

ECOMORPHOLOGY, PERFORMANCE CAPABILITY, AND SCALING OF WEST INDIAN *ANOLIS* LIZARDS: AN EVOLUTIONARY ANALYSIS¹

JONATHAN B. LOSOS

*Museum of Vertebrate Zoology and Department of Zoology, University of California,
Berkeley, California 94720 USA*

Abstract. Studies of ecomorphology—the relationship among species between morphology and ecology—contain two implicit and rarely tested hypotheses: (1) that morphological differences among species result in differences in performance capability at ecologically relevant tasks, which, in turn, produce differences in behavior and ecology; and (2) that morphology, performance capability, ecology and behavior have evolved synchronously. I tested these hypotheses using the *Anolis* lizards of Jamaica and Puerto Rico. I measured morphological and performance variables on recently caught lizards. Movement, display rate and microhabitat measurements were made on lizards observed in the field.

Body size explained most of the variation in morphology and performance ability, but was not correlated with the ecological or behavioral variables. When the effect of body size is removed from the morphological and performance variables, the ecomorphological hypotheses were confirmed. Species that were similar morphologically were also similar in performance ability, ecology, and behavior. Evolutionary changes in morphology, performance, and ecology and behavior (ecobehavior) were correlated. The morphology–ecobehavior comparison revealed that: long-legged, heavy-bodied lizards jump farther in nature, jump and display more often, walk less often, and use wide perches that are distant from the nearest available perches; and that species with many subdigital lamellae perch lower, use narrower supports, and walk more frequently. Inclusion of performance parameters revealed a relationship, in agreement with biomechanical models, between body proportions and running and jumping capability; in turn, performance capability related to locomotor patterns and microhabitat use. Despite the relationship between lamellae number and ecobehavioral variables, clinging performance did not contribute to the correlations with either morphology or ecology.

Key words: adaptation; *Anolis*; ecomorphology; lizards; performance; scaling; size.

INTRODUCTION

That much can be inferred about the ecology of an organism from its morphology is axiomatic in biology; e.g., aquatic animals have flippers, diggers have powerful limbs and claws, flying organisms have wings. Williams (1972) and Karr and James (1975) independently coined the term ecomorphology for the relationship between more subtle aspects of morphology, ecology, and behavior. Numerous subsequent studies have shown correlations between morphology and aspects of ecology and/or behavior among members of a community (e.g., Gatz 1979, Ricklefs et al. 1981, Findley and Black 1983, Miles and Ricklefs 1984, Niemi 1985, McKenzie and Rolfe 1986, Pianka 1986, Aldridge and Rautenbach 1987, Scheibe 1987, Crome and Richards 1988, Kappelman 1988, Voss 1988). This approach has been criticized, however (e.g., Wiens and Rotenberry 1980, Lederer 1984, Wiens 1984), and several studies have failed to discover a relationship between morphology and ecology (Wiens and Rotenberry

1980, MacNally and Doolan 1986). Two problems are crucial:

1) Ecomorphological hypotheses must assume that differences in morphology translate into differences in performance capability, which, in turn, result in differences in ecology or behavior. Recent advances in the ability to measure the performance capability of small vertebrates at ecologically relevant tasks provide an opportunity, heretofore unexploited, to rigorously quantify ecomorphological relationships. Few studies, however, have quantified the interspecific relationship between morphology and performance capability (e.g., Zug 1972, Zug and Altig 1978, Emerson and Diehl 1980, Alberch 1981, Green 1981), and rarely have such studies been coupled with field studies to thoroughly investigate ecomorphological hypotheses (e.g., Grant 1986, Wainwright 1988), an approach originally proposed by Bock and von Wahlert (1965) and reiterated by Huey and Bennett (1986).

2) As a corollary, ecomorphological hypotheses imply that the evolution of morphology and of performance capability are tightly linked. Increasingly, ecologists are realizing that evolutionary history can be a major factor determining present-day patterns and that

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BACKGROUND INFORMATION ON *ANOLIS*

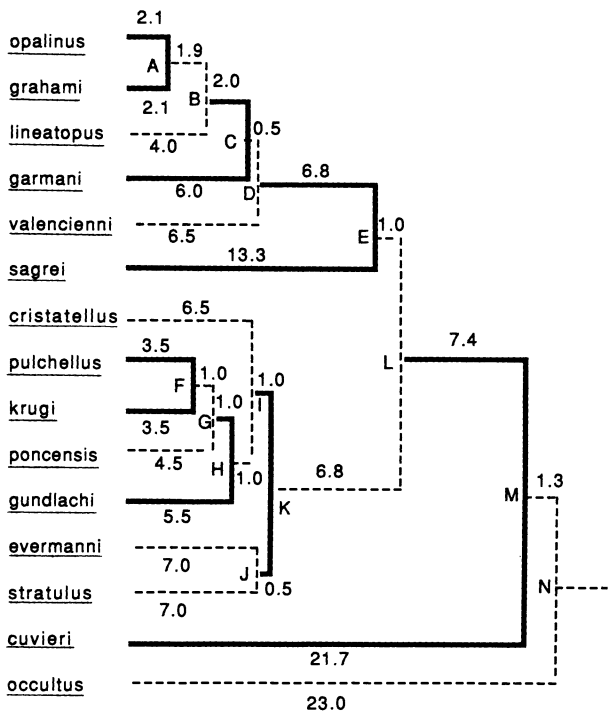


FIG. 1. Phylogenetic relationships among Jamaican and Puerto Rican *Anolis*. The top six species are from Jamaica; the remainder are from Puerto Rico. This phylogeny is not meant to imply that the Jamaican and Puerto Rican anole radiations are sister taxa or monophyletic in the strict sense of including all descendant taxa. Numbers represent the relative length of each branch. The 13 independent contrasts are indicated by the line type (— — — or ———).

phylogenetic information must be incorporated to interpret them (Harvey and Mace 1982, Ridley 1983, Clutton-Brock and Harvey 1984, Cheverud et al. 1985, Gittleman 1985, 1986a, b, Huey 1987). Indeed, to the extent that species share similar attributes due to recent common ancestry, they do not constitute independent points for statistical analysis (Clutton-Brock and Harvey 1984). A phylogenetic approach can circumvent this difficulty (Felsenstein 1985a, 1988). By analyzing morphology, performance capability, and relevant ecological and behavioral parameters in a phylogenetic context, one can determine whether the evolution of morphology and performance are linked and, if so, whether their evolution might have occurred adaptively with regard to ecology and behavior (Greene 1986, Schaefer and Lauder 1986, Huey and Bennett 1987, Donoghue 1989, Wainwright and Lauder, *in press*).

An appropriate evolutionary ecomorphological analysis requires a group that has radiated extensively, producing species that differ in morphology, ecology, and behavior; that is amenable to behavioral and ecological field studies; and for which the phylogenetic relationships are relatively well understood. The *Anolis* lizards of Jamaica and Puerto Rico meet these requirements.

Nearly 300 species of *Anolis* have been described, 122 of which occur on Caribbean islands (Henderson and Schwartz 1984, Schwartz and Henderson 1985). Anoles have radiated extensively in the Greater Antilles, producing 6 species (plus one recent colonist) in Jamaica, 11 in Puerto Rico, and ≈ 40 each in Hispaniola and Cuba (Williams 1972, Henderson and Schwartz 1984, Schwartz and Henderson 1985). Here I report studies on the anoles of Jamaica and Puerto Rico, the phylogenetic relationships of which are reasonably well understood (Underwood and Williams 1959, Williams 1972, Gorman et al. 1980a, b, 1983, Wyles and Gorman 1980, Shochat and Dessauer 1981; Fig. 1).

For the most part, intra-island differentiation has proceeded independently on the Greater Antillean islands, producing species that differ morphologically; they are termed "ecomorphs" and named for the microhabitat they usually occupy (grass-bush, trunk-ground, trunk, trunk-crown, crown giant, and twig [Williams 1972, 1983]). Inter-island comparisons reveal that the same set of ecomorphs has evolved repeatedly (Williams 1972, 1983, Mayer 1989). Furthermore, these morphologically convergent species also appear to have converged in behavior and ecology (Williams 1972, 1983, Losos 1990). Mayer (1989) has confirmed that ecologically similar species cluster together in a multidimensional morphospace defined by limb proportions and number of subdigital lamella (see also below).

These previous studies provide the ecomorphological hypotheses I tested: they predict that morphologically similar species should have similar performance capabilities; species with similar abilities, in turn, should be similar in ecology and behavior. The null hypothesis is that the morphological grouping of species bears no relationship to groupings based on either performance capability or ecology and behavior.

In addition, my analysis provides a test of the hypothesis (Peters 1983, Calder 1984) that body size is the most important factor accounting for interspecific variation. With several exceptions, species in the same ecomorph category are similar in size (Williams 1983). Consequently, I investigated to what extent size and shape account for variation in and explain correlations among morphology, performance ability, and ecology and behavior among species.

MATERIALS AND METHODS

Field studies

Field studies were conducted during the summer of 1987 and 1988 in Jamaica and Puerto Rico. Localities are listed in Appendix 1. Ecological data were collected during "Rand censuses" (Rand 1964, 1967, Schoener and Schoener 1971a, b); for each lizard sighted, the observer noted its species, perch (tree, ground, etc.), height above the ground, perch diameter,

distance to the closest perch in the following three diameter categories: (1) 0.2–1.0 cm; (2) 1.0–1.5 cm; and (3) ≥ 1.5 cm. A compound index of the distance to the nearest available perch (modified from Pounds 1988) was calculated for each species as

$$D_k = \sum_{i=1}^3 P_i D_i$$

where i = perch diameter category, P_i = the proportion of all lizards observed using that category, and D_i = the mean distance to perches of that category. At each locality, paths were selected to sample all habitats available. Only animals that were spotted before they fled were included.

Behavioral focal samples were conducted following Moermond (1979a, b) and Pounds (1988). Each lizard was watched from a distance of 2–10 m. Lizards were observed for 20 min or until they disappeared. All movements were noted (walk, run, or jump); the distance of all jumps was measured, when possible, or estimated at the conclusion of each session. Jumps in which the lizard descended ≥ 28 cm were excluded because they inflate the horizontal distance of the jump (28 cm was selected to standardize with the jumping performance measures described below). The amount of time spent displaying (bobbing and/or dewlapping) was recorded with a stopwatch, and was recorded as the proportion of total time observed. Only animals that made ≥ 5 moves were included in the analyses below because animals that made fewer moves may have been disturbed by the observer. Movement and display rates were calculated only for individuals observed for ≥ 5 min. Including animals that disappeared quickly would have artificially inflated movement rates because their periods of inactivity were not observed (in any case, analyses using all individuals did not differ qualitatively). Observations were not conducted during inclement weather or early in the morning or late in the afternoon, when lizards may not have been able to thermoregulate at preferred temperatures.

Performance and morphological measurements

I measured performance capability at the following three tasks:

1) Running—lizards were placed at the lower end of a 2.25 m race track covered with a rough rubber surface and angled up at 37° (anoles placed on flat surfaces tend to hop [van Berkum 1986, J. B. Losos, *personal observation*]), and were induced to run by repeated taps to the tail (protocol following Huey [1982], Garland [1985], van Berkum [1986], Losos et al. [1989]). As the lizard ran, it interrupted light beams stationed every 0.25 m. The time elapsed during each interval was computed by a Compaq portable computer; the fastest single interval during five trials, conducted at hourly intervals, was considered the maximum speed for that

lizard (sprinting ability is measured as time elapsed, not rate of travel).

2) Jumping distance—lizards were placed on a flat board covered with a rough rubber surface 28 cm above the floor and induced to jump by a tap to the tail. This procedure was repeated twice at hourly intervals, and the longest jump was considered the maximum for each individual.

3) Sticking ability—lizards were placed on a flat smooth plate of plexiglass with a noose around their waist connected to a Pesola spring scale calibrated in grams. The scale was gradually pulled backward. The lizard began sliding backward as the force exerted approached the lizard's maximum sticking ability. The point at which the lizard moved backward at the same rate as the scale, resulting in no increase in the force measured on the scale, was considered maximum sticking ability. This procedure was repeated twice in rapid succession. The data were converted to newtons (1 "gram force" = 9.80665 mN).

Most performance measurements were conducted at the field site within 2 d of capture. *Anolis poncensis* was transported to the El Verde Field Station and tested within 3 d of capture. In 1987, Jamaican anoles were returned to Berkeley for sprint-speed measurements, maintained at appropriate temperatures with food and water supplied ad libitum, and tested within 3 wk of capture. In 1988, they were transported to the El Verde Field Station and tested within 1 wk of capture. In most cases, jumping and sticking ability were measured on the 1st d and sprint speed on the 2nd d. All performance measurements were conducted at a body temperature of 30°C , which is at or near the optimal temperature for performance for these species (Huey and Webster 1976, Huey 1983, van Berkum 1986, R. B. Huey, *personal communication*). Trials in which the lizards performed sub-optimally, as recognized by jump posture and trajectory, running gait, and clinging posture (lizards clinging maximally had all four legs completely stretched forward), were excluded. Lizards with only one acceptable sprint trial were not included in the sprint-speed calculations. Neither the jumping nor clinging calculations included animals with no acceptable trials.

The following morphological measurements were taken on all animals utilized: snout–vent length (svl), mass, foreleg and hindleg length (from the tip of the most distal toe on the right side of the body to the insertion of the limb in the body wall), and tail length (excluding individuals with regenerated tails). Sub-digital lamella number for the fourth toe on the hind foot of each species was taken from Mayer (1989). Although geographical or temporal variation may exist between Mayer's animals and mine, these differences are probably relatively minor compared to interspecific differences (Mayer 1989).

Previous discussion of ecomorphological differences among *Anolis* have focused on adult males (Rand and

TABLE 1. Morphological, performance, and ecobehavioral data* for *Anolis* spp. Data are mean values \pm 1 SE for all individuals of a species.

	Morphological measurements†					
	Snout-vent length (mm)	Mass (g)	Foreleg (mm)	Hindleg (mm)	Tail (mm)	Lamella number
<i>cristatellus</i>	63.8 \pm 0.58	8.1 \pm 0.26	32.1 \pm 0.26	53.8 \pm 0.42	114.6 \pm 2.21	19.6
<i>cuvieri</i>	127.0 \pm 3.30	44.5 \pm 3.98	59.7 \pm 1.62	95.5 \pm 2.24	275.5 \pm 9.15	30.1
<i>evermanni</i>	62.3 \pm 0.63	5.6 \pm 0.28	30.9 \pm 0.25	47.9 \pm 0.42	109.6 \pm 1.34	25.8
<i>gundlachi</i>	65.1 \pm 0.49	7.1 \pm 0.18	33.2 \pm 0.22	57.6 \pm 0.45	122.2 \pm 2.41	17.5
<i>krugi</i>	48.6 \pm 0.45	2.4 \pm 0.09	21.1 \pm 0.24	38.9 \pm 0.38	128.3 \pm 2.40	19.5
<i>occultus</i>	38.1 \pm 0.50	0.5 \pm 0.04	10.9 \pm 0.17	16.5 \pm 0.22	39.1 \pm 1.70	18.0
<i>poncensis</i>	43.9 \pm 0.52	1.6 \pm 0.08	17.2 \pm 0.22	31.2 \pm 0.33	112.1 \pm 1.48	17.1
<i>pulchellus</i>	43.6 \pm 0.34	1.5 \pm 0.04	17.6 \pm 0.17	32.5 \pm 0.38	113.2 \pm 1.48	17.8
<i>stratulus</i>	44.5 \pm 0.46	1.9 \pm 0.10	21.5 \pm 0.19	32.8 \pm 0.30	71.7 \pm 1.23	19.0
<i>garmani</i>	109.3 \pm 1.50	31.7 \pm 1.50	47.4 \pm 0.65	80.0 \pm 1.52	216.7 \pm 3.23	28.4
<i>grahami</i>	61.6 \pm 0.93	6.2 \pm 0.23	28.4 \pm 0.43	45.6 \pm 0.80	108.3 \pm 3.80	25.9
<i>lineatopus</i>	57.2 \pm 0.51	4.6 \pm 0.51	26.7 \pm 0.25	46.1 \pm 0.40	107.6 \pm 1.95	18.4
<i>opalinus</i>	47.7 \pm 0.47	2.1 \pm 0.08	22.3 \pm 0.25	34.1 \pm 0.38	78.7 \pm 3.23	21.2
<i>sagrei</i>	48.8 \pm 0.48	2.9 \pm 0.09	21.2 \pm 0.21	36.2 \pm 0.32	94.9 \pm 2.63	18.1
<i>valencienni</i>	72.1 \pm 1.69	6.8 \pm 0.73	26.0 \pm 0.98	38.5 \pm 0.76	90.5 \pm 4.04	22.6

	Performance measurements‡			Ecological measurements§		
	Sprint (s)	Jump (cm)	Cling (N)	Height (m)	Diameter (cm)	Nearest perch (cm)
<i>cristatellus</i>	0.116 \pm 0.002	84.9 \pm 1.43	2.837 \pm 0.335	1.2 \pm 0.06	13.3 \pm 3.41	52.8
<i>cuvieri</i>	0.114 \pm 0.006	73.5 \pm 4.20	14.857 \pm 0.485
<i>evermanni</i>	0.137 \pm 0.003	67.0 \pm 1.70	3.148 \pm 0.223	3.4 \pm 0.87	35.3 \pm 5.69	51.7
<i>gundlachi</i>	0.116 \pm 0.002	81.4 \pm 1.89	2.305 \pm 0.228	1.3 \pm 0.08	33.5 \pm 5.35	59.5
<i>krugi</i>	0.140 \pm 0.003	67.8 \pm 1.07	2.162 \pm 0.122	0.6 \pm 0.08	5.7 \pm 1.74	28.1
<i>occultus</i>	...	27.7 \pm 1.46	0.834 \pm 0.159
<i>poncensis</i>	0.142 \pm 0.003	60.9 \pm 1.36	1.312 \pm 0.124	0.9 \pm 0.16	3.6 \pm 0.36	45.8
<i>pulchellus</i>	0.147 \pm 0.007	57.9 \pm 1.40	1.463 \pm 0.147	0.3 \pm 0.03	1.4 \pm 0.29	11.8
<i>stratulus</i>	0.168 \pm 0.007	55.1 \pm 1.83	1.471 \pm 0.119	7.0 \pm 1.38	9.4 \pm 1.91	50.1
<i>garmani</i>	0.101 \pm 0.003	97.0 \pm 2.73	13.484 \pm 1.728	3.5 \pm 0.35	33.2 \pm 4.59	44.1
<i>grahami</i>	0.129 \pm 0.005	74.3 \pm 2.40	2.344 \pm 0.200	2.5 \pm 0.29	17.7 \pm 3.94	28.8
<i>lineatopus</i>	0.123 \pm 0.002	75.7 \pm 2.53	1.876 \pm 0.244	1.0 \pm 0.07	26.0 \pm 4.78	34.5
<i>opalinus</i>	0.142 \pm 0.003	55.5 \pm 1.62	1.275 \pm 0.165	1.4 \pm 0.09	24.2 \pm 6.58	37.5
<i>sagrei</i>	0.138 \pm 0.004	61.6 \pm 1.29	1.136 \pm 0.132	0.4 \pm 0.09	15.4 \pm 3.45	38.4
<i>valencienni</i>	0.153 \pm 0.004	56.6 \pm 1.52	3.102 \pm 0.210	2.3 \pm 0.41	6.0 \pm 2.01	26.4

	Behavioral measurements¶					
	Display rate	% walks	% runs	% jumps	Moves/min	Distance jumped in nature
<i>cristatellus</i>	0.043 \pm 0.008	0.271 \pm 0.059	0.583 \pm 0.063	0.146 \pm 0.02	1.10 \pm 0.11	45.7 \pm 6.1
<i>cuvieri</i>
<i>evermanni</i>	0.056 \pm 0.010	0.536 \pm 0.043	0.319 \pm 0.046	0.146 \pm 0.02	1.27 \pm 0.12	39.3 \pm 3.9
<i>gundlachi</i>	0.055 \pm 0.010	0.339 \pm 0.052	0.429 \pm 0.042	0.231 \pm 0.02	0.73 \pm 0.08	36.4 \pm 4.0
<i>krugi</i>	0.040 \pm 0.008	0.496 \pm 0.053	0.258 \pm 0.060	0.247 \pm 0.03	0.84 \pm 0.10	28.2 \pm 3.2
<i>occultus</i>
<i>poncensis</i>	0.012 \pm 0.004	0.435 \pm 0.072	0.376 \pm 0.054	0.189 \pm 0.05	0.58 \pm 0.12	32.0 \pm 5.2
<i>pulchellus</i>	0.033 \pm 0.008	0.610 \pm 0.047	0.191 \pm 0.038	0.200 \pm 0.02	0.99 \pm 0.13	19.3 \pm 4.1
<i>stratulus</i>	0.083 \pm 0.017	0.348 \pm 0.060	0.553 \pm 0.062	0.099 \pm 0.02	1.84 \pm 0.27	31.3 \pm 4.7
<i>garmani</i>	0.054 \pm 0.013	0.451 \pm 0.069	0.454 \pm 0.075	0.095 \pm 0.02	0.81 \pm 0.08	50.8 \pm 6.9
<i>grahami</i>	0.097 \pm 0.020	0.315 \pm 0.047	0.493 \pm 0.043	0.192 \pm 0.02	1.74 \pm 0.26	41.0 \pm 4.6
<i>lineatopus</i>	0.031 \pm 0.007	0.153 \pm 0.034	0.575 \pm 0.046	0.273 \pm 0.03	0.82 \pm 0.09	35.8 \pm 3.6
<i>opalinus</i>	0.078 \pm 0.013	0.198 \pm 0.036	0.696 \pm 0.038	0.106 \pm 0.02	1.74 \pm 0.19	30.3 \pm 4.7
<i>sagrei</i>	0.100 \pm 0.019	0.185 \pm 0.046	0.558 \pm 0.045	0.256 \pm 0.03	0.90 \pm 0.13	28.3 \pm 2.6
<i>valencienni</i>	0.015 \pm 0.007	0.719 \pm 0.049	0.166 \pm 0.041	0.114 \pm 0.01	1.55 \pm 0.16	28.8 \pm 7.5

* Some of these data have also been presented elsewhere (Losos, *in press a, b*).

† All morphological measurements were made on a minimum of 20 specimens, except for *cuvieri* (6), *occultus* (11), and *poncensis* (16). Tail measurements exclude specimens with regenerated tails. Lamella number is from Mayer (1989), based on specimens primarily from the same sites as the specimens I used.

‡ All performance measurements were made on a minimum of 15 specimens, except for *cuvieri* (6) and *occultus* (11). Among the performance measurements, sprint speed is the fastest time over a 0.25-m interval, not the rate of travel when crossing that distance.

§ All ecological measurements were based on a minimum of 40 individuals per species except for *poncensis* (18). Nearest perch is the statistic D_k (modified from Pounds [1988]), which is a weighted average of the proportion of time a lizard uses a perch size class multiplied by the average distance of perches of that class (see text).

Williams 1969, Williams 1972, 1983). Considerable sexual dimorphism exists in most species for both size and body proportions (J. B. Losos, *personal observation*); interspecific differences among females are much less pronounced than among males. Consequently, only relatively large adult males are used in all analyses (with the exception of two relatively rare species, *A. cuvieri* and *A. occultus*, for which adult females were included as well. Excluding those females does not qualitatively alter the results.). Using only large adults also avoids the confounding effect of intraspecific allometric variation.

Statistical analysis

The mean value of each variable for each species is used in subsequent analyses (Table 1). Principal components analyses based on correlation matrices were performed separately on the morphological, performance, and ecobehavioral (i.e., ecological and behavioral) variables to reduce the dimensionality of the data. All variables were ln-transformed except display rate and the proportion of all moves that were walks, runs, and jumps, which were arcsine-transformed. All morphological and performance variables scaled allometrically with body size. Two sets of analyses were conducted. In the first set, unadjusted data were used. Almost all of the variation in the morphological and performance variables was explained on the first principal component axis, which could readily be interpreted as an indicator of overall size; little variation remained to be explained by body shape. To assess the importance of shape, in the second set of analyses, the effect of size on all morphological and performance variables was removed by using the residuals of each of these variables regressed on svl (I use svl as a proxy variable for body size because, among species, all morphological and performance variables are highly correlated with svl [Losos, *in press*; J. B. Losos, *unpublished manuscript*]; the transformations produce svl-allometry free shape variables [sensu Bookstein 1989]). Of the ecological and behavioral variables, only maximum jump distance displayed a significant relationship with body size; consequently, no adjustment was needed for this data set. To maintain its comparability to the other ecological and behavioral variables, the residual value for maximum jump distance in nature was not used.

Canonical correlation analysis was used to assess the degree of similarity of the position of species in morphological, performance, and ecobehavioral space. The use of canonical correlation in ecomorphological stud-

ies is explained in detail in Miles and Ricklefs (1984) and Miles et al. (1987); I have followed their methodology exactly. In essence, canonical correlation rotates a space encompassing the coordinates for species based on one set of data (e.g., morphology) to maximize the correlation with the corresponding coordinates in a space based on a second set (e.g., performance; Miles and Ricklefs 1984). The null hypothesis that the i^{th} correlation axis and all that follow are zero can be tested using Bartlett's approximation of Wilks' λ , which has a χ^2 distribution (Miles and Ricklefs 1984). Note that the formula for calculation of Bartlett's approximation in Miles and Ricklefs (1984) should read: $\chi^2 = -[(N - 1) - (p + q + 1)/2] \ln \Lambda$, where the Wilks' likelihood ratio $\Lambda = \prod_{k=1}^s (1 - r_k^2)$, N is the number of species, p and q are the number of variables in the two data sets, r_k is the k^{th} canonical correlation, and the value for χ^2 has $(p + 1 - i)(q + 1 - i)$ degrees of freedom (D. B. Miles, *personal communication*). Canonical correlation analysis is a conservative test, particularly when the number of variables approaches the number of species (Miles and Ricklefs 1984, D. B. Miles, *personal communication*). To reduce the number of variables, principal components scores for each species, rather than the original variables, were used in the canonical correlation analyses (Miles and Ricklefs 1984).

Phylogenetic analysis

The comparative approach, as its name implies, is based on comparing whether variation in two characters of interest is associated among species. Because species are linked by a network of shared ancestry, however, species may be similar in a character or characters solely because these characters have been inherited from a common ancestor. Because character states among species are consequently not independent, statistical analyses based on among-species comparisons are invalid (Felsenstein 1985a, 1988).

To circumvent this difficulty, two methods—the ancestor reconstruction approach and the contrast approach—have been advanced recently (they are discussed in detail in Appendix 2). These methods have the added advantage that they explicitly test the hypothesis implicit in the comparative approach, i.e., that two characters have evolved synchronously. Evolutionary conclusions cannot be drawn from analyses that do not incorporate phylogenetic information.

To assess the degree to which variables (in this case, scores on principal components axes) have evolved

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|| Cling forces were measured with a spring scale calibrated in grams. Statistical analyses were based on the raw ("gram-force") values, rather than the converted (newton) values. 1 "gram-force" = 9.80665 mN.

¶ All behavioral measurements were made on a minimum of 28 individuals for Puerto Rican species, with the exception of *poncensis* (18), and 18 individuals for Jamaican species. Display rate is the mean proportion of time spent displaying. % walks, runs, and jumps are relative to total number of movements.

synchronously, the ancestor reconstruction method estimates the values of the variables for all hypothetical ancestral taxa (the nodes on the phylogeny labeled with letters in Fig. 1). Then, by comparing the value for a trait in an ancestor and in a descendant, one can determine the magnitude and direction the trait evolved along that branch of the tree. When the amount of change is calculated for all ancestor–descendant pairs of taxa for all variables, one can determine to what extent evolutionary change in one set (e.g., morphology variables) is associated with evolutionary change in another (e.g., performance variables [Huey and Bennett 1987]).

I calculated the amount of evolutionary change in the value for all principal component axes along all 26 branches of the phylogeny in Fig. 1 (see Appendix 2 for details of calculations) and used these values in subsequent canonical correlation analyses. Statistical inferences based on these analyses must be received cautiously, however, because (see Appendix 2 for further discussion): (1) change partitioned along one branch of the phylogenetic tree is not independent of change on other branches; and (2) from n species, the algorithm generates information on $2N - 1$ taxa (hypothetical and extant) and $2N - 2$ ancestor–descendant pairs of taxa (Huey 1987, Felsenstein 1988, Martins and Garland, *in press*). To avoid inflating the sample size in the canonical correlation analyses, I used the number of extant species, rather than the number of ancestor–descendant pairs of taxa, as the sample size, N .

Felsenstein (1985a; see also Sessions and Larson 1987) developed an algorithm that circumvents these difficulties by calculating independent contrasts for each variable. Starting with sister species, the difference in value for the variable in question is calculated (i.e., the contrast) and the species are removed from the tree. The node on the tree representing their common ancestor is assigned a value which is the mean of the value for each descendant weighted by a function of the length (in time) of the branch leading to it. The contrast between this node and its sister taxa (either an extant species or another internal node of the tree) can similarly be calculated, and so on, producing $N - 1$ contrasts (where N is the number of species; see Appendix 2 for details of calculating and scaling contrasts). Contrasts, identified in Fig. 1, were calculated for each set of principal component axis scores and used in subsequent canonical correlations analyses.

The phylogeny used as the basis for these analyses (Fig. 1) is a composite of several systematic studies. The relationships of the Puerto Rican *crisatellus* group (all Puerto Rican species except *cuvieri* and *occultus*) follow the electrophoretic and karyological analyses of Gorman et al. (1983), which agree closely with Williams' (1972) primarily osteological work. The relationships of the Jamaican anoles are based on osteological (Underwood and Williams 1959) and

immunological (Shochat and Dessauer 1981) studies, which are in close agreement. All studies of these taxa consider *cuvieri* and *occultus* to be relatively primitive. Their positioning relative to each other follows Williams (1972) and Wyles and Gorman (1980).

To calculate contrasts, one needs not only data on extant species and an understanding of their phylogenetic relationships, but also information on the length of the branches in the phylogenetic tree. For the species in this study, enough data are available to allow an estimation of the branch lengths in Fig. 1. These estimates must be treated as extremely tentative because they are drawn by extrapolation from several studies, each on a subset of the species involved. Branch lengths were assigned to a previously derived phylogenetic tree based on immunological (primarily Shochat and Dessauer 1981, also Wyles and Gorman 1980) and electrophoretic (Gorman et al. 1983, B. Hedges, *personal communication*) studies, with the much-debated assumption that the distance values generated are proportional to time-since-divergence. Note that the tree is not a phenogram based on these biochemical studies; rather, estimates of branch lengths have been drawn from these studies and applied to the already established tree topology. Branch lengths were calculated as follows: First, the distances between several species (*cuvieri*, *evermanni*, *crisatellus*, and *valencienni*) were calculated based on immunological studies (Wyles and Gorman 1980, Shochat and Dessauer 1981) using J. Felsenstein's algorithm Kitsch in Phylip version 2.8 (Felsenstein 1985b). These groups are the only ones for which reciprocal immunological crosses have been conducted. Distances of other species to these four were calculated or estimated based on one-way immunological or electrophoretic studies; in the latter case, immunological and electrophoretic distances were calibrated utilizing pairs of species for which both immunological and electrophoretic data are available (Wyles and Gorman [1980] demonstrate that among *Anolis*, electrophoretic and immunological differentiation are tightly correlated). When no suitable information was available, distance was partitioned equally among branches (e.g., in Fig. 1, available data indicate that *pulchellus* and *krugi* are 3.5 units apart, and that the distance from their common ancestor [node F] to node K is 7.5 units. How to partition the remaining 4 units to the four branches between F and K is uncertain; hence, each has been assigned a distance of 1 unit).

I used both evolutionary approaches because of the uncertainty in both the ancestor-reconstruction approach due to non-independence of branch lengths and estimation of $2N - 2$ points from only N original points, and in the contrast approach due to the tentative estimation of branch lengths. One can be confident in relationships determined to be significant by both approaches; how to interpret cases in which they differ is as yet uncertain. In this analysis, most of the discrep-

TABLE 2. Principal component (PC) axis loadings.

a) Morphology (data ln-transformed)			
	PC 1	PC 2	
% variation accounted for	88.1	7.9	
Snout-vent length	0.971	-0.095	
Foreleg length	0.982	0.061	
Hindleg length	0.971	0.205	
Weight	0.988	0.012	
Lamella number	0.807	-0.567	
Tail length	0.898	0.310	
b) Performance (data ln-transformed)			
	PC 1	PC 2	
% variation accounted for	83.6	14.0	
Sprint*	-0.961	0.195	
Jump	0.941	-0.287	
Pull	0.836	0.548	
c) Ecobehavior (data ln- or arcsine-transformed)			
	PC 1	PC 2	PC 3
% variation accounted for	44.6	24.3	16.5
Moves/min	0.307	-0.594	-0.683
Jump	-0.333	0.829	0.054
Walk	-0.633	-0.687	0.250
Run	0.806	0.395	-0.259
Display	0.624	0.136	-0.614
Jump in nature	0.772	-0.089	0.494
Perch height	0.639	-0.694	0.131
Perch diameter	0.871	0.107	0.172
Nearest perch	0.780	0.050	0.466

* Sprint = time to run 0.25-m intervals, not speed over that distance.

ancies concern relatively minor issues. The ancestor-reconstruction approach allows one to reconstruct character evolution as well as to statistically analyze the resultant patterns. Node values calculated in the contrast approach should not be considered to be reconstructions of hypothetical ancestral taxa because they are the result of averaging the values of their descendants and scaling them by time-since-differentiation. Consequently, I used the values generated in the ancestor-reconstruction approach to investigate which variables are most responsible for the significant canonical correlations among morphology, performance capability, and ecology and behavior.

RESULTS

Size analyses

The results of the principal components analyses using non-size-corrected data are presented in Table 2. In the morphological analysis, the first axis represents size, loading strongly and positively for all variables and accounting for 88.1% of the variation. The second axis accounts for most of the remaining variation and loads most strongly for lamella number. The first performance PC axis, which accounts for 83.6% of the variation, indicates that running, jumping, and clinging

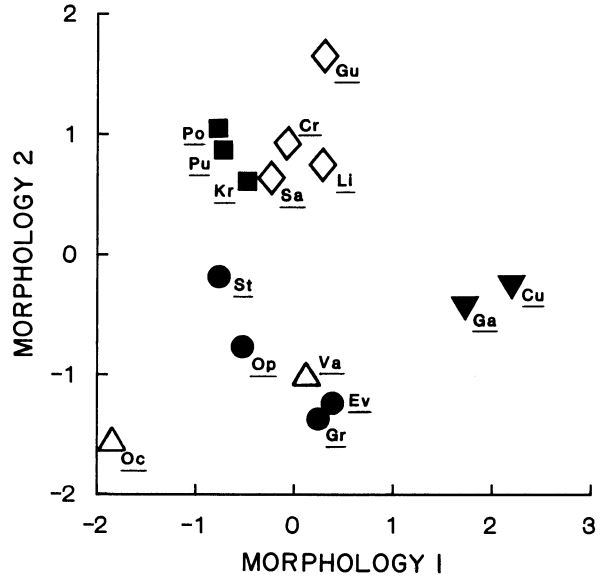


FIG. 2. The distribution of *Anolis* species in a two-dimensional morphospace, based on scores from the first two morphology principal component axes (PC 1 = size; PC 2 = inverse of lamella no.) using non-size-adjusted data. The ecomorph categories to which species belong are: \diamond trunk-ground: *A. cristatellus*, *A. gundlachi*, *A. lineatopus*, *A. sagrei*; \bullet trunk-crown: *A. evermanni*, *A. stratulus*, *A. grahami*, *A. opalinus*; \blacksquare grass: *A. krugi*, *A. poncensis*, *A. pulchellus*; \triangle twig: *A. occultus*, *A. valencienni*; \blacktriangledown crown-giant: *A. cuvieri*, *A. garmani*.

ability are strongly and positively associated among species (the negative sign for running results because the fastest animals have the lowest time elapsed per 0.25-m interval). Clinging, which loads less strongly than running and jumping on PC 1, loads most strongly on the second axis. The first three ecology and behavior PC axes (hereafter referred to as "ecobehavior") account for 85.4% of the variation. The first axis indicates that species that walk relatively infrequently tend to

TABLE 3. Summary of the canonical correlation analyses using non-size-adjusted values for extant species.

Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
			χ^2	df	P
a) Morphology-Performance					
1	0.981	0.962	44.46	4	<.0005
2	0.513	0.263	7.56	1	<.01
b) Performance-Ecology					
1	0.904	0.817	21.15	6	<.005
2	0.669	0.448	5.31	2	<.10
c) Morphology-Ecobehavior					
1	0.829	0.687	16.29	6	<.025
2	0.689	0.475	5.76	2	<.10
3	0.291	0.085	0.76	1	<.40

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

TABLE 4. Summary of the canonical correlation analyses for non-size-adjusted ancestor-reconstruction values.

Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
			χ^2	df	P
a) Morphological evolution–Performance evolution					
1	0.984	0.468	40.85	4	<.0005
2	0.602	0.362	4.71	1	<.05
b) Performance evolution–Ecobehavioral evolution					
1	0.854	0.729	15.30	6	<.025
2	0.569	0.324	3.51	2	<.20
c) Morphological evolution–Ecobehavioral evolution					
1	0.739	0.546	9.90	6	<.20
2	0.518	0.268	2.81	4	<.30
3	0.030	0.001	0.02	1	<.90

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

run relatively frequently, display often, jump far, and perch high on large-diameter objects that are distant from other perch sites. The second axis reveals that species that move infrequently tend to jump relatively frequently, walk relatively infrequently, and use low perches. The third axis indicates that species that move frequently also display frequently.

Figs. 2–4 illustrate the position of species using their scores on the two morphology, two performance, and three ecobehavior PC axes. Fig. 2 indicates that size (PC 1) and lamella number (PC 2) are sufficient to essentially separate the ecomorph categories, with the exception of the twig and crown giant anoles. The ecomorphs also can be distinguished by their position in ecobehavioral space (Fig. 3), but their separation is less clear-cut based on performance ability (Fig. 4). Canonical correlation analysis was used to assess to what degree position in, for example, a two-dimensional “morphospace,” determined by species’ scores on the

TABLE 5. Summary of the canonical correlation analyses using non-size-adjusted contrast values.

Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
			χ^2	df	P
a) Morphology contrasts–Performance contrasts					
1	0.982	0.964	38.65	4	<0.0005
2	0.548	0.300	3.75	1	<0.055
b) Performance contrasts–Ecobehavioral contrasts					
1	0.830	0.689	12.44	6	<0.054
2	0.439	0.193	1.93	2	<0.40
c) Morphological contrasts–Ecobehavioral contrasts					
1	0.815	0.664	11.25	6	<0.10
2	0.383	0.147	1.43	2	<0.50
3	0.022	0.000	0.00	1	<1.0

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

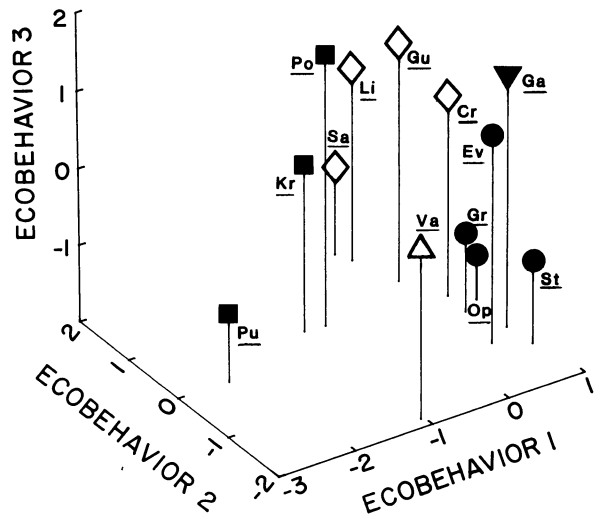


FIG. 3. Ecobehavior space, based on the first three ecobehavior principal component axes. Ecomorph category symbols as in Fig. 2. No ecobehavioral data were available for *Anolis occultus* and *A. cuvieri*.

morphological PC axes, is correlated with position in a two-dimensional “performance” space or three-dimensional “ecobehavioral space.” The analyses using data from extant species indicates that the first two canonical axes for each of the three comparisons are statistically significant, or nearly so (Table 3). However, the evolutionary analyses (Tables 4 and 5) indicate that some of these correlations are not significant when the effect of phylogenetic relationships is includ-

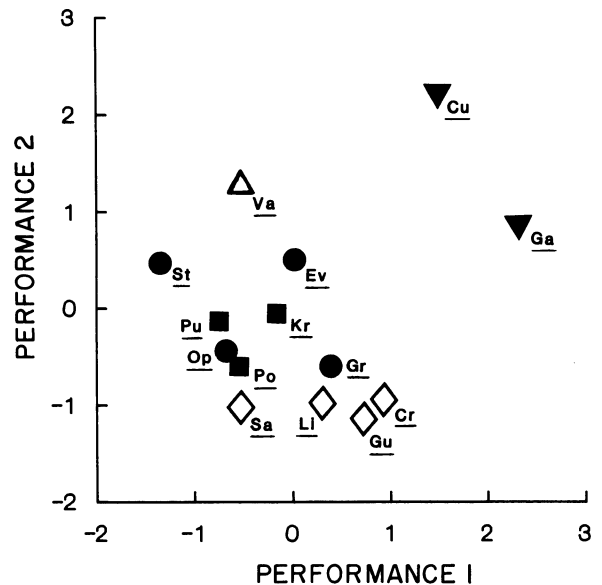


FIG. 4. Performance space, based on the first two principal component axes using non-size-adjusted data. Ecomorph category symbols as in Fig. 2. No sprint data were available for *Anolis occultus*.

TABLE 6. Variance (r^2) explained by the significant canonical correlation (CC) axes in the non-sized-adjusted analyses, using correlations based on principal components (PC) scores for each species in the ancestor-reconstruction analyses.

a) Morphology-Performance					
	Morphology			Performance	
	CC 1	CC 2		CC 1	CC 2
Morphology PC 1	1.000	0.000	Performance PC 1	0.893	0.108
Morphology PC 2	0.067	0.933	Performance PC 2	0.311	0.689

b) Performance-Ecobehavior					
	Performance			Ecobehavior	
	CC 1	CC 2		CC 1	CC 2
Performance PC 1	0.028		Ecobehavior PC 1	0.098	
Performance PC 2	0.943		Ecobehavior PC 2	0.109	
			Ecobehavior PC 3	0.895	

ed. Both the ancestor-reconstruction and contrast analyses indicate that the first two canonical axes in the morphology-performance analysis and the first axis in the performance-ecobehavior analysis are significant, or nearly so ($P < .055$). However, both approaches reveal that morphology and ecology have not evolved concordantly; the significant result in Table 3c is an artifact resulting from the failure to consider phylogenetic information.

Loadings on the canonical axes can be examined to determine which variables are responsible for the significant correlations. Table 6 presents the amount of variation in each variable explained by the significant canonical axes in the morphology-performance and performance-ecobehavior ancestor-reconstruction analyses. In the morphology-performance analysis, morphological PC 1 and performance PC 1 load strongly on canonical axis 1, which indicates that larger species have greater capability at all three performance measures. Canonical axis 2 indicates a relationship between

lamella number (morphological PC 2) and clinging ability (performance PC 2). However, the relationship is weak, given that the second principal component axes for both morphology and performance explain so little of the variance (Table 2). Canonical axis 1 in the performance-ecobehavior analysis loads strongly for clinging ability (performance PC 2) and movement and display rate (ecobehavior PC 3). General performance ability (performance PC 1) is not significantly related to any ecological or behavioral variables. The lack of significance in the morphology-ecobehavior analysis indicates that size (morphological PC 1) is not related to ecological or behavioral variables.

Shape analyses

The results of the morphology and performance principal components analyses using size-corrected

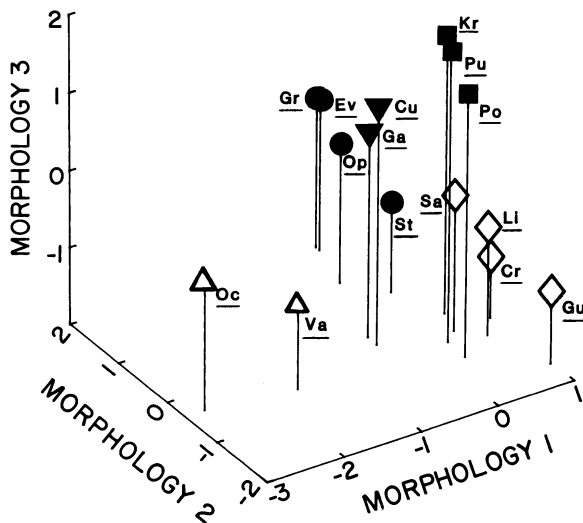


FIG. 5. Morphospace, based on the first three morphology principal component axes using size-adjusted data. Ecomorph category symbols as in Fig. 2.

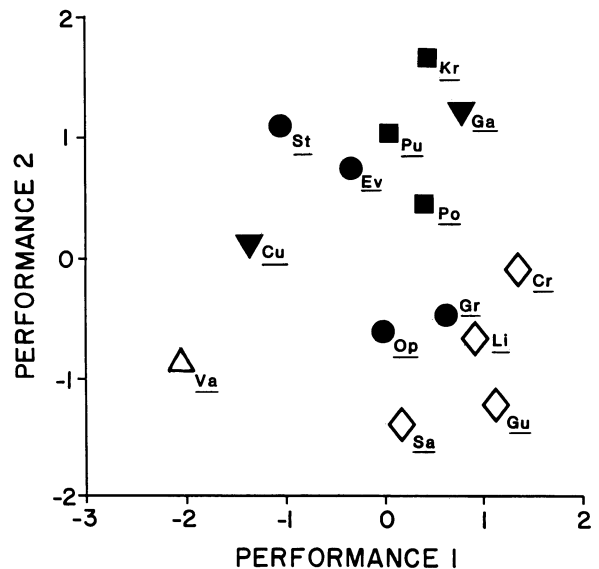


FIG. 6. Performance space, based on the first two performance principal component axes using size-adjusted data. Ecomorph category symbols as in Fig. 2. No sprint data were available for *Anolis occutus*.

TABLE 7. Principal component (PC) axis loadings for size-corrected variables. svl = snout-vent length.

a) Morphology (residuals of regression against svl, data ln-transformed)			
	PC 1	PC 2	PC 3
% variation accounted for	64.2	19.5	13.1
Foreleg length	0.910	0.274	-0.221
Hindleg length	0.991	0.015	0.046
Mass	0.898	0.143	-0.290
Lamella number	-0.302	0.925	0.227
Tail length	0.709	-0.159	0.685
b) Performance (residuals of regression against svl, data ln-transformed)			
	PC 1	PC 2	
% variation accounted for	59.7	34.1	
Sprint*	-0.943	0.142	
Jump	0.948	0.097	
Pull	0.042	0.996	

* Sprint = time to run 0.25-m intervals, not speed over that distance.

morphology and performance data are presented in Table 7. The first three axes using the morphological data account for 96.8% of the variation. The first axis loads strongly for all variables except lamella number, indicating that species with relatively long forelegs (with the effect of size removed), for example, also have relatively long hindlegs and tail, and are heavier. Garland (1985) and Losos et al. (1989) found a similar relationship among individuals of two species of agamid lizards. The second axis refers solely to lamella number, and the third to tail length. The first two performance principal component axes account for 93.8% of the variation. The first axis loads strongly for sprinting and jumping ability, whereas the second axis emphasizes sticking ability.

Fig. 5 indicates that the ecomorphs separate cleanly

TABLE 8. Summary of the canonical correlation analyses using size-adjusted values for extant species.

	Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
				χ^2	df	P
a) Morphology-Performance						
1	0.772	0.596	15.30	6	<.025	
2	0.681	0.464	6.24	2	<.05	
b) Performance-Ecology						
1	0.876	0.767	13.82	6	<.05	
2	0.276	0.076	0.71	2	<.80	
c) Morphology-Ecobehavior						
1	0.890	0.792	22.06	9	<.01	
2	0.780	0.608	8.81	4	<.10	
3	0.291	0.085	0.76	1	<.40	

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

TABLE 9. Summary of the canonical correlation analyses for size-adjusted ancestor-reconstruction values.

	Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
				χ^2	df	P
a) Morphological evolution-Performance evolution						
1	0.881	0.776	19.92	6	<.005	
2	0.625	0.391	4.96	2	<.10	
b) Performance evolution-Ecobehavioral evolution						
1	0.867	0.752	14.01	6	<.05	
2	0.387	0.150	1.46	2	<.50	
c) Morphological evolution-Ecobehavioral evolution						
1	0.917	0.841	19.80	9	<.025	
2	0.622	0.387	4.17	4	<.40	
3	0.030	0.001	0.01	1	<.95	

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

based on morphological shape. Although members of some ecomorphs group together in a size-adjusted performance space (Fig. 6), other ecomorphs are widely dispersed.

Canonical correlation indicated significant correlations between position in ecobehavioral space (which had no size component and thus was not adjusted) and size-independent morphological and performance spaces (Table 8). The first canonical axis in all three analyses, and the second axis in the morphology-performance analysis, are significant. The evolutionary analyses (Tables 9 and 10) confirm that morphological shape has evolved concordantly with both performance and ecobehavior, but differ on whether performance and ecobehavior have coevolved. Because the ancestor-reconstruction analysis found a significant performance-ecobehavior correlation and the probability value, though non-significant, was high ($P < .15$)

TABLE 10. Summary of the canonical correlation analyses for size-adjusted contrast values.

	Canonical variates	Canonical correlation	Canonical r^2	Statistical tests*		
				χ^2	df	P
a) Morphology contrasts-Performance contrasts						
1	0.840	0.706	17.19	6	<.005	
2	0.706	0.498	6.21	2	<.05	
b) Performance contrasts-Ecobehavioral contrasts						
1	0.828	0.686	9.90	6	<.15	
2	0.276	0.076	0.63	2	<.80	
c) Morphological contrasts-Ecobehavioral contrasts						
1	0.915	0.837	24.31	9	<.005	
2	0.840	0.706	12.09	4	<.05	
3	0.022	0.000	0.00	1	<.10	

* Tests of the null hypotheses that the correlation in the current row and all that follow within the same analysis are zero.

TABLE 11. Variance (r^2) explained by the significant canonical correlation (CC) axes in the analyses of size-adjusted variables using correlations based on principal components (PC) scores for each species in the ancestor-reconstruction analyses.

a) Morphology–Performance					
	Morphology			Performance	
	CC 1	CC 2		CC 1	CC 2
Morphology PC 1	0.922	0.077	Performance PC 1	0.878	0.122
Morphology PC 2	0.005	0.223	Performance PC 2	0.077	0.924
Morphology PC 3	0.078	0.672			

b) Performance–Ecobehavior			
	Performance		Ecobehavior
	CC 1		CC 1
Performance PC 1	0.874	Ecobehavior PC 1	0.321
Performance PC 2	0.068	Ecobehavior PC 2	0.828
		Ecobehavior PC 3	0.064

c) Morphology–Ecobehavior					
	Morphology			Ecobehavior	
	CC 1	CC 2		CC 1	CC 2
Morphology PC 1	0.951	0.029	Ecobehavior PC 1	0.233	0.507
Morphology PC 2	0.036	0.623	Ecobehavior PC 2	0.931	0.060
Morphology PC 3	0.000	0.329	Ecobehavior PC 3	0.001	0.144

in the corresponding contrast analysis, I treat this correlation as significant, though further work is necessary to resolve this discrepancy.

The evolutionary analyses also differed on which canonical axes are statistically significant. Based on the three analyses (two evolutionary, one non-evolutionary), the first two canonical axes on the morphology–performance and morphology–ecobehavior analyses and the first canonical axis on the performance–ecobehavior analyses are clearly or potentially significant. Table 11 indicates which variables load strongly on these axes. The first axis in the morphology–performance analysis indicates a relationship between general body proportions (morphology PC 1) and sprinting and jumping ability (performance PC 1). The second canonical axis suggests a relationship between tail length (morphological PC 3) and clinging ability (performance PC 2).

The only significant canonical correlation axis in the performance–ecobehavior analysis reveals a relationship between sprinting and jumping ability (performance PC 1) and movement rate, jumping, running, and walking frequency, and perch height (ecobehavior PC 2). In the morphology–ecobehavior analysis, the first canonical axis reveals an inverse relationship between general body proportions (morphological PC 1) and ecobehavior PC 2, as one would expect, given that performance PC 1 is correlated with both. The second canonical axis indicates a relationship, not suggested by the analyses involving performance capability, between lamella number (morphological PC 2) and all ecobehavioral variables except jumping and walking frequency (ecobehavior PC 1).

DISCUSSION

The importance of body size

Much of the variation among organisms and species is attributable to differences in body size. Allometric effects on morphological shape, physiology, and biomechanical function have long been recognized (e.g., Thompson 1917, Huxley 1932, Kleiber 1961). Two recent compilations (Peters 1983, Calder 1984) have argued convincingly that size also has a pervasive effect on the ecology of organisms. For example, much of the variation in life history patterns among mammals and reptiles is due solely to size differences (e.g., Stearns 1983, Dunham et al. 1988).

Despite the recognition of six morphotypic categories based primarily on shape, most of the morphological variation among *Anolis* is explained by body size. Similarly, most of the variation in performance ability also results from body size differences. However, this analysis indicates that size is not significantly related to behavior and ecology. In fact, of all of the ecological and behavioral variables, size is correlated only with distance jumped in nature (J. B. Losos, *personal observation*). For example, species occurring on wide perches (i.e., trunks) include the crown giant *A. garmani*, intermediate-sized species such as *A. evermanni*, and the small *A. opalinus*. By contrast, morphological shape is significantly related to the ecological and behavioral variables.

The lack of a size effect may be attributable to two factors. First, locomotor and display behavior are not influenced by size, but are directly related to size-independent limb parameters (Losos 1990). Second, although members of each ecomorph category are rel-

atively uniform ecologically, enough intra-ecomorph size variation exists (e.g., the trunk-crown anoles range in SVL from 44.5 to 62.3 mm) to obscure any size effect on ecology.

The ecomorph concept in Anolis

Williams (Rand and Williams 1969, Williams 1972, 1983), referring to *Anolis*, coined the term "ecomorph," which he defined as "species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phylogenetically" (1972: 82). I have shown that the ecomorphs are readily distinguishable in a size-independent morphospace (see also Mayer [1989]). Further, my original hypotheses are confirmed: the relative position of species in morphospace correlates with their arrangement in performance and ecobehavioral space; and morphology, performance ability, and ecology and behavior have evolved synchronously.

Williams (1983) differentiated the ecomorphs morphologically by leg proportions, mass (stocky to slender), tail length, and head length. No readily apparent relationship exists between head length and the performance parameters in this study; hence, I did not measure it. I included lamella number because differences exist among ecomorphs (Collette 1961, Mayer 1989). The principal components analysis indicates that all of these variables, with the effect of size removed, are important in defining the ecomorph categories. The most important distinction among species is general body proportions. At the extremes, trunk-ground species (see Fig. 2 legend for ecomorph identifications) are stocky, with long forelegs, hindlegs, and tails, whereas twig anoles are elongate, with short forelegs, hindlegs, and tails. Lamella number and tail length independent of general body proportions also help distinguish the ecomorphs.

Biomechanical models

Biomechanical models predict that species with relatively long hindlegs should be able to run faster (Hildebrand 1974, Bakker 1975, Coombs 1978) and jump farther (Emerson 1978, 1985, Pounds 1988). In support of these predictions, the principal components analysis indicates that running and jumping ability among species are tightly correlated. Lamellar pad structure might increase clinging capability in two ways. Dry adhesion results from the intermolecular forces between the substrate and the microscopic setal hairs found on lamellar scales (Hiller 1975, Peterson and Williams 1981). Consequently, ignoring interspecific differences in setal hair density and form (which are just now receiving preliminary analysis—see Peterson and Williams 1981, Peterson 1983), clinging ability on a smooth surface should be a function of lamellar pad area irrespective of lamella number. Increased lamella number, however, should enhance the capability of the pad to mold its shape to surface irregularities, increas-

ing clinging ability on rough surfaces (Cartmill 1985). Running, jumping, and clinging ability, which are related to different morphological features, would not be expected to be correlated among species. The principal components analysis demonstrates their independence.

Morphology, ecology, and behavior

The relationships among morphology, microhabitat use and locomotor behavior are complex. The habitat matrix model (Moermond 1979a, b, Pounds 1988) predicts that both morphology and behavior reflect interspecific microhabitat differences. Basically, the model predicts that species will jump more often when available structures are nearby, though more-distant perches will require greater jumping capability. On broad surfaces lizards will run more often, but narrower perches make running more difficult, resulting in slower progression. Whereas running and jumping favor long limbs, locomotion on narrow perches favors short legs, which enhance stability and minimize the risk of toppling (Cartmill 1985, Pounds 1988), and increased number of lamellae, which enhance gripping ability. Williams (1983), following Rand (1964, 1967, Rand and Williams 1969), Schoener and Schoener (1971a, b) and others, included perch height as a characteristic differing among ecomorphs. Several studies (Collette 1961, Lister 1976) have noted a correlation between arboreality and number of subdigital lamellae in anoles (which is confounded by the larger size of more arboreal species), but a functional explanation for this pattern is not obvious (Moermond 1979a).

Previous analyses (Losos 1990) indicated that ecomorphs differ in the rate of display behavior. In particular, Hicks and Trivers (1983) showed that the specialized crawling species, *A. valencienni*, forages widely and actively, in contrast to many *Anolis*, and consequently is less territorial and displays less than other species. I included display rate to determine whether differences among ecomorphs in social behavior are correlated with either morphology or performance ability.

The ecobehavioral principal components analysis supports many of these predictions. The first axis indicates that species that occur on broad perches in microhabitats with distant nearest available perches tend to run relatively often and walk relatively infrequently. Not surprisingly, when they do jump, these species tend to make relatively long jumps. These species also occur high in trees and display frequently. Walking frequency also is associated with perch height on the second axis. The first and third axes confirm that display frequency is also a variable distinguishing the ecomorph categories.

The canonical correlation analyses indicate that morphology, performance capability, and ecology and behavior are closely related. Examination of the loadings of the variables onto the canonical axes allows

identification of the variables most responsible for these associations. Interpreting the results is difficult, however, because compound variables (the principal components scores) were used in the canonical correlation analyses rather than the original variables. As future work increases the sample of species studied, I will be able to use the original variables, which will hopefully increase the clarity of the results.

The morphology–ecobehavior comparison reveals that: (1) long-legged, long-tailed and heavy-bodied lizards jump and run more often, walk and move less often, and use low perches; and (2) species with many lamellae walk more often, run and display less often, make shorter jumps, and use perches that are narrow, low, and closely spaced.

*Performance capability as the
mechanistic link?*

These findings support the ecomorphological predictions above, but the inclusion of performance measurements only partially provides a mechanistic explanation for them. In comparing the morphology–performance and performance–ecobehavior analyses, the first pattern is readily explainable in terms of performance capability. In accord with biomechanical models, relatively long-legged species can run faster and jump farther for their size (the relationship between limb proportions and sprinting and jumping ability is explored in detail in Losos [*in press*]). These species run more often, walk less often, use broad perches in habitats with distant nearest perches, and make longer jumps than other species. The independence of non-size-corrected performance ability and ecology, however, suggests that running and jumping ability are not the only factors mediating these ecomorphological relationships.

Knowledge of performance capability does not elucidate the relationship between lamella number (both absolute and size-adjusted) and walking frequency, height, and perch diameter. My analysis demonstrates that the oft-noted relationship between lamella number and perch height is not a simple allometric consequence of more-arboreal species being larger. The functional basis for this relationship, however, is unclear; none of the analyses suggested a relationship between clinging capability and either morphology or ecology. Possibly the relevant performance parameter was not measured. Increased numbers of lamellae may contribute to ability to grasp irregular or small perches but total pad area may be more important for clinging to smooth surfaces. No explanation is readily apparent for the relationship that is weakly suggested between tail length and clinging capability. Clinging capability is not a function of total body surface area; lizards generated frictional force only when applying their lamellar pads to the plexiglass. Most likely, tail length is correlated to some unmeasured variable (perhaps lamellar pad area?) which is important for clinging.

Ecomorphological evolution

Ecomorphological hypotheses are essentially predictions about the adaptive (*sensu* Williams 1966, Gould and Vrba 1982) relationship between morphology and ecology (James 1982, Niemi 1985, Voss 1988). This study, however, is the first to examine the evolution of ecomorphological relationships in a strictly phylogenetic context. The analyses confirm that morphology, performance capability, and ecology and behavior have coevolved. I have shown that general body proportions and running and jumping performance coevolve, and that evolution of these features is coincident with evolutionary change in aspects of the organisms' ecology. Hence, to the extent that adaptation can be inferred in the past, these interspecific morphological differences represent adaptations for utilization of different microhabitats (see Greene 1986).

A phylogenetic approach is important not simply because it allows one to test predictions implicit in ecomorphological hypotheses. By ignoring phylogeny, one risks confounding cases in which several species share similar morphological and ecological features due solely to descent from a common ancestor, with instances in which distantly related species have convergently evolved the same morphology as a response to the same selective factor in the environment. (Presence of the same morphological and ecological feature in all members of a monophyletic group does not preclude the possibility that the feature arose as an adaptation in the common ancestor and has been maintained adaptively in all descendants. In such cases, "phylogenetic inertia" cannot be distinguished from adaptation without further information [Derrickson and Ricklefs 1988, Greene 1988].) As a result, one may overestimate the amount of adaptive evolution that has occurred (Lauder 1981, Huey 1987, Donoghue 1989).

In the present case, both evolutionary and non-evolutionary analyses come to many of the same conclusions. The reason is that convergent evolution has been rampant among West Indian *Anolis*. For example, the trunk–ground ecomorph has evolved minimally three times among these species (and possibly at least once more in Hispaniola [Williams 1983]): *A. gundlachi*–*A. cristatellus*, *A. lineatopus*, and *A. sagrei*. Multiple evolution has occurred in the twig (twice), crown giant (twice), and trunk–crown (twice) ecomorphs. Consequently, to a large extent, extant species are statistically independent points. Despite the general agreement of results, however, the phylogenetic analyses confirm that non-evolutionary analyses usually overestimate statistical relationships and produce spurious significant results, as predicted by Felsenstein (1985, 1988) and Martins and Garland (*in press*).

Although the analyses confirmed the relationships among morphology, performance capability, and ecology and behavior, considerable variation remained unexplained in most cases (variance explained in a

canonical correlation is the product of a variable's loading on a canonical axis multiplied by the canonical correlation of that axis [Miles and Ricklefs 1984]). For example, <15% of the variation in ecobehavior PC 3 was explained by either morphology or performance (Table 11). This suggests either that much variation in each category (e.g., ecology or performance ability) is unrelated to the others, or that more variables need to be examined. For example, the performance parameters measured were simplistic. More sophisticated procedures (e.g., investigations of agility or performance on different substrates [Losos and Sinervo 1989]) could increase the explanatory power of these analyses. Similarly, other morphological (e.g., head and muscle proportions, lamellar pad area) and ecological (e.g., diet, sleeping perches, microclimate) variables could be addressed. Unexplained variation notwithstanding, this study amply confirms Williams' (1972, 1983, Rand and Williams 1969) claim that the radiation of West Indian *Anolis* has been adaptive.

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APPENDIX 1

Anolis species abbreviations.—*crstatellus* (cr), *cuvieri* (cu), *evermanni* (ev), *gundlachi* (gu), *krugi* (kr), *occultus* (oc), *poncensis* (po), *pulchellus* (pu), *stratulus* (st), *garmani* (ga), *grahami* (gr), *lineatopus* (li), *opalinus* (op), *sagrei* (sa), and *valencienni* (va).

FIELD LOCALITIES

Jamaica.—Discovery Bay, St. Ann Parish—Discovery Bay Marine Laboratory grounds (ga, gr, li, sa, va); Mona, St. Andrew Parish—grounds of University of the West Indies and

fields on Long Mountain (gr, li, op, va); Negril, Westmoreland Parish—lots surrounding Gold Nugget Hotel, lots surrounding Villas Negril (ga, gr, li, op, va); San San, Portland Parish—grounds of Frenchman's Cove and nearby fields (li, op); Southfield, St. Elizabeth Parish—study site of Trivers (1976, ga, va).

Puerto Rico.—Caribbean National Forest—grounds of El Verde Biological Field Station and surrounding forest (cr, ev, gu, kr, pu, st) and forest near El Yunque (cu, oc); El Verde—private road 4.8 km S Hwy. 3 on Hwy. 186 (cr, kr, pu, st); Parguera—0.2 km S Hwy. 116 on Hwy. 304 (po).

APPENDIX 2

Two general methods, the analysis-of-variance and phylogenetic approaches, have been proposed to incorporate information on evolutionary relationships into comparative analyses.

ANOVA approach

The analysis of variance approach was first suggested by Clutton-Brock and Harvey (1977) and subsequently employed, with various modifications, by many others (see recent treatments by Pagel and Harvey [1988] and Bell [1989]). It identifies the lowest level of the taxonomic hierarchy that explains the greatest proportion of the statistically detectable variance for two variables, and then determines whether, at that level, the variables are related.

Although this approach is preferable to ignoring phylogenetic information entirely, it has several flaws (see Felsenstein 1988):

- 1) By concentrating on only one hierarchical level, variance at other levels is ignored and some proportion of the phylogenetic information is lost (some approaches [e.g., Bell 1989] attempt to circumvent this difficulty);
- 2) It assumes that all recognized taxa are monophyletic. This is often not the case, and leads to an unknown degree of error;
- 3) Phylogenetic information within a given hierarchical level is not utilized (e.g., all genera within a family are not equally distantly related to all other genera). Consequently, within that level, all taxa are treated as independent points, exactly the situation these methods were devised to circumvent;
- 4) It cannot be used for studies involving only one level of the taxonomic hierarchy. This study includes 15 species of *Anolis*. I would need to create several intrageneric hierarchical levels to use the analysis-of-variance approach.

Phylogenetic approaches

Because of these difficulties, methods that utilize all available phylogenetic information are superior. Although to date the methods delineated below have only been employed on fully resolved phylogenies, these methods could readily be modified to accommodate phylogenetic trees with unresolved polychotomies.

Two phylogenetic methods have been proposed: the ancestor-reconstruction approach and the contrast approach. The ancestor-reconstruction approach assigns values of a variable to hypothetical ancestral taxa and then calculates how much evolutionary change occurred along each branch of the tree.

Ancestor-reconstruction.—There are two methods for reconstructing the value of quantitative traits for hypothetical ancestral taxa.

1. *Linear parsimony.*—The first method, derived from Farris's (1970) algorithm for optimizing character states on a phylogeny, minimizes the sum of the evolutionary change along the branches of the tree ($\sum_{i=1}^k$ evolutionary change on the *k*th branch).

Swofford and Maddison (1987) demonstrated that Farris's optimization finds only one or a few of the often many possible, equally parsimonious reconstructions of ancestral values. All equally parsimonious reconstructions can be determined by using a three-step algorithm (Maddison and Maddison 1987, following Swofford and Maddison 1987), illustrated with a hypothetical example in Fig. A1. *Step 1:* starting at the top of the tree, assign each hypothetical ancestor a range of values based on the following rule: if the values of its two descendants do not overlap, then the range for the node is the interval between the values for its two descendants; if the values or ranges for the descendants abut or overlap, then the range for the node is the point of abutment or the range of overlap. *Step 2:* beginning at the node one removed from the root of the tree, assign each node a second value using the same rule, except in this case, instead of comparing

the values of the node's two descendants, compare the range calculated in Step 1 for the sister taxon of the node with the range calculated in Step 2 for the ancestor of that node (for the comparison for the first node above the root of the tree, use the range calculated in Step 1 for the root). *Step 3:* compare the values calculated in Step 1 for both of the node's descendants (or the actual values if descendants are extant taxa) with the value calculated in Step 2 for the node itself. For this step, a different rule is employed: if all three ranges overlap for at least one point, then the assigned range for the node is the range of overlap; if one range overlaps both of the others, which do not overlap each other, then the assigned range is the range between the two non-overlapping ranges; if none of the ranges overlap, then the assigned range is the range that lies between the other two ranges; if two ranges (range A and range B) overlap and neither overlaps range C, then the assigned range is the portion of A that does not overlap B, or the portion of B that does not overlap A, depending on which is nearer to C. The range of possible values for a node is the range calculated in Step 3. Inspection is necessary to see which combinations of values at different nodes produce minimal amounts of evolutionary change; all combinations of the possibilities at each node are not equally parsimonious. MacClade (Maddison and Maddison 1987) can be used to find all possible optimizations at each node and the most parsimonious combinations of these values; PAUP (Swofford 1985) gives all possible states at each node and can find a subset of the possible optimizations.

In the hypothetical example, given the values of the variable for five species in the ingroup (Fig. A1: species B–F) and one outgroup species (Fig. A1: A), Figs. A2 and A3 present the two most extreme of the possible equally parsimonious reconstructions for the four hypothetical taxa in the ingroup clade (the state of the ancestor to all species is almost always ambiguous and not included in analyses of evolution within the ingroup clade); Fig. A4 presents an intermediate reconstruction. All of the reconstructions require evolutionary change of 23 units. The first reconstruction (Fig. A2) suggests early evolution of high value for the variable, with a reversal on the branch leading to the ancestor of D and E, whereas the second reconstruction (Fig. A3) indicates later convergent evolution of high value on the branches leading to species C and F. The third reconstruction (Fig. A4) reveals moderate levels of convergence and reversal.

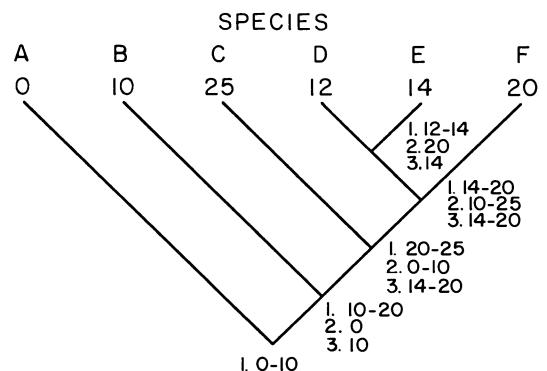


FIG. A1. Results of the three steps in the Swofford-Maddison ancestor-reconstruction algorithm. Numbers by each node are the results for that hypothetical ancestral taxon.

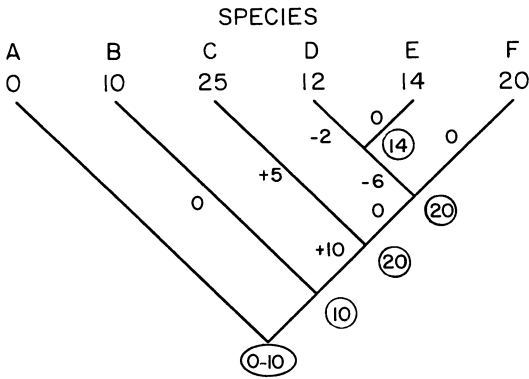


FIG. A2. One possible reconstruction of ancestral character states using the Swofford-Maddison algorithm.

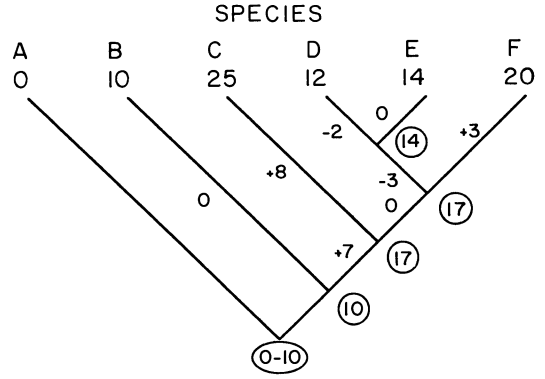


FIG. A4. A third possible reconstruction of ancestral character states using the Swofford-Maddison algorithm.

2. *Squared-change parsimony.*—An alternative approach for reconstructing ancestral variable values, which minimizes the sum of the squares of evolutionary change along each

branch ($\sum_{i=1}^k [\text{evolutionary change}]^2$ on k th branch), was pro-

posed by Huey and Bennett (1987). Moving down the tree from its terminal tips, the algorithm works by initially seeding each hypothetical ancestor with the mean value of its two descendants. Then, again starting from the tips of the tree and working toward the bottom, ancestral taxa are assigned the mean value of the three most proximate taxa (two descendants and one ancestor). The procedure is reiterated until the ancestral values do not change. The algorithms used by Huey and Bennett (1987), Martins and Garland (*in press*), and me differ in how the value of the root node is assigned. Because this node does not have three proximate taxa, I have left it

with its original seeded value. Fig. A5 illustrates this method, using the same phylogeny and variable values as in Fig. A1. The sum of the changes along the branches (24.1, excluding $D \rightarrow C$) is greater than in the linear parsimony approach, but the sum of squared changes (111) is less than for any of the linear parsimony reconstructions (135, 165, or 176).

Discussion.—The advantages of the two reconstruction approaches differ. Most parsimony approaches attempt to minimize the absolute amount of evolutionary change required. The interpretation of a reconstruction that minimizes the sum of evolutionary changes squared is less intuitive. In the linear parsimony approach, many ancestral taxa will have variable values identical to those exhibited by living taxa. However, most continuous variables evolve readily (Falconer 1981); it is unrealistic to postulate that many ancestral taxa (e.g., Fig. A1: the nodes with values of 10 and 14) had values identical to those of their ancestors. In these cases, however, one may

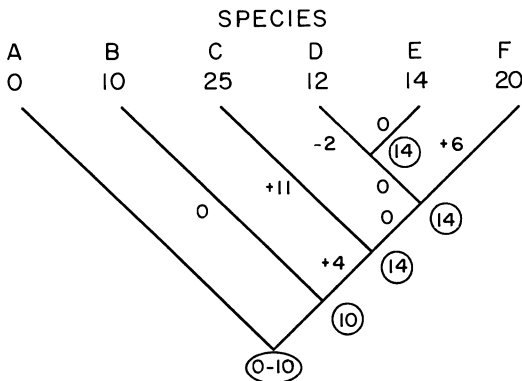


FIG. A3. A second possible reconstruction of ancestral character states using the Swofford-Maddison algorithm.

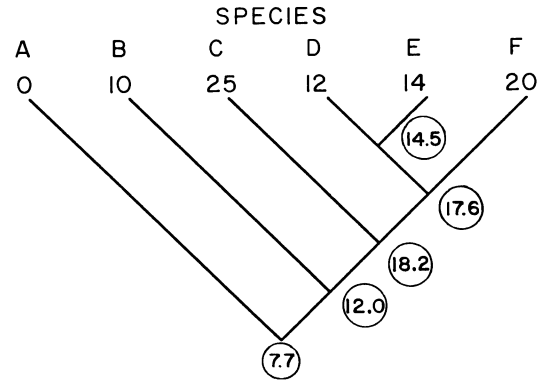


FIG. A5. Reconstructed ancestral character states using the Huey-Bennett algorithm.

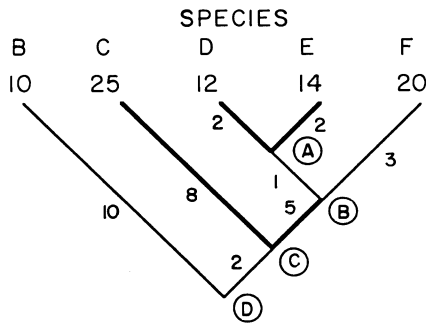


FIG. A6. The four independent contrasts are identified by letters. Contrast A considers the evolution along the top part of the tree indicated by a thicker line; Contrast B considers evolution along the slighter line in the center of the tree, and so on.

view the reconstructed values as estimates that ancestors and descendants were similar, rather than actually identical. In contrast, the squared-change parsimony approach spreads evolutionary change over all branches of the tree, rather than localizing it on a few branches with many branches indicating no change. Consequently, in some cases ancestral nodes have values that lie outside the range of all of their descendants (e.g., the node ancestral to species D and E in Fig. A5), which is not possible in approaches that minimize the absolute amount of evolutionary change.

The squared-change parsimony algorithm may also suggest more certainty than is warranted in the reconstruction of ancestral values. For example, the linear parsimony algorithm suggests a number of possibilities in the evolution of the character, including extreme reversal (Fig. A2), convergence (Fig. A3), and moderate convergence and reversal (Fig. A4). The squared-change parsimony approach only identifies the third possibility.

The major advantage of the squared-change parsimony approach is its analytical tractability. Because the algorithm produces only one reconstruction for each variable, it is simple to test whether evolutionary change in two variables is related. By contrast, the linear parsimony approach generates multiple possible trees for each variable. Because evolutionary change in each variable is presumed to be independent, the number of possible composite reconstructions for multiple variables increases rapidly; the number of scenarios is the product of the number of reconstructions for each variable. For example, if one wanted to test whether evolution of the variable in Fig. A1 was related to change in another variable that similarly had an ambiguity with two possible extreme reconstructions, then one would have to analyze four combinations of reconstructions: variable 1, reconstruction 1 – variable 2, reconstruction 1; variable 1, reconstruction 1 –

variable 2, reconstruction 2; and so on. All four contingencies could be analyzed, and one could report the results based on each possibility. However, in my study there are 15 extant taxa and 5–10 possible reconstructions for each variable. In my analyses I investigated whether evolution in three variables is related to evolution in another three variables. Based on the multiple reconstructions for each variable, there are 15 624–1 000 000 different possible composite reconstructions of all six variables. Presently, there are no analytical or simulation methods available to deal with so many equally parsimonious possibilities; analyzing each possibility separately is infeasible. Consequently, in this analysis, I have used the squared-change parsimony approach.

Independent contrasts. — Felsenstein (1985a) developed an alternative method. Every hypothetical ancestor in a phylogenetic tree has two descendant clades. The degree to which these clades differ in a given trait reflects the amount of evolution since their divergence and can be summarized by Felsenstein’s “contrasts”; each contrast is independent of evolutionary change occurring at other hypothetical ancestral nodes on the tree. For a tree with N extant species, there are $N - 1$ independent contrasts (Fig. A6). One can ask whether the calculated differences in these contrasts for one variable are related to differences in a second variable; i.e., is differentiation in these variables associated? If one assumes that random changes accumulate in time in a manner similar to Brownian motion (i.e., small and independent change between generations), then each contrast can be scaled by a function of the time elapsed since the two descendants differentiated, to guarantee equal variance among contrasts. The hypothesis that the two characters have evolved concordantly can then be tested by using parametric or non-parametric tests of association. To calculate contrasts, one needs not only data on extant species and an understanding of their phylogenetic relationships, but also information on the length of the branches in the phylogenetic tree.

Contrasts are determined by calculating (following Felsenstein [1985a] and A. Larson [*personal communication*]):

- 1) for each node, beginning near the top of the tree, the uncorrected contrast ($x_i - x_j$), which is the variable value for one descendant (x_i) minus that of the other descendant (x_j);
- 2) the variance proportion ($v_i + v_j$), which is the sum of the branch lengths leading from the node to the two descendants (v_i and v_j , respectively);
- 3) the corrected contrast, which is the uncorrected contrast divided by the square root of the variance proportion;
- 4) the variance adjustment to the branch length leading to the node (v_k), which is adjusted to $v_k + [v_i \cdot v_j / (v_i + v_j)]$. This adjustment is necessary because the weighted average in (5) is estimated with error;
- 5) the adjusted value for the hypothetical taxon represented by the node (x_k) used in calculating subsequent contrasts. It is a weighted average of the values of its two descendants, with the weights proportional to the inverses of the variances v_i and v_j . $x_k = [x_i/v_i + (x_j/v_j)] / [(1/v_i) + (1/v_j)]$.

These calculations are reported in Table A1 for the now-familiar Fig. A6, which has been assigned branch lengths. The values in column 3, the corrected contrasts, are used in subsequent statistical analyses.

Discussion

Statistical results generated by both the ancestor-reconstruction and contrast approaches are valid only if the phylogenetic hypothesis they utilize is correct. Methods need to be developed that incorporate multiple, alternative phylogenetic hypotheses. Further, perhaps these methods could weight statistical results from the different hypotheses by some estimate of the likelihood that each hypothesis is correct. In my analysis, though the exact placement of several species may be debatable, the phylogeny as a whole is robust. Only a phy-

TABLE A1. Contrast calculations.

Node	$x_i - x_j$	$v_i + v_j$	$(x_i - x_j) / \sqrt{(v_i + v_j)}$	$v_k + [v_i \cdot v_j / (v_i + v_j)]$	x_k
A	-8	6.0	-3.27	6.5	16.0
B	9	14.5	2.36	5.6	20.0
C	-10	15.6	-2.54

logenetic hypothesis that minimized the convergent evolution of ecomorphs (i.e., by placing members of an ecomorph category in a monophyletic group) could lead to non-significant statistical results. All available evidence contradicts such a phylogenetic hypothesis.

The ancestor-reconstruction and contrast approaches each have one major drawback. From a tree with N extant taxa, the ancestor-reconstruction approach produces information on the degree of change along $2N - 2$ branches. Further, the amount of change along one branch is not independent of the amount of change inferred on other branches. Consequently,

the underlying statistical distributions, and particularly the appropriate degrees of freedom, are unknown (Felsenstein 1988, Martins and Garland, *in press*). The contrast approach is statistically robust (Felsenstein 1985a, Martins and Garland, *in press*), but requires information not only on phylogenetic topology, but also on the length of branches, which often is not available (though Martins and Garland [*in press*] indicate that even with substantial errors in branch lengths, the contrast method still performs as well as the ancestor-reconstruction or non-phylogenetic approaches).