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Evolution and ecology of developmental processes and of the resulting morphology: directional asymmetry in hindlimbs of Agamidae and Lacertidae (Reptilia: Lacertilia)

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In this paper, the evolution and ecology of directional asymmetry (DA) during the developmental trajectory (DT) is compared with that of its product, morphological DA (MDA). DT and MDA are calculated for two bilateral morphological scale characters of lizards, the number of subdigital lamellae beneath the fourth toe in 10 agamid and 28 lacertid taxa, and the number of rows of ventral scales in 12 lacertid taxa. MDA, the subtraction between left and right sides (classical measure of DA), is functional in adult animals. Results confirm the hypothesis that, in DT, the regression parameters *a* (constant) and *b* (regression slope) of counts on the right side with those on the left describe a developmental process. No phylogenetic or environmental effects were observed on *a* and *b*, but analyses considering both *a* and *b* together show non-random phyletic patterns. Independent analyses deduced the same ancestral DT in Agamidae and Lacertidae. In Lacertidae, distance between pairs of taxa in $a+b$ (standardized values) correlates positively with the phylogenetic distance between taxa. Phyletic trends in MDA are indirect, and due to the link of MDA with $a+b$. The MDA of species is more dissimilar in sympatry than in allopatry. The phyletic trends suggest evolution of DT, while the association of MDA with sympatry suggests that ecological pressures shape MDA in adult animals. Evolution of DT is independent from that of its product, MDA—adaptive determinism defines the result of, but not the mechanistic process of, development. Deterministic environmental processes define MDA, and deterministic evolutionary processes define the interactive result of *a* and *b*, but not each separately. According to circumstances, different DTs produce similar or different MDA, and a particular DT can produce different MDAs.

ADDITIONAL KEY WORDS:—allometry – developmental trajectory – injury – ovary – pholidosis – subdigital lamellae – unsuccessful predation.

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INTRODUCTION

The geometry of the primitive organism is approximately spherical. The major steps in the evolution of form involve the specialization of regions of this sphere, resulting in a loss of symmetry. Initially, the dorsal and ventral sides differentiate, then the anterior and posterior. The last step occurring in metazoans differentiates left and right sides, although secondary reversals to bilateral symmetry also exist in early chordates (Jefferies, Brown & Daley, 1996). Hence the study of asymmetries is at the core of macro-evolution. In animals possessing bilateral symmetry, several types of conspicuous, functional asymmetry sometimes occur (for review, see Palmer & Strobeck, 1986). However, the existence and function of evolutionary incipient stages are unknown (Palmer, Strobeck & Chippindale, 1993). Most studies deal with the ubiquitous fluctuating asymmetry (FA), a randomly distributed difference between right and left sides. Sometimes, asymmetry is directional (DA): either the right or the left side is systematically dominant in most individuals, as shown by a significant difference between the right and left sides (see review by Ludwig, 1932).

The classical measure of asymmetry, the difference between measures of a trait on left and right sides (in the following, MDA), fails to yield scale-independent measures of FA and DA, which can impede studies on evolutionary links between them (Palmer, 1996). In addition, these measures of FA and DA are not independent. Graham *et al.* (1998) proposed quantifying FA by the residual variance of the regression between left and right sides, and DA by the parameters of the regression between values on each side. This yields *a* (constant) and *b* (slope), together defining a developmental trajectory (DT). They interpret the regression parameters as follows. A regression constant *a*, significantly different from zero, indicates which side begins

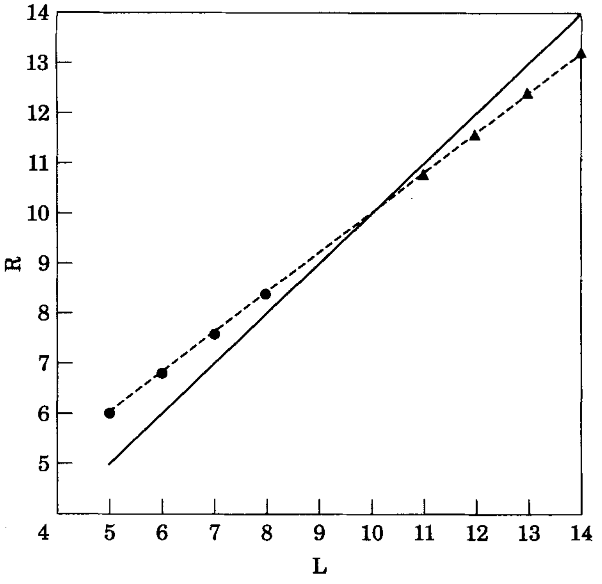

Figure 1. Plot of right (R) versus left (L) side character values. An imaginary example is given. Symbols represent observations on individual specimens. The interrupted line is the least square regression, using R as dependent and L as independent. The continuous line shows R = L. The regression parameters (constant and slope) are proposed as quantifications of directional asymmetry, the correlation coefficient as a quantification of fluctuating asymmetry.

first to develop; slope *b*, when significantly different from 1, indicates which side develops faster, an allometric component of DA. MDA describes the phenotype, while DT describes the components, *a* and *b*, of a process from which results the phenotype.

Figure 1 shows that both methods are complementary for describing DA. The dotted line is the regression line between left (L) and right (R) sides for an imaginary trait, and the continuous line represents perfect symmetry, R = L. MDA is opposite, where all pairs of observations on individuals yield points in the region where R>L (●), or where L>R (▲), but *a* and *b* are unchanged.

The effects of evolution and environmental conditions on MDA with those on DT were compared in order to explore the possibility of functional relationships between process and product. Behind this approach is the question whether the process of development is geared towards a particular result, as suggested for regeneration by Spilsbury (1961).

The first part of this study examines the empirical evidence for functional importance of minor MDA and tests the developmental interpretation of the regression parameters *a* (which side begins to develop first) and *b* (which develops fastest). The second part analyses phyletic trends and compares links between evolution, ecology and process with those with its product.

In an interspecies comparison of Agamidae, Seligmann (1998) showed a positive correlation between MDA of hindlimb morphology and DA in frequency of injury to hindlimbs (IDA). The causal direction of this correlation is not immediately evident, but it involves an association between enhanced probability of injury and the morphologically more developed side. Hence parameters *a* and *b*, because they do not quantify which side is most developed, are not expected to be correlated with IDA, while MDA is. Below, these correlations in Lacertidae and in Agamidae are explored.

Preliminary observations on pregnant lacertids show that when different numbers of eggs develop in the two ovaries, in most cases the right ovary has the higher number of eggs. It seems improbable that MDA in the number of rows of ventral scales correlates with directional asymmetry in egg number (EDA). However, the hypothesis that *a* and *b* determined for this character correlate positively with EDA seems more plausible, because DT and EDA measure relative dominance during developmental processes of the same region of the body. A significant correlation between EDA and DT would be evidence in favour of developmental interpretations of *a* and *b*.

Analysis of phenetic correlation matrices reveals important information on co-regulation of development of (often homologous) characters, as in the wings of butterflies (Monteiro, Brakefield & French, 1994, 1997; Paulsen, 1994, 1996; Paulsen & Nijhout, 1993). However, Steppan (1997a,b) showed in rodents that these matrices contain no or little information for deducing phylogenetic relationships, while the means of the morphological characters from which the matrices were calculated do. This finding suggests that evolution and environment define the 'ideal' morphology, but not the developmental process that underlies it, which is characterized by the covariance between characters. Haeckel (1870) long ago observed that vertebrates with very different developmental pathways develop—according to the phase of development—highly similar or different forms. This apparent finalism of developmental processes is also observed in regeneration. For example, several processes, according to the species, regenerate teleost pectoral fins, and each differs from the original process of development; however, all produce a replacing tissue with the same function as the original (Wagner & Misof, 1992).

It is in light of these considerations that in the second part of this study I compare associations of phylogeny and environment with MDA and DT, in order to explore the link between the deterministic pressures on the phenotype and the developmental process that produces it.

MATERIAL AND METHODS

Specimens examined

Lacertid specimens from four collections were examined. Sample sizes of specimens from each collection follow the taxon name in parentheses. The first number indicates specimens from the Hebrew University of Jerusalem, the second from Tel-Aviv University, the third from the Natural History Museum, London, and the fourth from the American Museum of Natural History, New York. *Acanthodactylus boskianus* (300/2/163/0), *A. cantoris* (0/0/59/28), *A. erythrurus* (0/0/56/0), *A. grandis* (52/1/13/0), *A. longipes* (30/42/20/0), *A. maculatus* (0/0/122/8), *A. opheodurus* (53/8/43/0), *A. pardalis* (E) (9/0/18/0), *A. pardalis* (N) (135/119/0/0), *A. schmidti* (0/0/164/0), *A. schreiberi* (134/105/0/0), *A. scutellatus* (N) (89/30/0/0), *A. scutellatus* (P) (53/42/0/0), *Adolfus africanus* (0/0/0/90), *Eremias argus* (0/0/0/170), *Heliobolus lugubris* (0/0/50/27), *Ichnotropis squamulosa* (0/0/20/7), *Lacerta laevis* (128/68/0/0), *Meroles* *suborbitalis* (0/0/30/12), *Mesalina brevirostris* (55/0/43/0), *M. guttulata* (563/0/0/0), *M. oliveiri* (121/0/0/0), *Ophisops elegans* (475/0/0/0), *Pedioplanis lineoocellata* (1/0/82/10), *P. namaquensis* (2/0/35/8), *Podarcis melisellensis* (12/0/0/0), *P. muralis* (16/0/0/0), *P. sicula* (33/0/0/0) and *Takydromus smaragdinus* (0/0/0/95). Additional specimens of *A. pardalis* (E) examined were: 41 (Field Museum of Natural History, Chicago), 3 (Museo Zoologico de 'La Specola', Firenze), 11 (National Museum, Prague), 20 (Smithsonian Institution, Washington) and 7 (Zoologisches Museum, Humboldt Universität, Berlin). Additional material of *A. pardalis* (N) was: 1 (Museo Zoologico de 'La Specola', Firenze) and 11 (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn). *A. pardalis* (E) and *A. pardalis* (N) are geographically isolated populations from the Mediterranean region of Egypt and Northern Cyrenaica (Libya) and from the central Negev (Israel), respectively. *A. scutellatus* (N) and *A. scutellatus* (P) indicate respectively populations inhabiting the dunes from the central region of the Negev and from the dunes along the coastal plain bordering the Mediterranean Sea in Israel. Populations from these biogeographical and climatological regions are likely to differ (unpublished results). Seventy specimens of *P. muralis* at the National Museum, Prague, were examined. In Agamidae, 87 *Agama colonorum* and 127 *A. cyanogaster* from the American Museum of Natural History were included in the analyses, in addition to data from eight other species from Seligmann (1998).

Frequency of injury

Frequency of injury (%I) on the right and left hindlimbs is the percentage of individual lizards lacking at least one part of that hindlimb, not including claws. %I increases with the longevity of animals (Schall & Pianka, 1980). As a consequence, in long-lived species, few animals undergo exposure times to injury inducing agents equivalent to those experienced by members of the comparatively more numerous species with shorter longevity. Hence variation in longevity may result in differences in both frequency of injury and accuracy of the injury. The difference between %I on right and left sides (R-L) quantifies directional asymmetry in injury frequency on hindlimbs (IDA). When making interspecies comparisons, differences in longevity should be taken into account, as indicated by the results of Bustard & Hughes (1966). The comparison between %I on right and left sides with equal longevities probably cancels most effects on IDA of variation in longevity. IDA is a valid quantification of asymmetry in frequency of injury based on the condition that the probability of injury on one side is independent of injury on the other. 2 × 2 contingency tables were used to test this assumption. The low frequency of limb injuries does not allow for statistically significant comparison between sexes, hence estimates are pooled.

Asymmetry in ovary fertility

I used data collected by Frankenberg & Werner both published in their 1991 study and available at the Hebrew University on fertility of reptiles derived from x-ray photographs. Additional data from photographs made by Y. L. Werner of Egyptian *A. pardalis* from the Natural History Museum, London, were used. I quantified DA in fertility by the mean of the difference between egg numbers counted in the right and left ovaries. Sign tests determine whether the number of females with more eggs on the right side differs significantly from half of the sample. Data on fertility asymmetry were available from 12 lacertids.

Morphological characters: subdigital lamellae of the fourth toe and numbers of ventral rows

Ontogenetic changes are likely in mensural characters. In order to avoid this difficulty, I chose scale characters to quantify DA because these characters are determined during embryogenesis (Maderson, 1965). Thus placing an adult animal on the developmental trajectory shown in Figure 1 would not be determined by the size of the animal (or its age), but by the embryological differentiation rate of the character, or the time at which this character stopped differentiating. Problems in the use of highly discrete, meristic characters for this kind of study were discussed by Swain (1987) who advised the use of characters with more than five different counts, a condition fulfilled by the characters used in this study. The subdigital lamellae (for illustration, see Smith, 1935) of the fourth toe were counted bilaterally. DA in subdigital lamellae of the fourth toe in one species is quantified by two methods. (I) MDA is the difference between numbers counted on right and left sides (R-L), divided by the mean of the subdigital lamellae beneath the fourth toe on both sides. Size scaling has to be justified by statistical means, but I did not find qualitatively different results when analysing data without it. I settled on size scaling because a difference between sides of a unit has a different meaning if the character count is 5 (asymmetry accounts for 20% of the character) or 20 (asymmetry accounts for 5%). In addition, previous publications on other taxa used this method to quantify MDA (i.e. Werner, Rothenstein & Sivan, 1991), and future studies might gain from uniformity in methodology, especially for comparing between data originating from different studies. MDA in each species is the mean MDA for all individuals examined. Tests for statistical significance of MDA and sexual dimorphism in MDA were as used by Werner *et al.* (1991). (II) a and b are the parameters (constant and slope, respectively) of the reduced major axis regression between counts on right (dependent) and left (independent) sides. The slope of the regression between left side as dependent and right as independent is a simple transformation of a ($1/a$). Therefore I calculate only the regression between left (x-axis) and right (y-axis) sides. MDA results from the joint effects of a and b, therefore I quantify the relative importance of a versus b. This is particularly relevant, because in all the cases of this study, a and b were negatively correlated ($r = -0.99$). Hence, each component a and b of DT indicates opposite dominance during the developmental process. The residual of b as a function of a gives an indication on which among a or b has the strongest effect. Positive values indicate that the tendency towards right side dominance in b is stronger than the associated opposite tendency towards left side dominance in a. This residual of b as a function of a is in our particular case mathematically equivalent to the sum of the standardized values (z scores) of a and b, and is referred to in the following as $a+b$. All hypotheses were tested on a, b, and $a+b$, but results quote $a+b$ only in cases where qualitatively different results were obtained for this index. The same procedures quantify DA in the number of ventral rows in the 12 lacertids for which fertility data were available, but only counts on females were included in the calculations. For MDA, sexes were pooled because *t*-tests revealed significant differences between sexes in none of the species examined, even at $P<0.05$. Analyses of covariance between R and L, in which the effect of sex on *b* was estimated by a dummy, binary variable (males = 1, females = 0), and on the slope *a* by a half dummy variable (the product of the count on the left side L and the first dummy variable), did not reveal any significant effect of sex on the parameters of the regression at $P<0.05$ in any species. Hence estimates of regression parameters are for pooled sexes.

Grouping taxa within developmental trajectories

I aimed to test whether modalities exist in DT, because discontinuities might exist in the distributions of *a* and *b*. In other words, to determine whether it is justified to group several taxa into one DT. In each family, for the number of subdigital lamellae, I tested the significance of difference between DT of each taxon as compared to pooled taxa: lizards from all taxa were pooled, and R was regressed as a function of L, and of 2*k dummy variables (k = the number of taxa). For each taxon i, one dummy variable (value 1 for individuals of taxon i, and 0 for all others) tests for the difference of *a* in that particular taxon with *a* for the pool of all other taxa. The other dummy variable (the product of the first dummy variable with L) tests the homogeneity of the slope of that taxon with that of pooled other taxa. After a first run of this test, it was run a second time, including only taxa with at least one of their regression parameters significantly different from those of the other pooled taxa. This procedure was repeated until taxa grouped were homogenous in both *a* and *b*: no dummy variable indicated statistically significant difference with the regression parameters of the pooled taxa included in that analysis at $P<0.05$. I describe the DT of taxa for which it did not differ significantly by the weighted means of *a* and *b*, according to sample sizes.

The relationship between subdigital lamellae counts and toe length

I calculated the correlation between the length (measured to an accuracy of 0.1 mm with calipers) and the number of subdigital lamellae of the fourth toe, when measurements available. Allometric size effects on toe length were accounted for by calculating the residual of toe length from the regression between toe length (dependent) and rostrum–anus length (measured to the nearest 0.5 mm), as discussed by Reist (1985).

Phylogenetic analyses

Interspecies comparisons have to take into account the phylogenetic relationships of the taxa involved. Phylogenetic hypotheses were constructed for Lacertidae according to Arnold (1983, 1989, 1991), and for ten Agamidae according to Moody (1980). Relationships among closely related species as the three *Trapelus* spp. cannot be deduced from phylogenies of Moody (1980). I assumed that the psammophile species *T. savignii* is a derived form, and supposed that *T. pallidus* and *T. ruderata* are sister taxa. Using similar rationals in Lacertidae, I considered *M. brevirostris* to be derived, *M. olivieri* and *M. guttulata* to be sister taxa, and *A. scutellatus* from the coastal plain to be derived as compared to *A. scutellatus* from the central Negev. Correlations with alternative evolutionary scenarios were also tested: results were qualitatively similar. The correlations between IDA and the various measures of DA were tested by least square correlation coefficients, for values and phylogenetic contrasts (Felsenstein, 1985) calculated according to the phylogenetic hypotheses (Table 1). Correlations based on phylogenetic contrasts did not differ qualitatively from regular analyses: results presented do not include analyses of phylogenetic contrasts.

For the number of subdigital lamellae in Lacertidae, I tested for association between phylogenetic processes and the variation of L and R, the mean number of subdigital lamellae on left and right sides, MDA, a, b, and $a+b$. The absolute value of the difference between all combinations of two species for each of the former characters was calculated. These distance matrices will henceforth be referred to as mL, mR, mMDA, ma, mb, m$a+b$. Phylogenetic distances between all the combinations of two species were quantified by the number of changes in character states since the most recent common ancestor, using morphological data published by Arnold (1983, 1989, 1991, 1997) and confirmed by mitochondrial DNA data of Harris, Arnold & Thomas (1998). Testing the statistical significance of correlations and regressions between matrices is problematic, because the observations, the different values in each matrix, are not independent. I used the most conservative procedure to resolve this problem: correlation and regression coefficients are transformed into t values according to usual methods, but I tested their significance by using as number of degrees of freedom the number of entries to the matrix, hence the number of taxa involved, and not the number of combinations between taxa. The phylogenetic hypothesis of Moody (1980) has still not been confirmed by other workers and methods, hence a precise quantitative phylogenetic analysis was not performed in Agamidae.

RESULTS

Directional asymmetry in hindlimbs: mean difference method

Tables 1 and 2 present the frequencies of injuries (I) on right and left hindlimbs in 28 taxa of Lacertidae and 10 of Agamidae, respectively. In Agamidae, the lack of animals with injury on both hindlimbs suggested that in this family injuries are independent: the occurrence of an injury does not increase the risk for injury on the other side. Contingency tables (2 × 2) did not reveal a significant negative association between injury on one side and injury on the other side. In contrast, for pooled Lacertidae, a 2 × 2 contingency table shows a significant association between injury occurrence on left and right sides: there were a total of 19 individuals with both right and left hindlimbs injured, which is much more than would be expected by chance. But injuries on limbs are rare, and the joint occurrence of injuries on

TABLE 1. Percentage of injured left and right limbs and quantifications of directional asymmetry in subdigital lamellae beneath the fourth toe for 28 taxa of Lacertidae. %I(l) and %I(r) are the percentages of individuals with injury on left, respectively right hindlimbs. *N* is the sample size of specimens examined for injuries. MDA is the mean of the subtraction of the count of subdigital lamellae on the left side from the right side, divided by the mean count for both sides. R and L are the mean number of subdigital lamellae on right and left sides, respectively. Numbers following means are standard deviations. r^2 is the square of the correlation coefficient between subdigital lamellae counts on right and left sides. *a* is the constant and *b* is the regression coefficient of the regression between counts on left and right sides, where the left side is the x-axis. *r* is the correlation coefficient between the size adjusted length of the fourth toe (regression method) and the mean count of subdigital lamellae on both sides. Bilateral counts of the subdigital lamellae were on *n* specimens

Species	%I(l)	%I(r)	*N*	L	R	MDA	r^2	*a*	*b*	*r*	*n*
Acanthodactylus boskianus	3.44	1.51	465	21.56, 1.53	21.79, 1.53	0.0024	0.68	0.5677	0.9777	0.21	159
A. cantoris	6.90	4.60	87	21.81, 1.33	21.84, 1.55	0.0098	0.55	−3.6605	1.1691		48
A. erythrurus	5.36	3.57	56	22.40, 1.50	22.50, 1.57	0.0043	0.59	−0.9265	1.0458		20
A. grandis	3.39	1.70	66	22.65, 1.62	22.62, 1.63	0.0040	0.69	−0.1964	1.0073	0.22	52
A. longipes	0.00	0.00	92	24.08, 1.27	24.03, 1.48	0.0116	0.64	−4.0984	1.1683	0.29	70
A. maculatus	0.91	0.91	130	20.36, 1.57	20.33, 1.73	−0.0005	0.36	−2.1459	1.1042		28
A. opheodurus	0.00	0.01	104	21.10, 1.61	21.10, 1.51	0.0168	0.68	1.1817	0.9439	0.19	34
A. pardalis (E)	3.00	7.10	109	20.48, 1.56	20.56, 1.60	0.0045	0.68	−0.3190	1.0197	0.27	109
A. pardalis (I)	2.30	2.30	266	19.86, 1.27	19.88, 1.27	0.0027	0.57	−0.0267	1.0023	0.24	266
A. schmidti	1.39	2.08	164	21.80, 1.21	22.40, 1.32	0.0269	0.42	−1.3988	1.0917		20
A. schreiberi	9.00	9.00	239	20.83, 1.09	20.41, 1.43	0.0041	0.55	−6.5663	1.3188	0.10	190
A. scutellatus (N)	2.78	0.00	119	22.70, 1.78	22.80, 1.60	−0.0002	0.62	2.4776	0.8955	0.17	119
A. scutellatus (P)	2.68	0.67	95	23.91, 1.96	23.87, 1.96	0.0025	0.52	0.0343	0.9970	0.15	91
Adolfus africanus	1.11	2.22	90	18.27, 1.20	18.92, 1.34	0.0348	0.65	−1.5077	1.1182		90
Eremias argus	0.60	0.60	170	21.56, 1.70	22.06, 1.76	0.0228	0.46	−0.2081	1.0328		32
Heliobolus lugubris	5.19	5.19	77	26.20, 1.72	26.29, 1.62	0.0042	0.62	2.1744	0.9207		52
Ichnotropis squamulosa	7.41	0.00	27	20.07, 2.04	20.07, 2.07	0.0001	0.64	−0.3689	1.0184		27
Lacerta laevis	1.53	3.57	196	30.18, 2.48	30.30, 2.53	0.0136	0.75	−0.4952	1.0206	0.32	196
Mesalina brevirostris	0.00	0.00	98	23.20, 1.36	23.33, 1.32	0.0059	0.52	0.8391	0.9694		55
M. guttulata	0.71	0.53	563	22.17, 1.07	22.36, 1.17	0.0200	0.51	−1.9424	1.0959	−0.10	70
M. oliveiri	0.83	0.83	121	21.59, 1.36	21.69, 1.38	−0.0032	0.72	−0.1323	1.0106	0.25	121
Meroles suborbitalis	7.14	2.38	42	25.03, 2.04	25.00, 2.13	−0.0016	0.66	−1.0972	1.0425		31
Ophisops elegans	2.30	1.30	475	22.29, 2.11	22.41, 2.03	0.0178	0.70	0.9611	0.9620	0.32	187
Pedioplanis lineoocellata	10.75	6.45	93	26.00, 2.06	26.15, 2.21	0.0080	0.18	−1.6899	1.0708		33
P. namaquensis	6.67	8.89	45	26.55, 2.32	26.69, 2.24	0.0089	0.58	1.1261	0.9628		32
Podarcis muralis	3.49	3.49	86	25.08, 1.86	25.48, 2.08	0.0121	0.77	−2.5895	1.1193		25
P. sicula			33	26.77, 2.33	27.13, 2.66	−0.0128	0.80	−3.2592	1.1355		33
Takydromus smaragdinus	0.00	1.05	95	28.05, 2.33	28.30, 2.43	0.0086	0.68	−0.9830	1.0439		20

TABLE 2. Percentage of injured left and right limbs and quantifications of directional asymmetry in subdigital lamellae beneath the fourth toe for 10 agamid taxa. Abbreviations as in Table 1

Species	%I(l)	%I(r)	*N*	MDA	L
Agama colonorum	0.71	2.14	140	−0.0197	21.70, 1.59
A. cyanogaster	0.00	2.36	110	0.0055	22.41, 1.42
Ctenophorus reticulatus	0.00	0.00	35	−0.0016	22.86, 1.99
Laudakia stellio	3.00	2.75	397	−0.0007	20.41, 2.46
Pseudotrapelus sinaitus	3.11	0.60	86	−0.0022	21.95, 1.61
Trapelus pallidus	0.82	1.65	209	0.0016	18.11, 1.80
T. ruderata	1.72	5.17	48	0.0059	18.76, 1.73
T. savignii	3.19	4.26	45	0.0029	23.87, 2.07
Uromastyx aegyptius	0.81	1.61	49	0.0008	20.65, 1.62
U. ornatus	3.45	13.79	26	0.0197	16.26, 1.19

Species	R	r^2	*a*	*b*	*n*
Agama colonorum	21.27, 1.53	0.29	0.4543	0.9595	27
A. cyanogaster	22.54, 1.88	0.51	−7.1186	1.3235	33
Ctenophorus reticulatus	22.80, 1.70	0.58	3.2079	0.8572	35
Laudakia stellio	20.40, 2.49	0.83	−0.3248	1.0153	397
Pseudotrapelus sinaitus	21.98, 1.67	0.45	−0.7857	1.0370	86
Trapelus pallidus	18.10, 1.79	0.56	0.0882	0.9948	209
T. ruderata	18.94, 2.10	0.48	−3.8111	1.2131	48
T. savignii	23.82, 2.02	0.79	0.4400	0.9794	45
Uromastyx aegyptius	20.69, 1.66	0.65	−0.4679	1.0244	49
U. ornatus	16.48, 1.10	0.40	1.4282	0.9260	26

both sides is even rarer, even in a situation that suggests a probability higher than expected by chance of such an event. Hence sample sizes did not enable to test for association between injury on both sides in single species. Sexes were pooled because differences between sexes in MDA were never significant (data not shown). This is in agreement with a study on *Ptyodactylus* (Gekkonidae) (Werner *et al.*, 1991) and on Agamidae (Seligmann, 1998) where sexual dimorphism in MDA was never significant in any species. Statistically significant MDA was rare: MDA was significantly different from zero (two-tailed *t*-tests) in 4/28 species (*A. boskianus*, $P=0.023$; *A. schmidtii*, $P=0.038$; *E. argus*, $P=0.048$; and *L. laevis*, $P=0.011$), which is more than the 1.4 cases (5%) which might be expected by pure chance. This contrasts with the study on *Ptyodactylus* spp. A significant tendency at the family level for phenotypic right side dominance exists in Lacertidae (MDA was positive in 23/28 taxa, $P<0.02$).

Directional asymmetry in hindlimbs: regression parameters

Statistically significant DA in DT was rare in Lacertidae: *t*-tests yielded $P<0.05$ in 3/28 species for *a* and *b* in Table 1 (*Adolfus africanus*, $P=0.02$ and $P=0.005$; *A. longipes*, $P=0.03$ each; and *A. schreiberi*, $P=0.0001$ each), which is more than 1.4 cases which might be expected by pure chance. In Lacertidae, $a<0$ and $b>1$ in 20/28 taxa. This result suggests that in Lacertidae the right side develops faster, but the left side begins developing first. No tendency was observed at the family level in Agamidae. In Agamidae, significant side dominance was found in three taxa in *a* (*A. cyanogaster*, *Ctenophorus* and *T. ruderatus*, Table 2), which is more than 0.5 cases expected by pure chance.

TABLE 3. Means of developmental trajectories (DT) of taxa with homogeneous DT. The weighted mean of *a* and *b* was calculated for taxa with no significant difference in DT. Weighting was according to sample size. The column headed by 'Y=X' indicates the lack of difference with perfect bilateral symmetry. DTs in Agamidae and Lacertidae merged together are indicated below the column headed by 'Similar to'. 'Polarity' indicates which DTs are supposed primitive and derived according to the phylogenies of each family. DT1 is for *L. stellio*, DT2 for *A. colonorum*, *P. sinaitus* and *T. pallidus*, DT0 for the rest of Agamidae. DT3 is for *A. scutellatus* (N), DT4 for *P. sicula*, DT5 for *A. maculatus*, *A. pardalis* (I), *Adolfus* and *Heliobolus*, DT6 for the rest of Lacertidae

DT	*a*	*b*	Y=X	Similar to	Polarity
0	−1.15	1.06	No	DT6	Primitive
1	−0.33	1.02	Yes	DT5	Derived
2	−0.12	1.00	Yes		Derived
3	2.49	0.90	No		Derived
4	−3.26	1.14	No		Derived
5	−0.21	1.02	Yes	DT1	Derived
6	−1.14	1.06	No	DT0	Primitive

Regression analyses between MDA and *a* and *b* separately, and multiple regression between MDA (dependent) and *a* and *b* (independent) did not detect any significant relationship between MDA and *a* and *b* in Agamidae. In Lacertidae, the simple regression analyses did not detect any significant relationship of any regression parameter with MDA ($P>0.40$), but the multiple regression is significant ($r=0.61$, $P<0.001$), and each *a* and *b* affect positively MDA ($P<0.001$). Similarly, MDA and $a+b$ were significantly correlated in this family ($r=0.50$, $P<0.01$).

Grouping taxa within a few DTs

I found significant differences between DTs for subdigital lamellae of several taxa in each family, suggesting discontinuities in the variations of *a* and *b*: not all DTs are equiprobable. In Agamidae, a first run of analyses separates the slopes of *P. sinaitus* and *T. pallidus*, the constant of *L. stellio*, and both parameters of *A. colonorum* from the DT of the pool of all other taxa. Hence *A. cyanogaster*, *Ctenophorus*, *T. savignyi*, *T. ruderatus* and the two *Uromastyx* can be considered as having the same DT: DT0. This group also includes the three taxa in which *a* was shown to be significantly different from 0. Although no significant difference between Y=X was found for any of the remaining species, a second run separates *L. stellio* (DT1) from *A. colonorum*, *P. sinaitus* and *T. pallidus*. A third analysis including only the latter species did not detect differences in DT among them. They were hence assigned to DT2. Both *a* and *b* of DT1 were intermediary between DT2 and DT0: the hierarchy of right side dominance for *b* is DT2>DT1>DT0, and the opposite hierarchy was found for *a*. Similar analyses in Lacertidae detect DT3, *A. scutellatus* (N); DT4, *P. sicula*; DT5, *A. maculatus*, *A. pardalis* (I), *Adolfus* and *Heliobolus*; and DT6, the rest of the species. Table 3 shows that DT0 and DT6 are similar and thus pooled within DT0′, and that DT1 and DT5 are similar, thus pooled within DT1′. DT0′, DT3 and DT4 differ from Y=X. DT3 is outstanding among DTs as it is the only case where *a*

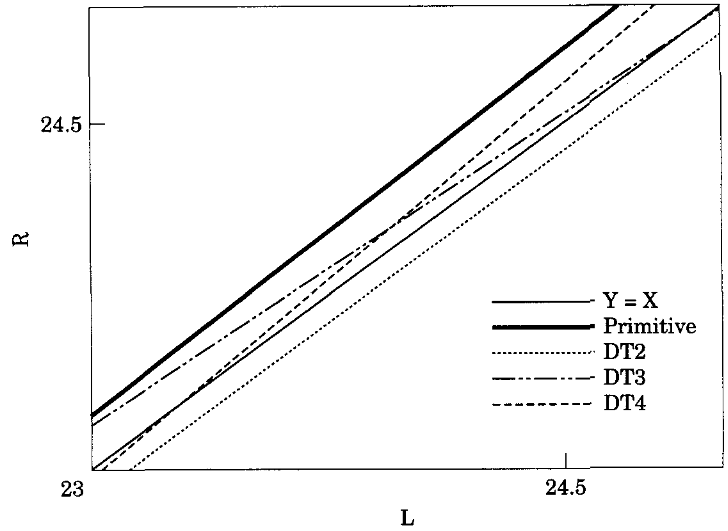

Figure 2. Plot of regression lines of right (R) versus left (L) side for the number of subdigital lamellae beneath the fourth toe for four representative DTs. DT0′ is the developmental trajectory found primitive in both Agamidae and Lacertidae. The line of bilateral symmetry Y = X is indicated, as well as DT2, a derived DT found in the Agamidae, *A. colonorum*, *P. sinaitus* and *T. pallidus*, and two derived DTs found in Lacertidae, DT3, *A. scutellatus* (N), and DT4, *P. sicula*.

indicates right side and *b* left-side dominance. Figure 2 displays DT0′, DT1, DT3 and DT4.

Relationships between asymmetry in injury frequency and morphological asymmetries

The correlation between MDA and IDA was stronger (*t*-test, $P<0.05$) in Agamidae than in Lacertidae ($r=0.66$ and $r=0.37$, respectively). This is probably because calculating IDA by the difference between injury frequency on each side implies the assumption that injury occurrence on one side is independent from the occurrence of injury on the other. This assumption is verified in Agamidae, but not in Lacertidae, and is the probable reason for the decreased correlation between MDA and IDA in this family. No significant correlations were found between IDA and *a* or *b*, and by multiple regression between IDA (dependent) and *a* and *b*, in none of the families.

DA in fertility and in number of transverse ventral rows of scales

Table 4 presents EDA, asymmetry in egg numbers between left and right sides, and MDA, *a* and *b* for the number of rows of ventral scales in females of 12 Lacertidae. There is a significant tendency over all taxa for dominance of the fertility of the right side (sign test, $P<0.01$). This difference is significant also inside some taxa: *A. boskianus*, *A. scutellatus* (N), *L. laevis* and *M. guttulata*.

MDA in numbers of ventral rows was significantly different from zero in two among 12 taxa (*A. pardalis* (I), $P=0.04$; and *M. guttulata*, $P=0.006$), which is more than the 0.6 cases that would be expected by pure chance. Both *a* and *b* showed

TABLE 4. Directional asymmetry in the number of eggs in ovaries (EDA) and in counts of ventral rows in females of 12 lacertid taxa. Underlined values of EDA show significant discrepancies from 0 (sign tests); values between parentheses are sample sizes of pregnant females. L and R constitute the mean number of ventral rows for left and right sides, respectively, for all females (*N*). MDA is the mean of the difference between counts of ventral rows on right and left sides, divided by the mean of the sides. *a* and *b* are the constant and coefficient of the reduced major axis regression between R (dependent) and L (independent). r^2 is the square of the correlation coefficient between R and L. Standard deviations are in italics

Species	EDA	*N*	L	R	MDA	r^2	*a*	*b*
Acanthodactylus boskianus	0.25 (26)	93	26.91 *1.78*	26.96 *2.02*	0.0007 *0.0354*	0.77	−3.5783 *1.4895*	1.1348 *0.0552*
A. opheodurus	0.25 (2)	51	26.31 *1.38*	26.53 *1.14*	0.0086 *0.0376*	0.50	4.7957 *2.1931*	0.8261 *0.0832*
A. pardalis (E)	0.29 (7)	39	32.18 *1.60*	32.33 *1.69*	0.0046 *0.0236*	0.81	−1.6601 *2.4442*	1.0563 *0.0759*
A. pardalis (I)	0.03 (44)	138	35.26 *1.54*	35.09 *1.68*	−0.0049 *0.0278*	0.67	−3.3755 *1.8975*	1.0906 *0.0538*
A. schreiberi	0.14 (14)	100	32.33 *1.80*	32.40 *1.86*	0.0024 *0.0285*	0.76	−1.0077 *1.6672*	1.0333 *0.0515*
A. scutellatus (N)	0.22 (16)	60	34.51 *1.90*	34.23 *1.66*	−0.0066 *0.0359*	0.58	4.0792 *2.5858*	0.8737 *0.0748*
A. scutellatus (P)	0.13 (4)	49	34.83 *1.59*	34.59 *1.59*	−0.0073 *0.0322*	0.56	−0.2400 *3.3755*	1.0000 *0.0968*
Lacerta agilis	−0.25 (2)	8	28.00 *1.63*	27.71 *1.70*	−0.0065 *0.0267*	0.91	−1.5090 *0.8358*	1.0436 *0.2483*
L. laevis	−0.22 (16)	90	27.98 *1.46*	27.88 *1.49*	−0.0036 *0.0280*	0.76	−0.6749 *1.5135*	1.0205 *0.0540*
Mesalina guttulata	0.22 (64)	27	31.22 *1.72*	31.70 *1.56*	0.0156 *0.0272*	0.76	3.3842 *2.8071*	0.9070 *0.0898*
Ophisops elegans	0.06 (16)	56	29.46 *1.80*	29.45 *1.81*	−0.0032 *0.0252*	0.82	−0.1737 *1.7241*	1.0056 *0.0583*
Podarcis melleselensis	0.38 (4)	12	28.50 *1.09*	29.00 *1.54*	0.0168 *0.0377*	0.50	−11.2661 *9.0185*	1.4128 *0.3162*

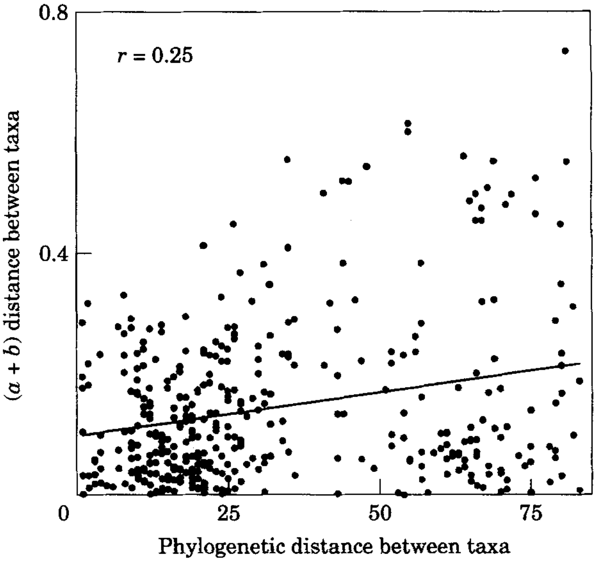

Figure 3. Divergence between species in $a+b$ as a function of their phylogenetic divergence (PD). Each data point represents a comparison between a pair of species. The y-axis is the absolute value of the difference between the residual of b as a function of a, in pairs of species. The x-axis is the number of changes in character states since the most recent common ancestor between the same pair of species.

significant dominance of one side in *A. boskianus* ($P<0.02$) and *A. opheodurus* ($P<0.05$), which is more than the 0.6 cases that would be expected by pure chance. I used weighted multiple regression to test the relationships between EDA (dependent) and a and b (independent) because of large differences in sample sizes of pregnant females ($r=0.59$, $P<0.05$). Regression coefficients of each a and b were significant and positive ($P<0.05$, one-tailed t-tests).

Phylogenetic analyses in Lacertidae

I calculated the absolute value of the difference between MDA values for all pairs of taxa and obtained phenotypic distance matrices for MDA. A similar matrix was calculated for L, R, a, b, and $a+b$. I calculated the correlation between each of these distance matrices and the matrix of phylogenetic distances (PD) between the same taxa, estimated by the number of character changes since the most recent ancestor. There were significant correlations between PD and each mL (0.49, $P<0.001$), mR (0.49, $P<0.001$), mMDA ($r=0.19$, $P<0.05$), m$a+b$ ($r=0.25$, $P<0.02$), but there was no significant effect of PD on each ma and mb ($r=0.009$ and -0.003, respectively). Partial correlation analyses revealed that the correlation between PD and mMDA is due to the correlation between MDA and $a+b$ ($r=0.51$, $P<0.001$), and not to a direct association between PD and mMDA. Hence only m$a+b$ correlates with PD (Fig.3), but neither of its components a and b, or the product of DT, MDA, correlated with PD. I calculated the distance matrix between species pairs for residuals of MDA from the regression between MDA and $a+b$, in order to test the association between sympatry and MDA, without the confounding effect of $a+b$. These residuals were consistently higher between sympatric pairs of species than between allopatric pairs of species ($t=2.20$, $df=26$, $P<0.05$), a result also found for mMDA itself. The effect of sympatry on mL and mR is opposite: at the same PD, sympatric species are less divergent in L and R than are allopatric species.

DISCUSSION

Significance of different measures of DA

The predictions made in the introduction on the significance of regression parameters are verified by the results. The fact that multiple regressions between MDA and a and b in some cases are significant (Lacertidae), and in other cases not (Agamidae), suggests that a and b are not equivalent to MDA. The relationship between the process and its result is complex. It is most likely that these methods quantify different aspects of DA: regression parameters are probably relevant to DA in developmental processes, and MDA measures the mean phenotypic result of these processes. Hence regression parameters cannot replace subtractions between left and right sides as quantifications of DA, but these methods are complementary.

Causes of DA

The correlation reported by Seligmann (1998) between IDA and MDA in Agamidae is confirmed in that family after the addition of two species to the analysis, and exists also in Lacertidae. In both families, the side with the higher scale count under the fourth toe has the highest frequency of injury. Injuries on toes are caused by intraspecific combats (Vitt *et al.*, 1974; Schoener & Schoener, 1980), but result probably mainly from unsuccessful predation attempts. Assuming that the causal direction of the relationship IDA-MDA is from IDA to MDA, the results would fit the frame set by Vermeij (1982) of unsuccessful predation as a major evolutionary factor. The positive association between injury probability on each hindlimb in Lacertidae contrasts with the lack of association in Agamidae. This situation probably reflects differences in the intensity of use of limbs in both families: although variation in foraging mode exists among Lacertidae (Perry *et al.*, 1990), this family can be considered as more actively foraging than Agamidae. Hence the frequent use of limbs for locomotion after injury is likely to increase the probability of further injury, as compared to lizards whose lifestyle might be compatible with injury to one hindlimb without increasing the probability of injury to the other. This hypothesis is strengthened by the interactive effect of experimentally induced toe loss with size on sprint performance in the teid *Cnemidophorus* (Dodd, 1993), an active forager.

The right antler in the fallow deer (*Dama dama*) is both morphologically more developed and more active during male combats (Alvarez, 1995). This observation suggests that IDA reflects 'handedness' in intensity of use of limbs. Hence the results presented above could be interpreted as that the limbs more intensively used (and more often injured) are also more developed. Ineich (1987) found a positive correlation between lengths and injury frequencies of fingers and toes in several

Scincidae and Gekkonidae, an observation confirmed on several species of other skinks by Hudson (1996). Hence the correlations between IDA and MDA at the interspecific level might result from the positive correlation between injury frequency and limb length. But the causal relationship between IDA and MDA remains obscure for the following reason. I did not find any correlation at the individual level between the injured side and the side with higher scale counts in either a single taxon or for pooled individuals from all taxa. At the inter-individual level, lizards with longer toes tend to have more subdigital lamellae; results therefore indicate that correlations between MDA in scale counts and IDA at the interspecific level do not result from increased injury frequencies on longer limbs. It seems that the correlation between IDA and MDA is due to a third, unknown factor, which affects at the level of individual lizards independently injury frequency and morphology. I suggest that each species has an overall level of relative dominance of one side over the other for all traits. Hence behavioural laterality in limb use might cause IDA at the population level. Independently, the same overall tendency for dominance of the same side causes DA in morphology; hence, at the level of intertaxa comparisons, a correlation appears between IDA and MDA which does not exist at the level of individuals. A similar hypothesis fits the results for egg number asymmetry: there was no correlation at the individual level between side dominance in ventral row counts and in egg numbers in any single taxon or pooled taxa; however, at the level of interspecies comparisons, EDA is correlated with *a* and *b*.

In the light of the results of this study, variations in individual levels of handedness, such as observed for example in hunting lions (*Panthera leo*) (Stander, 1992), do not correlate to pre-existing morphological differences between sides in the individual. Also in the example of *Dama dama*, the inter-individual variation in degree of laterality of use of antlers would not correlate with the level of morphological asymmetry. Unfortunately, the data cannot be adapted to test this hypothesis.

The interspecies correlations described in this study suggest that MDA levels are determined by evolutionary processes. The fact that the correlations are not observed at the level of individuals suggests that causation due to classical natural selection cannot be advocated in this case. Random drifts are unlikely, as there are overall tendencies for dominance of one side (e.g. the right side in Lacertidae), over all taxa. In addition, the correlation between morphological DA and traits obviously related to fitness (DA in injury frequency and fertility) makes an adaptive causation of the phenomena described here likely. Palmer (1996) stated that he finds it difficult to escape the conclusion that the evolution of DA has to be explained by direct environmental imprinting of embryo development, and his view fits the results of this study.

The correlation observed between DA in ovary fertility and in ventral scale rows strengthens the hypothesis of an overall tendency over all traits for a given level of dominance of one side, because scale counts are determined in embryos, while egg differentiation occurs in adult females. Hence the same unknown factor determines tendencies to side dominance at species levels, and influences at different phases the development of organisms.

Macro-evolution of DA

The overall tendency of the right ovary to produce more eggs in 12 lacertid taxa contrasts with the situation known in birds, where the right ovary is absent in adults

(Lofts & Murton, 1973), but concords with observations on DA in fertility between ovaries of mammals (Lopez-Gatius, 1997). It is doubtful but possible that the observation in Lacertidae is relevant to the conspicuous DAs in snake anatomy: the right ovary is more proximal than the left; and the lack of development of the left lung in advanced snakes (Goin *et al.*, 1962). It is probable that the constraints of locomotion modes in snakes and birds caused these asymmetries. But the variation observed in Lacertidae might reflect the situation existing in the ancestors of these groups before locomotion specialization. This consideration could be tested in the future by comparing DA in lizards with varying levels of limb reduction.

Other considerations suggest a link between locomotion and DA, and are compatible with the increased level of DA in snakes and birds as compared to lizards. Elitzur (1997) observed at the level of interphyletic comparisons in metazoans that evolution of active locomotion is positively correlated with the specialization of different parts of the body, as seen in the loss of radial, and in later evolutionary events, of bilateral, symmetries. He suggests that mobile animals can control the part of their body that they expose to defined situations or environments. The loss of bilateral symmetry in the specialization of left versus right limbs is apparent comparing MDA in the less mobile Agamidae to MDA in the more active Lacertidae. The repartition among left and right side dominance in MDA of subdigital lamellae is almost equal (4 left, 6 right) in Agamidae, indicating a kind of FA at the level of the family. But in Lacertidae, 23 among 28 taxa are right side dominant in MDA, suggesting in this family a strong evolutionary trend towards right side dominance in hindlimbs.

The primitive state in developmental trajectories of DA of the number of subdigital lamellae

The analysis of homogeneity of DTs revealed three separate DTs in Agamidae and four in Lacertidae. In Agamidae, DT0 involves the least derived species, *Uromastyx* and *Ctenophorus*, while the more derived species split into DT1 and DT2. It is interesting to note that DT0 includes species for which DT was significantly different from Y = X, while the derived DT1 and DT2, although significantly different from each other, do not differ significantly from Y = X. Hence the primitive state in Agamidae indicates DA in the development of subdigital lamellae, and the derived DTs suggest evolution towards symmetry.

In Lacertidae, DT6 includes most taxa, and among them all the most basal taxa, excluding *P. sicula* (DT4). DT3 was found only in *A. scutellatus* (N), and several species were grouped into DT5, including two taxa from the *pardalis* species complex, *A. pardalis* (I) and *A. maculatus*. Hence DT6 seems to describe the primitive DT in Lacertidae, while other DTs are derived. Comparisons among DTs from both families showed a high similarity between DT0 and DT6, justifying their merging into DT0′, from a strictly numerical point of view. This strengthens their status as primitive states in each of the families, and makes probable that DT0′ describes the primitive DT of that character in Lacertilia. Additional analyses of similar data from other lizard families could test this hypothesis.

Micro-evolution of process and product

The correlations between DA in injury frequency and morphological DA confirm that even minor MDA has significance. MDA probably also reflects adaptations to the habitat of a lizard species: higher morphological divergence in MDA exists between sympatric species. Sympatric species of lizards tend to occupy different habitats from the point of view of substrate, as shown for part of the species involved in this study by ecological descriptions of lizard communities in Morocco (Pérez-Mellado, 1992), in the central Negev (Shenbrot & Krasnov, 1997), and in Arabia (Arnold, 1984). The association between sympatry and increased divergence in MDA is probably a secondary effect of interspecific habitat displacement, and a primary result of adaptation to substrate, but both these statements should be considered as preliminary. Further comparative analyses might confirm the adaptation hypothesis, but experimental manipulation is the best way to test competitive niche displacement. Hence environmental constraints affect the phenotype of organisms, and even minor levels of MDA are no exception to this statement basic to adaptive theories of evolution. In contrast, the evolution of the mean number of subdigital lamellae, L and R, are directly affected by macroscopic parameters of the environment, because, controlling for variation in PD, sympatric species are more similar than allopatric species. This means that L and R are affected by variables such as climate: sympatric species might divide habitats according to substrate—which results in diverging adaptations at the level of MDA—but are exposed to similar overall climatic conditions. This rationale might suggest that adaptations to substrate are fast and reversible, and hence do not correlate with phylogeny, while adaptations to more general environmental conditions do.

Variation in MDA seems to be due to adaptations to immediate (ecological) constraints on the species, and only indirectly to historical (evolutionary) constraints, because the association between PD and MDA is through the intermediary of evolution of DT, the process from which MDA results. This suggests that adaptations in MDA can be considered as reversible, while changes in DT are less. It should be stressed that $a+b$, but not a or b, is correlated with PD. A deterministic process defines $a+b$, but no evolutionary constraint was apparent on a and b. Hence the adaptive and evolutionary trends in DA are emergent (in the sense of Gordon, 1991) because they cannot be observed at the level of the constitutive components of DT, a and b. This means that the components of the developmental process subjacent to MDA are relatively free to vary, and that this variation is independent from the processes acting on its product MDA. The environment determines MDA, but the subjacent process is not constrained by it in which ways it produces it. The question 'How do organisms do the right thing?' (Emlen *et al.*, 1998) is posed by the data presented here. There might be a parallel to draw with the adaptive determinism already described in plants of *Sorghum bicolor* exposed to salinity in conditions that induce physiological adaptation to salinity: Amzallag, Seligmann & Lerner (1995) suggested that the wide morphological variation among individual plants reflect the fact that individuals reach their goal, physiological adaptation, by different processes. In that system, there was even a positive correlation between the frequency at which plants developed different developmental pathways and the resulting levels of adaptation associated with these pathways in their new (saline) environment. Furthermore, small differences in environmental conditions besides salinity altered both the relative levels of resulting adaptation levels and the frequency with which plants entered developmental pathways. However, the positive correlation between adaptation level and the frequency (without selective mortality) of developmental pathways remained relatively constant (Seligmann & Amzallag, 1995). Hence in this experimental system, as in the evolutionary case described here, the environment defines the result, albeit not the precise process that produces adaptation to the environment.

The fact that the results of analyses of phenetic correlation matrices between morphological characters did not yield information relevant to the phylogenetic reconstruction of the relationships among mice taxa, while the states (means) of the same characters did, contradicts the results obtained here, where MDA, independently from DT, does not reveal phylogenetic patterns, while DT does. Differences in this respect are likely between taxa and characters. The fact that the separation between two halves of a developing egg after the initial cleavages results in the development of independent organisms in frogs, but in two halves of one organism in insects (Costello, 1955), suggests that the level of (pre)determination of the processes of development varies among taxa. From this point of view, the development of mice would appear as less determined than that of lizards, insofar as the analysis of DA in the number of subdigital lamellae in lizards is comparable with a large number of cranial characters in mice. But the main point that should be stressed is that the approach presented permits quantification of the characteristics of the process that produces MDA and the phenotypic result of the process.

CONCLUSIONS

(1) The slope and constant of the regression quantify an allometric and a constant component of directional asymmetry during developmental processes. They do not replace quantifications of DA based on subtraction between measures of sides, but are complementary in that they emphasize other aspects of the same phenomenon.

(2) In Lacertidae and Agamidae, directional asymmetry in frequency of hindlimb injury (IDA) and hindlimb morphology (MDA) are correlated, but statistically significant DA in the traits involved is rare.

(3) Variantion of MDA reflects reversible adaptations to the immediate environment of the species, while variation in the developmental trajectory (DT) that produces MDA is independent from the immediate environment of the species, but is determined by evolutionary processes.

(4) The environment defines the result of the process of development of MDA, but does not affect the mechanistic components of the process that produce MDA.

(5) The primitive state of DT is not bilateral symmetry in any of the families.

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