizards are the dominant abundant terrestrial vertebrates of neotropical areas. Morphologically they are characterized by expanded toepads that facilitate their usually arboreal lifestyle and an often colorful throat fan, or dewlap, used mainly in intraspecific signaling. *Anolis* have been model systems for a plethora of experimental and comparative studies, including studies of evolutionary convergence (Williams, 1983). Ernest Williams, Jonathan Losos, and collaborators

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have documented striking ecological and morphological convergence in *Anolis* lizards of the Greater Antilles (Williams, 1972, 1983; Losos, 1994; Losos et al., 1998). Jamaica, Puerto Rico, Cuba, and Hispaniola each contain an assemblage of *Anolis* species composed of distinct “ecomorph” types. An ecomorph is a suite of correlated ecological and morphological states associated with a particular niche (Williams, 1983). For example in *Anolis*, the “crown-giant” ecomorph includes large species with long tails that live high in trees, and the “twig” ecomorph includes small species with short limbs that live cryptically on narrow perches. Williams (1983) identified six ecomorph types in *Anolis* – crown-giant, grass-bush, trunk, trunk-crown, trunk-ground, twig – and Losos et al. (1998) demonstrated that these types are morphologically distinct from each other and that this similarity is usually (though not always) due to convergence of ecomorphs between islands. For example, the Jamaican crown-giant *A. garmani* is more closely related to other ecomorphs on Jamaica than it is to the Cuban crown-giant *A. equestris*. Losos et al. (1998) found a minimum of 17 evolutionary transitions between ecomorphs, including two cases of independent evolution of the same ecomorph within an island, indicating rampant convergence of ecomorphs.

Losos et al. (1998) used six morphological characters associated with habitat to differentiate ecomorphs: snout to vent length (SVL), mass, number of subdigital lamellae, forelimb length, hindlimb length, and tail length (size effects were removed from all characters except SVL). The convergence of ecomorphs suggests that these characters are not likely to be good phylogenetic markers. However, these characters have been used to differentiate species (e.g., Kohler, 2003), demarcate groups of species (e.g., Savage and Talbot, 1978), and help elucidate large-scale phylogeny (Poe, 2004). It is possible that these studies have been misled by convergence in these characters.

Here I test the phylogenetic utility of ecomorph characters in the entire clade of *Anolis* and among only the Greater Antillean species from which the ecomorph concept was originally developed.

Materials and methods

I obtained values for four of the ecomorph characters: SVL, hindlimb length (femoral length, FL), tail length (TL), and number of subdigital lamellae (SDL) for 174 *Anolis* species (91 Greater Antillean species) and seven outgroup species. The other two ecomorph characters mass and forelimb length are expected to be strongly correlated with SVL and FL, respectively, and so are not analyzed here. The sample of *Anolis* species used here was selected to encompass the geographic and phyloge-

netic diversity in the genus. I measured maximum SVL and average FL (measured from midline of body to knee) for each species (from 1 to 20 individuals per species) and obtained data for median TL and median SDL from the *Anolis* handlist (Williams et al., 1995), supplemented by personal observation. TL, FL, and SDL are correlated with SVL (Williams, 1963; Poe, 2004). I corrected for size in FL and SDL by regressing these variables on SVL and using the residuals in all analyses. Variables were natural-log transformed before regression. TL was recorded in units of body length and so no transformation was necessary. Raw values for SVL and residuals for FL, SDL, and TL were converted to phylogenetic characters using Thiele's (1993) method of gap-weighting. This procedure results in an ordered character (states $a \leftrightarrow z$) for which the parsimony cost of transitions between states is weighted by the magnitude of the quantitative difference between states. Species codes are listed in Table 1.

A phylogenetic estimate for the analyzed species was obtained by parsimony analysis of the data of Poe (2004) excluding characters 1 (SVL), 3 (FL), and 8 (TL). This matrix includes 1677 parsimony-informative characters from morphology, allozymes, chromosomes, immunology, and DNA sequences. Parsimony searches were performed on PAUP (Swofford, 2002) using 1000 random starting trees and the optimal trees of Poe (2004) as starting trees. Tree-bisection-reconnection branch swapping was used to find optimal trees.

I mapped each ecomorph character onto the resulting best estimate and obtained the parsimony length under Wagner optimization. This length is a measure of the correlation of the character with the phylogeny (Kluge and Farris, 1969). Shorter length means fewer evolutionary transitions and thus stronger correlation. In order to assess whether this correlation is statistically significant, I created 99 data sets with states of each ecomorph character randomized between species and tallied the lengths for each randomized data set for each character (Maddison and Slatkin, 1991). If the length of the tested ecomorph character on the phylogeny is less than (e.g., 95% of) the lengths of that character in the randomized data sets, the null hypothesis of no association between that character and phylogeny is rejected.

I performed the above test using two samples of taxa. The first sample included all 174 taxa. The second sample included only those taxa found in the Greater Antilles, where ecomorphs have been shown to be convergent (Losos et al., 1998).

Results

The optimal phylogenetic tree had length 16861474, Consistency Index (Kluge and Farris, 1969) 0.21,

Table 1. Phylogenetic codes for ecomorph characters

Species	SVL,FL,TL,SDL	Species	SVL,FL,TL,SDL
"C." <i>chamaeleonides</i>	yjhr	<i>longiceps</i>	mnvz
"C." <i>barbouri</i>	dtxa	<i>longitibialis</i>	kxvi
"P." <i>heterodermus</i>	lfhq	<i>loveridgei</i>	susp
"P." <i>nicefori</i>	i?mq	<i>loysianus</i>	bnau
<i>acutus</i>	jrpv	<i>luciae</i>	orpt
<i>aeneus</i>	lnpu	<i>lucius</i>	jvsy
<i>aequatorialis</i>	owzp	<i>luteogularis</i>	zosity
<i>agassizi</i>	tvsw	<i>luteosignifer</i>	grmq
<i>ahli</i>	html	<i>maculiventris</i>	dspq
<i>aliniger</i>	hnpx	<i>marcanoi</i>	hvsr
<i>allisoni</i>	onsx	<i>mariarum</i>	fpsn
<i>allogus</i>	ivpk	<i>marmoratus</i>	mrpu
<i>altae</i>	coso	<i>maynardi</i>	lnpy
<i>altavelensis</i>	fsmt	<i>megapholidotus</i>	fopl
<i>alutaceus</i>	arvv	<i>meridionalis</i>	hnsh
<i>angusticeps</i>	fhmt	<i>mestrei</i>	gpho
<i>antonii</i>	grso	<i>microlepidotus</i>	cnpo
<i>apollinaris</i>	qtzr	<i>microtus</i>	smvj
<i>aquaticus</i>	kwph	<i>monticola</i>	gwwq
<i>argenteolus</i>	gtsy	<i>nebuloides</i>	fs?m
<i>argillaceus</i>	empt	<i>nebulosus</i>	domi
<i>armouri</i>	jsml	<i>nitens</i>	lysi
<i>auratus</i>	fnzl	<i>noblei</i>	zqvu
<i>bahorucoensis</i>	fsvt	<i>notopholis</i>	evsi
<i>baleatus</i>	yqpo	<i>nubilis</i>	mtsy
<i>barahonae</i>	wpst	<i>occultus</i>	ceat
<i>barkeri</i>	pqpj	<i>oculatus</i>	ossq
<i>bartschi</i>	lwvw	<i>olssoni</i>	eoze
<i>bimaculatus</i>	ssps	<i>onca</i>	oqp?
<i>biporcatus</i>	ppvl	<i>opalinus</i>	gopv
<i>bitectus</i>	fvpj	<i>ophiolepis</i>	bkpq
<i>bonairensis</i>	krpy	<i>ortoni</i>	hopp
<i>brevirostris</i>	fthp	<i>oxylophus</i>	ltph
<i>brunneus</i>	lnsq	<i>parvicirculatus</i>	eypq
<i>capito</i>	oxpf	<i>paternus</i>	ekms
<i>carolinensis</i>	kmpv	<i>pentaprion</i>	llhp
<i>chloris</i>	ippo	<i>perracae</i>	fopn
<i>chlorocyanus</i>	mmsz	<i>petersi</i>	srxq
<i>christophei</i>	etmw	<i>placidus</i>	ddaq
<i>clivicola</i>	etvq	<i>poecilopus</i>	kwpl
<i>cobanensis</i>	hvsn	<i>polylepis</i>	gtpk
<i>coelestinus</i>	mnsj	<i>poncencis</i>	envq
<i>compressicauda</i>	fvpl	<i>porcatus</i>	llsz
<i>conspersus</i>	jqpu	<i>proboscis</i>	khmo
<i>crassulus</i>	fqsj	<i>pulchellus</i>	fovs
<i>cristatellus</i>	mtsn	<i>punctatus</i>	novv
<i>cupreus</i>	gssk	<i>quadriocellifer</i>	gqmo
<i>cuprinus</i>	jvsi	<i>reconditus</i>	pvsj
<i>cuvieri</i>	uust	<i>richardi</i>	ussk
<i>cyanopleurus</i>	cxrx	<i>ricordi</i>	wqpr
<i>cybotes</i>	mupl	<i>roosevelti</i>	wvst
<i>darlingtoni</i>	lkhr	<i>roquet</i>	nppu
<i>desechensis</i>	gtpy	<i>rubribarbus</i>	itmm
<i>distichus</i>	huhp	<i>ruizi</i>	glsr
<i>dollfusianus</i>	cspj	<i>sagrei</i>	jppo
<i>dunni</i>	hrsn	<i>semilineatus</i>	drzv
<i>equestris</i>	zosl	<i>sericeus</i>	fovl

Table 1. (continued)

Species	SVL,FL,TL,SDL	Species	SVL,FL,TL,SDL
<i>etheridgei</i>	czxw	<i>sheplani</i>	baau
<i>evermanni</i>	lrmv	<i>shrevei</i>	htpn
<i>fasciata</i>	kssr	<i>smallwoodi</i>	zosp
<i>fowleri</i>	lsxo	<i>smaragdinus</i>	gmsz
<i>fraseri</i>	qnsl	<i>sminthus</i>	hqsp
<i>frenatus</i>	vtsk	<i>solitarius</i>	flmr
<i>fuscoauratus</i>	drpq	<i>spectrum</i>	cpsp
<i>gadovii</i>	mvpn	<i>squamulatus</i>	osxq
<i>garmani</i>	tqvr	<i>strahmi</i>	mws1
<i>gingivinus</i>	kspr	<i>stratulus</i>	fqmv
<i>grahami</i>	lppw	<i>subocularis</i>	itmi
<i>granuliceps</i>	dwvn	<i>taylori</i>	lspm
<i>griseus</i>	utvp	<i>tolimensis</i>	gqpm
<i>gundlachi</i>	kwpl	<i>townsendi</i>	dtpr
<i>hendersoni</i>	fqzv	<i>transversalis</i>	lppt
<i>homolechis</i>	jghm	<i>trinitatis</i>	komw
<i>humilis</i>	cthk	<i>tropidogaster</i>	gvpk
<i>insignis</i>	xppe	<i>tropidolepis</i>	hvph
<i>insolitus</i>	dkhp	<i>tropidonotus</i>	gtmm
<i>intermedius</i>	fnpp	<i>valencienni</i>	nkhu
<i>isolepis</i>	fkhw	<i>vanidicus</i>	aqqq
<i>jacare</i>	knss	<i>ventrimaculatus</i>	mwxl
<i>jubar</i>	ishq	<i>vermiculatus</i>	ssms
<i>kemptoni</i>	fnsn	<i>vociferans</i>	glhq
<i>krugi</i>	gszv	<i>wattsi</i>	hppr
<i>laeviventris</i>	dlnn	<i>whitemani</i>	jupp
<i>latifrons</i>	uvvj	<i>Anisolepis undulatus</i>	jlv?
<i>leachii</i>	rssv	<i>Enyalius iheringi</i>	?t??
<i>lemurinus</i>	lspk	<i>Leiocephalus melanochlorus</i>	?q??
<i>limifrons</i>	etpn	<i>Leiocephalus schreibersi</i>	?m??
<i>lineatopus</i>	krps	<i>Polychrus acutirostris</i>	saz?
<i>lineatus</i>	kssp	<i>Polychrus marmoratus</i>	tlz?
<i>liogaster</i>	fssn	<i>Urostrophus vautieri</i>	mih?
<i>lividus</i>	mosp		

Earlier letters indicate smaller values. All species are *Anolis* unless otherwise indicated.

Retention Index (Farris, 1989) 0.46. It is very similar topologically to the tree in Poe (2004) and so is not figured here.

Fig. 1 shows the results for tests performed using the entire *Anolis* data set. The null hypothesis of no association with phylogeny is strongly rejected for all four ecomorph characters. For each character, all 99 randomized data sets produced parsimony lengths much greater than the test statistic.

The results are the same for the tests performed using only the Greater Antillean taxa (Fig. 2). All four ecomorph characters show a highly significant association with phylogeny.

Discussion

The ecomorph characters appear to be useful phylogenetic markers. The null hypothesis of no

association with phylogeny was strongly rejected for each ecomorph character, regardless of whether the test included all available species (Fig. 1) or was restricted to the Greater Antillean species for which the ecomorph concept was developed originally (Fig. 2). This latter result is especially surprising. It is not known whether the same sorts of ecomorphs occur on the mainland that occur in the Greater Antilles, let alone whether such ecomorphs evolve convergently there, so it would not be surprising if the ecomorph characters accurately track phylogeny in these species. But the presence of a strong phylogenetic correlation in the very species for which convergence has been demonstrated begs for explanation.

Given the demonstrated convergence of ecomorphs, why would the ecomorph characters be good phylogenetic markers? One possible reason is that the ecomorphs generally constitute mini-radiations within islands. For example, Hispaniola has three crown-giant

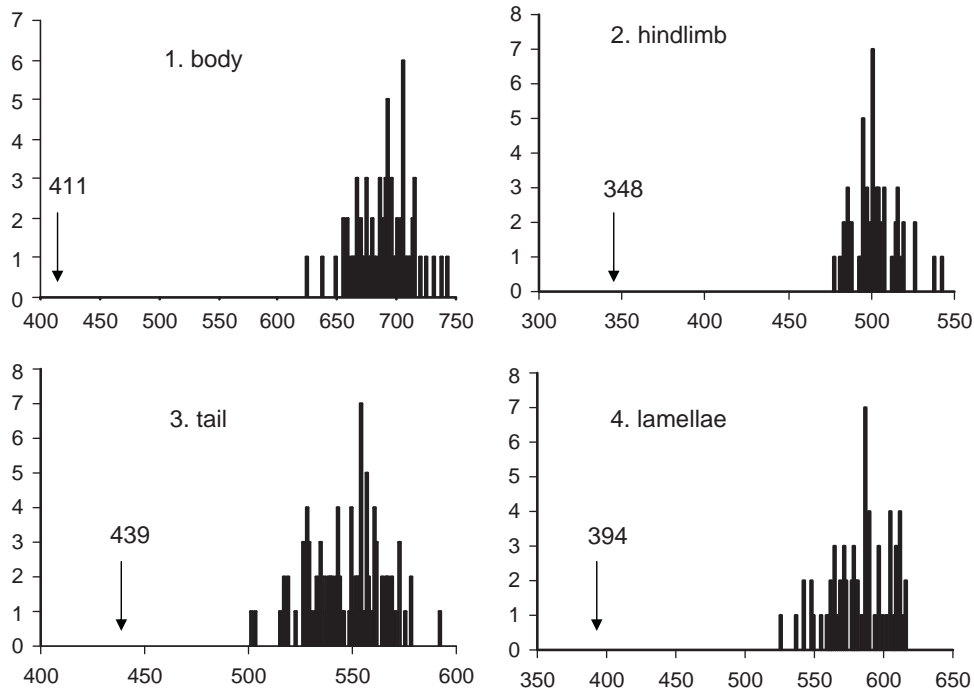


Fig. 1. Frequency distribution of randomized states for ecomorph characters on phylogeny, all taxa included. Test statistic is much lower than distribution for each character, indicating a significant phylogenetic signal.

species (*A. ricordi*, *A. barahonae*, *A. baleatus*) that almost certainly form a clade (Schwartz, 1974; Burnell and Hedges, 1990; Poe, 2004). Although there is convergence in crown-giant characters between these

species and, for example, Jamaican *Anolis garmani*, the crown-giant characters are good phylogenetic markers within Hispaniola. A second possible reason the ecomorph characters track phylogeny is the existence

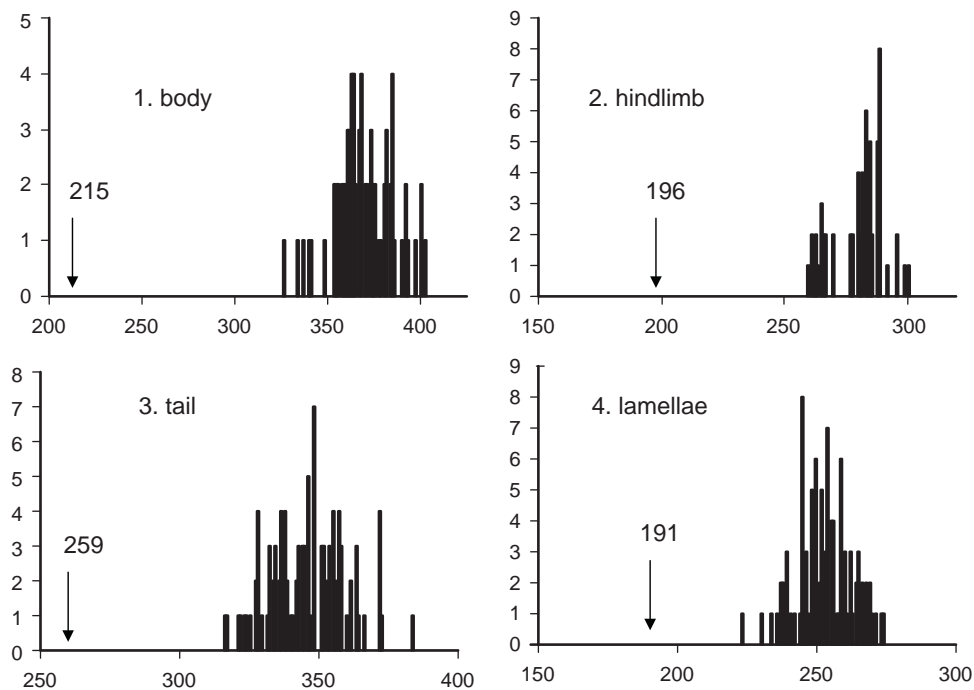


Fig. 2. Frequency distribution of randomized states for ecomorph characters on phylogeny, including only Greater Antillean taxa. Test statistic is much lower than distribution for each character, indicating a significant phylogenetic signal.

of several species that defy ecomorph characterization or occupy different ecomorphs but still share derived ecomorph characters and close relationship. For example, Cuban *A. bartschi* lives on rock cliffs and is sister species to the aquatic Cuban anole *A. vermiculatus* (Williams, 1976; Jackman et al., 1999; Poe, 2004). These two species are not members of any traditionally recognized ecomorph category and clearly occupy different niches, yet they share the condition of extremely long hindlimbs. Finally, some ecomorphs appear to be monophyletic across islands. For example, Puerto Rican crown giant *A. cuvieri* is more closely related to the crown giants on Hispaniola than to the other ecomorphs on Puerto Rico. In this case, ecomorph characters are a better predictor of phylogeny than island locality.

The specific message from the results presented here is clear: the ecomorph characters are adequate phylogenetic markers for *Anolis* lizards, in spite of correlated convergence in some cases in the Greater Antilles.

Are there any general rules to be gleaned from these results? Perhaps the message is that we should be careful in condemning any class of characters by virtue of argument by analogy. That is, the fact that a certain group of characters appears unreliable in a particular case does not necessarily mean that said characters are unreliable generally. Many molecular systematists have long recognized this fact in reference to particular gene regions. For example, the mitochondrial gene cytochrome-*b* appears useful for resolving recent but not ancient relationships of birds (Moore and DeFilippis, 1997). Likewise, viviparity has evolved multiple times within Squamata, but appears to be a reliable character within mammals. The complexity of evolution may dictate that we constantly should be evaluating the phylogenetic utility of characters on a case-by-case basis.

Acknowledgements

This paper is dedicated to Marvalee Wake. I thank her for guidance, scientific advice, and friendship during my postdoctoral tenure at Berkeley and afterwards. Thanks to Jim Mc Guire and Jonathan Losos for comments on the paper.

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