HERPETOZOA 14 (3/4): 153-162
Wien, 28. Februar 2002

Evolution among Lesser Antillean frogs of the genus *Eleutherodactylus*: ecological adaptation precedes morphological change

Evolution bei Fröschen der Gattung *Eleutherodactylus* von den Kleinen Antillen: Ökologische Anpassung geht morphologischer Veränderung voraus

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KURZFASSUNG

Am Beispiel einer kleinen Gruppe von Fröschen der Gattung *Eleutherodactylus* aus der östlichen Karibik untersuchte ich Unterschiede in der Körpergestalt und ihren Bezug zur Anpassung an das Leben in Bäumen. Während sich diese eng verwandten Arten in ihrer linearen Morphologie sehr ähnlich sind, sind sie adaptiv sehr differenziert und repräsentieren vier Ökomorphen: einen Generalisten (*E. johnstonei*), einen semiaquatischen Spezialisten (*E. barlagnei*), zwei dem Leben in Bäumen mäßig angepaßte Waldbewohner (*E. amplinympha*, *E. martinicensis*) und eine für das Leben unter Moos-Matten spezialisierte kleinwüchsige Art (*E. pinchoni*). Obwohl diese Arten ökologisch so verschieden sind, besteht dennoch eine enge Beziehung zwischen deren Morphologie und deren Anpassung an verschiedenste Lebensweisen. Dies drückt sich eindeutig im linearen Verhältnis zwischen Unterschenkel-Länge und Haftscheiben-Gesamtfläche aus, deren Größe auf die Fähigkeit, Bäume zu bewohnen, hindeutet.

ABSTRACT

I assessed morphometric divergence and arboreality in a small island radiation of frogs, genus *Eleutherodactylus* from the Eastern Caribbean. Whereas linear morphologies of these closely-related species remain highly similar, adaptive diversification is pronounced. Four ecomorphs are present: a generalist (*E. johnstonei*, a semi-aquatic specialist (*E. barlagnei*), two semi-arboreal forest-dwellers (*E. amplinympha*, *E. martinicensis*), and a miniaturized specialist adapted to life under moss mats (*E. pinchoni*). However, a close relationship between morphology and adaptation to specific life-styles among these taxa is demonstrated convincingly by the clear linear relationship of shank length, the single most important variable in the morphometric assessment, with total toepad area, an indicator of species arboreality.

KEY WORDS

Amphibia: Anura: Leptodactylidae: *Eleutherodactylus johnstonei*; *E. martinicensis*, *E. barlagnei*, *E. amplinympha*, *E. pinchoni*; ecology, morphology, ecomorphs, arboreality, toepads; Lesser Antilles, Caribbean

INTRODUCTION

Frogs of the genus *Eleutherodactylus* range throughout South and Central America and the West Indies (FROST 1985). With over 500 species (DUELLMAN 1993), it is the most diverse vertebrate genus, and many taxa are confined to narrow, isolated ranges. Although several species groups have been identified within *Eleutherodactylus* by morphological and biochemical analyses (e.g., LYNCH 1976; MIYAMOTO 1983; SAVAGE 1987), discussions of α-taxonomic issues are ongoing (e.g., HEDGES 1989; JOGLAR 1989; LYNCH & LA MARCA 1993). Their high inter- and intraspecific phenotypic variability, color polymorphisms, and sexual dimorphism have given *Eleutherodactylus* a bad name as a taxonomist's nightmare. However, this variability occurs within a morphologically conservative bauplan, and careful and detailed comparisons are invariably successful in resolving taxonomic problems (e.g., LYNCH & LA MARCA 1993; KAISER et al. 1994). Lesser Antillean *Eleutherodactylus* are also variable, but discrete island distributions (fig. 1) and sound knowledge of the fauna (e.g., HARDY 1982;

KAISER et al. 1994a, 1994b, 1994c, 1996; SCHWARTZ 1967) make them taxonomically manageable, in contrast to some of the larger, more unwieldy assemblages occurring elsewhere.

Five species of *Eleutherodactylus* are found in the Lesser Antilles (fig. 1), a group of small oceanic islands that is geographically located between the diverse *Eleutherodactylus*-faunas of the Greater Antilles and northern South America: *E. amplinympha* KAISER, GREEN & SCHMID, 1994; *E. barlagnei* SCHWARTZ, 1967; *E. johnstonei* BARBOUR, 1914; *E. martinicensis* (TSCHUDI, 1838); and *E. pinchoni* SCHWARTZ, 1967. In a prior systematic investigation using multiple data sets, I ascertained that these five species form a monophyletic group and are part of a larger, Caribbean *Eleutherodactylus*-clade (KAISER 1996).

Despite what might be considered a relatively low diversity of *Eleutherodactylus* in the Lesser Antilles, four adaptive lifestyles are utilized by these species. *Eleutherodactylus johnstonei* is a fiercely competitive ecological generalist with a superior ability to colonize dry or disturbed habitats (KAISER 1997; POUGH et al. 1977; STEWART 1977). *Eleutherodactylus martinicensis* is less competitive, though nearly equally as able to inhabit drier places (SCHWARTZ 1967; personal observation) whereas its sister species *E. amplinympha* is restricted to high-altitude forests on Dominica (KAISER et al. 1994). On the Basse-Terre portion of Guadeloupe (fig. 1), *E. johnstonei* and *E. martinicensis* are sympatric in various areas with *E. barlagnei* and *E. pinchoni*, frogs specialized for semi-aquatic and terrestrial life, respectively. *Eleutherodactylus pinchoni* is a minute frog that preferentially exploits the microhabitat beneath moss mats and retreats into shallow burrows when inactive or threatened (SCHWARTZ 1967; personal observation). The semi-aquatic *E. barlagnei* has webbed feet, a rare trait in *Eleutherodactylus*, and hides in rock cracks adjacent to or within fast-flowing mountain streams, with males calling from perches on wet boulder faces to attract mates (SCHWARTZ 1967; personal observation).

Statistical algorithms have long been used to assist in determining taxonomic groupings for systematic investigations. However, data from multivariate morphometrics are also useful to studies of morphological divergence and evolution (e.g., BAKER 1980; BOOKSTEIN et al. 1985; VOSS 1988). Lesser Antillean *Eleutherodactylus* are interesting study subjects for a variety of evolutionary and biogeographic reasons. Their ecological diversity yet great morphological similarity, combined with their existence on small, geologically young islands, make each of the species a discrete, isolated study group (species or populations on islands with gene flow near zero); together, these species form a study group composed of several independent evolutionary units (KAISER et al. 1994c; KAISER 1996). As with other such groups, most famously "Darwin's Finches" (genus *Geospiza*) in the Galapagos Archipelago (GRANT & GRANT 1989), a comprehensive morphometric study of these species can add to our understanding of the sequence in which adaptation, morphological diversification, and, ultimately, speciation occur (BARTON 1988; DIEHL & BUSH 1989; ENDLER 1989; MATSUDA 1987; NEVO 1989).

It has been postulated that the potential for evolutionary advancement, if gauged by speciation (WILLMANN 1988), is increased if stressful environments necessitate adaptation at a local level; the creation of peripheral isolates and, thus, an increased potential for premating isolation will often facilitate divergence (BARTON 1988; DIEHL & BUSH 1989; ENDLER 1989; MARCHETTI 1993; PARSONS 1988). The Lesser Antilles has always been a fluctuating environment, periodically disturbed by abiotic phenomena (e.g., volcanism, sea level changes, hurricanes). In order to survive, colonizers must display a certain propensity for rapid adaptation, particularly to changing physiological regimes (DAWSON et al. 1977; HOCHACHKA & SOMERO 1984). Thus, one might hypothesize that localized abiotic disturbances on Lesser Antillean islands may have given rise to phenotypic variants with higher fitness in the less than optimal habitats, resulting in ecological diversification among the native *Eleutherodactylus* but as yet in only limited morphological change. The morphometric data analyzed herein allow me to quantify divergence between taxa and the degree to which adaptations to a specific niche may be reflected by a morphometric change.

MATERIALS AND METHODS

Specimens and collecting

Specimens of *Eleutherodactylus amplinympha* (n = 58), *E. barlagnei* (n = 29), *E. charlottevillensis* (n = 25), *E. johnstonei* (n = 565), *E. martinicensis* (n = 161), and *E. pinchoni* (n = 32) were collected in the Lesser Antilles and on Tobago during several trips between 1989 and 1992. An additional 126 specimens from museum collections were examined, including the holotypes of all Lesser Antillean species, plus those of an unrelated ("outgroup") species of South American stock, *E. charlottevillensis* KAISER, DWYER, FEICHTINGER & SCHMID, 1955. Collecting and export permits were issued by local governments separately for each visit.

Measurements

Lengths. Measurements (table 1) were taken digitally on each frog and recorded to the nearest 0.1 mm. Measuring was accomplished using a dissecting microscope with camera lucida and a Numonics 2200™ digitizing tablet supported by Jandel Scientific Sigma Scan™ (version 3.10) software. Structures to be measured were placed under the microscope, and a digitizing mouse was used to click on and enter the extremes of a given structure. This technique was found to be superior to caliper measurements and reduced measurement errors to < 5% in trials at 4.5x and 9x magnification.

Toepad area. Toepads on the right side of the largest and smallest available specimens of each species were measured, as well as of several additional specimens chosen arbitrarily. The above digitizing setup was used at 18x total magnification to draw toepad outlines; Sigma Scan then automatically calculates the encircled area based on prior calibration. For ten measurements, the error was < 3%. Total toepad area, considered a reliable assessment of relative arboreality (GREEN 1979; GREEN & SIMON 1986), was calculated by doubling the sum of measurements for all toepads of each animal. This variable was corrected for size by scaling to mean snout-vent length (SVL) for each presumptive group. Scaling to weight might be considered a more appropriate means of standardizing since a given total toepad area will theoretically support a frog with a specific weight. However, weighing preserved and usually dissected animals would have introduced an unspecified amount of error into the data set. Data sets were transferred in ASCII format, and Systat™ software (version 5.2) was used on an Apple Macintosh LC™ (expanded memory) to perform statistical analyses.

Statistical analyses

After calculation of basic univariate statistics, principal components analysis (PCA) using log-transformed data in a variance-correlation matrix (WILKINSON et al. 1992) was used to explore how many informative variables in the data set determine whether species designations reflected morphometric groupings. Orthogonal variables in vector plots of the first five principal components were considered informative (WILKINSON et al. 1992). Multiple discriminant function analyses (MDAs) were conducted according to the algorithms and using the terminology of HAIR et al. (1992) to determine probabilities of group membership for each specimen, standardizing data within each assumed group (WILKINSON et al. 1992). Discriminant score (DS) plots were used to define group "morphospaces," which is the area of the 50% concentration ellipsoid resulting from DSs for all measured individuals in a pre-assigned group. Thus, "*E. barlagnei* morphospace" is defined to be that space on a DS plot of *E. barlagnei* which lies within and immediately around the 50% concentration ellipsoid for those specimens. This definition is not strict and requires recalculation with the addition or removal of specimens.

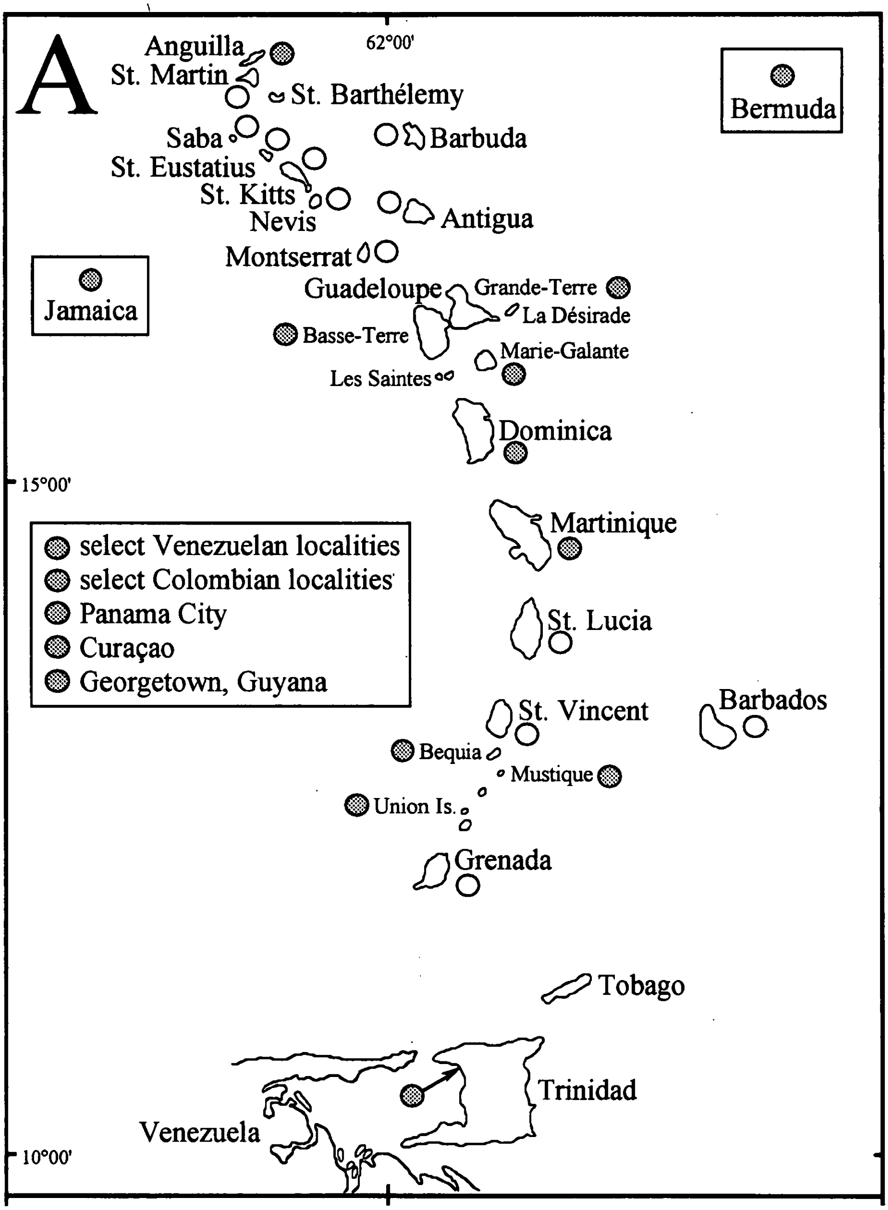

Fig. 1A: Distribution of Lesser Antillean *Eleutherodactylus*.
Distribution of *E. johnstonei*. Gray circles indicate introduction not due to colonial trade (KAISER 1992).

Abb. 1A: Verbreitung der Gattung *Eleutherodactylus* auf den Kleinen Antillen.
Verbreitung von *E. johnstonei*. Graue Kreise kennzeichnen Lokalitäten, in denen die Einführung dieser Art nicht dem Handel während der Kolonialzeit zuzuschreiben ist (KAISER 1992).

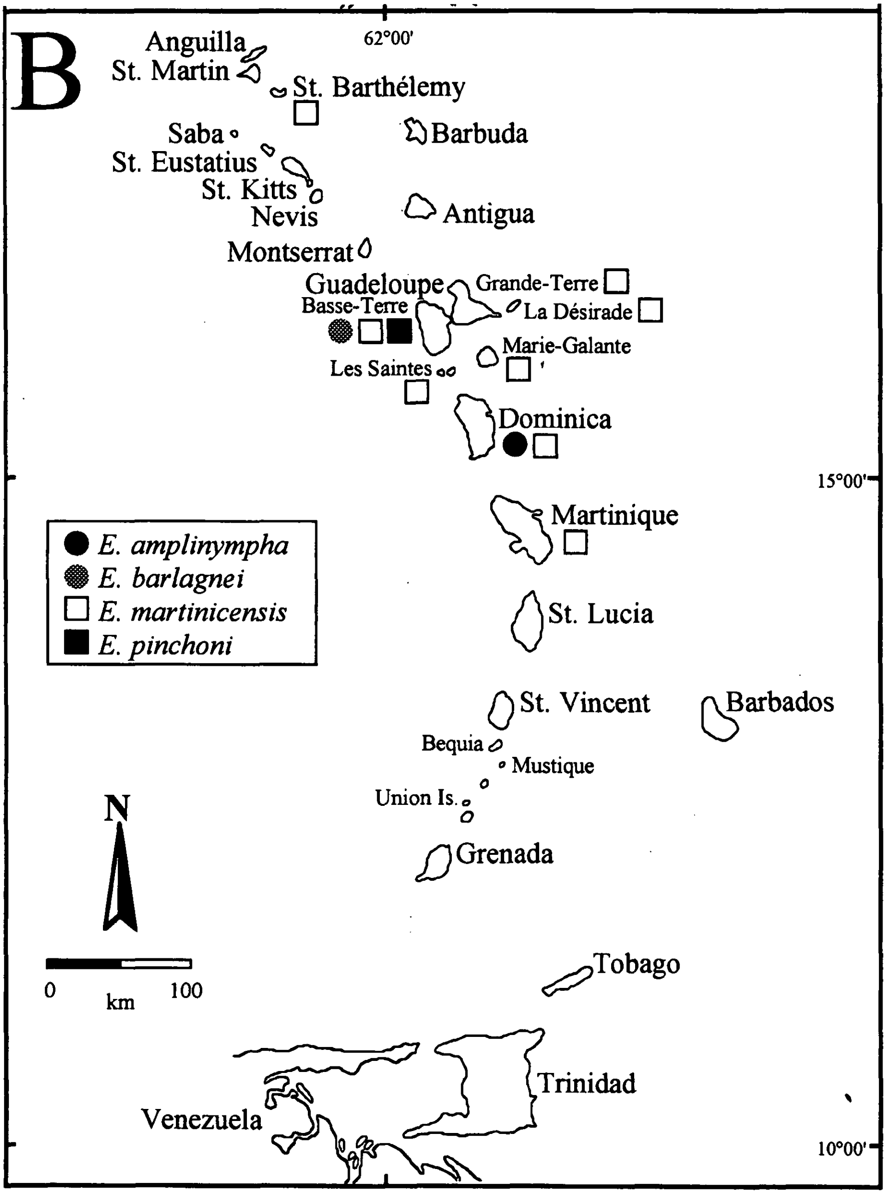

Fig. 1B: Distribution of Lesser Antillean *Eleutherodactylus*.
Distribution of *E. amplinympha*, *E. barlagnei*, *E. martinicensis*, and *E. pinchoni*.

Abb. 1B: Verbreitung der Gattung *Eleutherodactylus* auf den Kleinen Antillen.
Verbreitung von *E. amplinympha*, *E. barlagnei*, *E. martinicensis* und *E. pinchoni*.

RESULTS

Overall morphometry

PCA vector plots illustrated that ten of 20 measurements were suitable for assessing morphometric variability of Lesser Antillean *Eleutherodactylus* (head width, eye diameter, tympanum diameter, tympanum–eye distance, interorbital distance, snout length, internarial distance, tympanum–naris distance, snout–vent length, shank length). Species could be separated into groups using MDA data, but these groups were not well supported statistically: only 63.9% of specimens were identified correctly by their measurements alone.

A plot of DS1 against DS2 (fig. 2) illustrates that some differences exist between species along both the size (DS1) and shape (DS2) axis. However, this graphic representation produces greatly overlapping morphospaces. The morphometric data set is insufficient to produce discrete, species-level separation.

Table 1: List and description of 20 measurements taken from 870 specimens of Lesser Antillean *Eleutherodactylus*. All measurements were log-transformed before principal components and discriminant function analyses.

Tab. 1: Definition von 20 Meßstrecken, deren Längen bei der Untersuchung von 870 *Eleutherodactylus*-Exemplaren von den Kleinen Antillen gemessen wurden. Alle Meßwerte gingen log-transformiert in die Hauptkomponenten- und Diskriminanzanalyse ein.

Measurement Meßstrecke	Description Beschreibung
Head width Kopfbreite	distance between anterior edges of tympana Abstand zwischen den vorderen Trommelfellrändern
Eye diameter Augendurchmesser	greatest distance from anterior to posterior größte anterio-posteriore Ausdehnung
Eye–Naris distance Abstand Auge-Nasenöffnung	anterior edge of eye to posterior edge of naris vorderer Augenrand bis hinterer Nasenöffnungsrand
Tympanum diameter Trommelfelldurchmesser	from anterior to posterior extreme größte anterio-posteriore Ausdehnung
Tympanum–Eye distance Abstand Trommelfell-Auge	shortest distance from anterior edge of tympanum to posterior edge of eye / kürzeste Entfernung zwischen vorderem Trommelfellrand und hinterem Augenrand
Interorbital distance Augenhöhlenabstand	shortest distance between eyes across skull kürzester Augenabstand über den Schädel gemessen
Snout length Schnauzenlänge	tip of snout to mid-skull between eyes Schnauzenspitze bis Schädelmitte zwischen den Augen
Internarial distance Nasenöffnungsabstand	measured between medial edges of nares gemessen zwischen den inneren Rändern
Tympanum–Naris Abstand Trommelfell-Nasenöffnung	anterior edge of tympanum to posterior edge of naris vorderer Trommelfell- bis hinterer Nasenöffnungsrand
Snout–Vent length Kopf-Rumpf-Länge	tip of snout to posterior margin of vent von der Schnauzenspitze bis zur Afteröffnung
Finger lengths Fingerlängen	dorsal measurement from base to tip of finger dorsale Messung von der Basis zur Spitze des Fingers
Hand length Handlänge	tip of third finger to wrist von der Spitze des dritten Fingers bis zum Handgelenk
Length of longest toe Länge der längsten Zehe	dorsal measurement from base to tip of toe dorsale Messung von der Basis zur Spitze der Zehe
Foot length Fußlänge	tip of longest toe to back of heel von der Spitze der längsten Zehe bis zum Fersenende
Thigh length Oberschenkellänge	anus to knee vom After bis zum Knie
Shank length Unterschenkellänge	knee to heel vom Knie bis zur Ferse
Forearm length Unterarmlänge	wrist to elbow vom Handgelenk bis zum Ellenbogengelenk

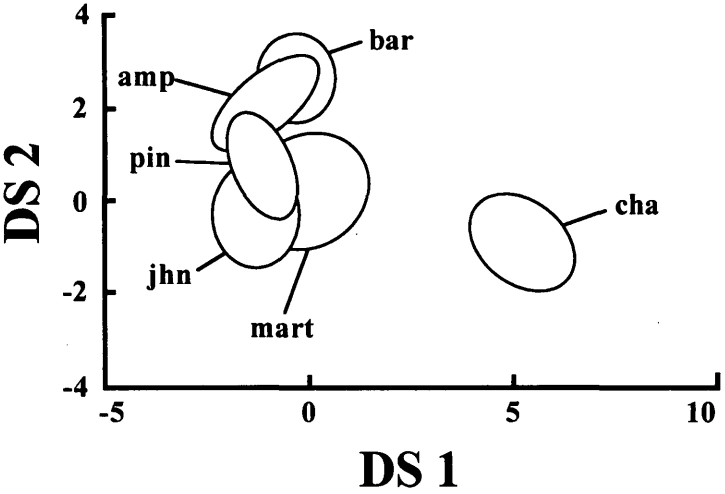

Fig. 2: Discriminant score (DS) plot for results of a multiple discriminant function analysis of 870 specimens of *Eleutherodactylus* from the Lesser Antilles. Species are coded as "amp" (*E. amplinympha*), "bar" (*E. barlagnei*), "cha" (*E. charlottevillensis*), "jhn" (*E. johnstonei*), "mart" (*E. martinicensis*), and "pin" (*E. pinchoni*).

Abb. 2: Grafische Darstellung der ersten zwei Diskriminanten aus einer multiplen Diskriminantfunktionsanalyse von 870 *Eleutherodactylus* - Exemplaren der Kleinen Antillen. Abkürzungen für die Arten sind wie folgt: "amp" (*E. amplinympha*), "bar" (*E. barlagnei*), "cha" (*E. charlottevillensis*), "jhn" (*E. johnstonei*), "mart" (*E. martinicensis*), "pin" (*E. pinchoni*).

Toepad area

Size-corrected toepad area differed among species. Among Lesser Antillean *Eleutherodactylus*, this variable was proportional to shank length, with species clustering quite tightly ($r^2 = 0.640$) around a line with a slope of 1.87 in a ln-ln plot (fig. 3). Neither SVL nor total toepad area were significant contributors to shank length in multiple regression analyses of mean values for all species separated or combined ($P \leq 0.05$), indicating the relative independence of these characters.

DISCUSSION

The morphometric data are insufficient to retrieve taxonomic information for Lesser Antillean *Eleutherodactylus* with a high degree of reproducibility, despite the fundamentally different life style adaptations. Although this outcome is not a surprise in view of the fact that taxonomists have struggled for centuries with the genus *Eleutherodactylus* because of its overall morphological similarity, it is interesting that there is no signal from morphometrics to reflect the diverse lifestyles of these taxa. This suggests that in these species behavioral and physiological adaptation precede morphological evolution.

Such a discrepancy between life-style diversity and morphometric homogeneity may be explained in terms of organismal and environmental interactions, and is attested to by adaptations as wide-ranging as beak specialization for seeds in finches of the genus *Geospiza* (GRANT & GRANT 1989), aquatic adaptations of behavior in Galapagos marine iguanas, genus *Amblyrhynchus* (DAWSON et al. 1977), or structure and function in Mesozoic reptiles (CALD-

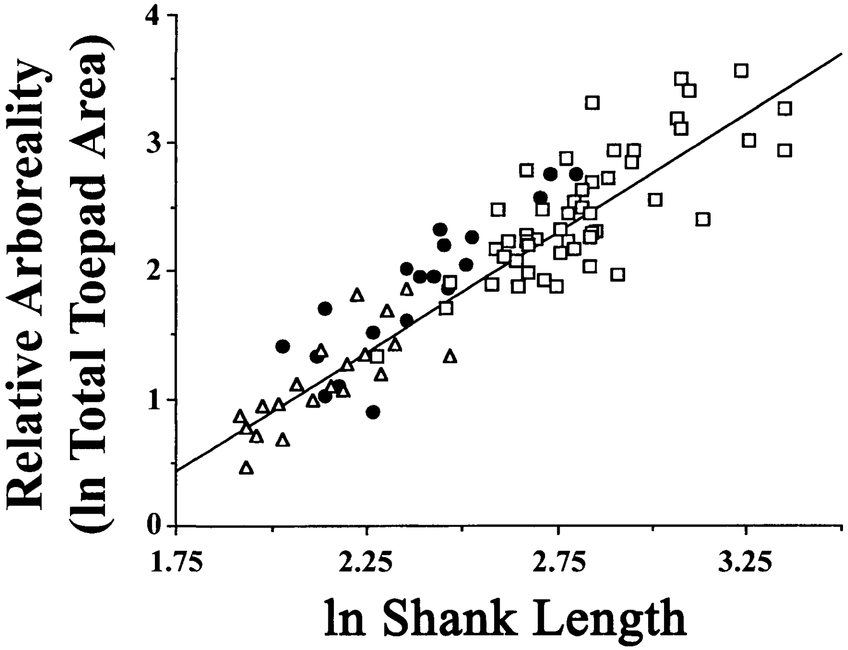

Fig. 3: Degree of arboreality of Lesser Antillean *Eleutherodactylus* as indicated by a plot of ln total toepad area against ln shank length. Total toepad area was size-corrected using snout-vent length. The regression line has a slope of 1.87 ($r^2 = 0.640$). The miniaturized, terrestrial species (*E. pinchoni*) is denoted by triangles, the ecological generalist *E. johnstonei* by closed circles, and the most arboreal species (*E. martinicensis*) by squares.

Abb. 3: Grafische Darstellung der Fähigkeit zum Baumbewohnen bei *Eleutherodactylus*-Arten der Kleinen Antillen. Die Relation der Haftscheiben-Gesamtfläche gegenüber der Unterschenkel-Länge ist hier in einem Schaubild von natürlichen Logarithmen verbildlicht. Die Größe der Haftscheiben-Gesamtfläche wurde hinsichtlich der Kopf-Rumpf-Länge korrigiert. Die Regression hat eine Steigung von 1,87 ($r^2 = 0,640$). Die kleinwüchsige, bodenbewohnende Spezies (*E. pinchoni*) ist durch Dreiecke gekennzeichnet, der ökologische Generalist *E. johnstonei* durch dunkle Kreise und die dem Leben in Bäumen am stärksten angepaßte Art (*E. martinicensis*) durch Vierecke.

WELL et al. 1995; CARROLL 1984). In *Geospiza*, the crucial factor affecting niche occupancy is beak size and shape, whereas in *Amblyrhynchus*, it is the development of a novel foraging behavior. For mosasaurs, plesiosaurs, and advanced ichthyosaurs, specializations for aquatic propulsion were apparently achieved by behaviorally modifying fore- and hindlimb movements, eventually resulting in changes of limb and limb girdle morphology while retaining a constant overall body form (CARROLL 1984). The data from Lesser Antillean *Eleutherodactylus* show that these frogs are becoming differentiating in size and shape, but more slowly than in their ecology and their concomitant physiology. This high degree of adaptability without the need for a priori phenotypic modification is probably a major factor in creating large radiations, such as *Bufo*, Greater Antillean *Eleutherodactylus*, Middle American *Hyla*, and Eurasian *Rana* among extant anuran genera, as well as several of the larger radiations of paleozoic amphibians or mesozoic reptiles (CARROLL 1988).

Comparative data from digital pad size provide further evidence for the influence of ecology/microhabitat on evolution. Different degrees of adaptation to climbing require appropriate development of toepads, and it has been shown that even within genera, variation in size and structure of toepads can be great (GREEN & SIMON 1986). Among Lesser Antillean *Eleutherodactylus*, toepad development reflects disparate life-styles. The species with the best developed toepads (*E. martinicensis*) is found at the upper extreme for both shank and toepad size (fig. 3) and is actually more arboreal than the others. Functional digital pads are progressively less important for semi-aquatic, generalist, and ground-dwelling life-styles, a prediction reflected by the data (fig. 3). The close quantitative relationship of these selected morphological and life-style characters shows that up to this point in the evolution of these species, the influence of ecology on morphology has been more significant than vice versa. Furthermore, I conclude that the disparate life-styles of these frogs have evolved by optimization of fitness through successful phenotypic adaptation in an environmental context, reflecting exactly the theory of REEVE & SHERMAN (1993).

ACKNOWLEDGEMENTS

I thank COURTNEY GEORGE (West Hartford, Connecticut, USA), HEATHER GRAY (Montréal, Canada), GUDRUN VON STÖSSER (Berlin, Germany), HELMUT SCHWARTEN (Malente-Gremsmühlen, Germany), TIM SHARBEL (Weimar, Germany), DOMINIC VON STÖSSER (Windhoek, Namibia), and AXEL WERRES (Hannover, Germany) for assistance in the field, and HENRY REISWIG (Montréal, Canada) for equipment and digitizing assistance. Discussions with CHRISTINE DWYER (Riverside, California, USA), DAVID GREEN (Montréal, Canada), and TIM SHARBEL were important in shaping some of the ideas presented here. Thanks to LEE GRISMER (Riverside, California, USA) for reading a first draft of the manuscript. My research was supported by grants from the Hans-Krüger-Stiftung and the Studienstiftung des Deutschen Volkes, Germany, by an NSERC Canada operating grant to DAVID GREEN, and by grants from the University Research Council and the College of Arts and Scienes at La Sierra University, Riverside.

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DATE OF SUBMISSION: October 30, 2001 Corresponding editor: Heinz Grillitsch

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Zeitschrift/Journal: Herpetozoa

Jahr/Year: 2002

Band/Volume: 14_3_4

Autor(en)/Author(s): Kaiser Hinrich

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