

Preliminary analysis of correlated evolution of morphology and ecological diversification in lacertid lizards

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Resum

S'ha investigat la diversitat morfològica en 129 espècies de lacèrtids i la seva relació amb l'ecologia, per mitjà de mètodes comparatius, utilitzant set variables morfomètriques. La mida corporal és la variable més important, determinant un gradient entre espècies de petita i gran mida independentment evolucionades al llarg de la filogènia dels lacèrtids. Aquesta variable està forta i positivament correlacionada amb les altres, emmascarant els patrons de diversitat morfològica. Anàlisis multivariants en les variables ajustades a la mida corporal mostren una covariació negativa entre les mides relatives de la cua i les extremitats.

Remarcablement, les espècies arborícoles i semiarborícoles (*Takydromus* i el clade africà equatorial) han aparegut dues vegades independentment durant l'evolució dels lacèrtids i es caracteritzen per cues extremadament llargues i extremitats anteriors relativament llargues en comparació a les posteriors. El llangardaix arborícola i planador *Holaspis*, amb la seva cua curta, constitueix l'única excepció. Un altre cas de convergència ha estat trobat en algunes espècies que es mouen dins de vegetació densa o herba (*Tropidosaura*, *Lacerta agilis*, *Takydromus amurensis* o *Zootoca*) que presenten cues llargues i extremitats curtes. Al contrari, les espècies que viuen en deserts, estepes o matollars amb escassa vegetació aïllada dins grans espais oberts han desenvolupat extremitats posteriors llargues i anteriors curtes per tal d'assolir elevades velocitats i maniobrabilitat. Aquest és el cas especialment de *Acanthodactylus* i *Eremias*

Abstract

Morphologic diversity was studied in 129 species of lacertid lizards and their relationship with ecology by means of comparative analysis on seven linear morphometric measurements. Body size is the most important variable determining, a continuum among small bodied species and larger ones independently evolved through the lacertid phylogeny. This variable is strongly and positively correlated with the others masking the patterns of morphologic diversity. Multivariate analysis on size-adjusted variables show a negative covariation among relative tail and limb length. Remarkably, arboreal and semiarboreal species (*Takydromus* and the Equatorial African clade) appeared two times independently during the evolution of lacertids and are characterized by extremely long tails, and relatively long forelimbs in comparison with hindlimb length. The arboreal and glider lizard *Holaspis* with their short tail constitute the only exception. Another case of convergence is found by

some species dwelling into dense vegetation or grass (*Tropidosaura*, *Lacerta agilis*, *Takydromus amurensis* or *Zootoca*) which have long tails and short limbs. On the opposite, species living in deserts, steppes or scrublands with scarce vegetation isolated into extended open areas have developed long hindlimbs and short forelimbs to achieve higher speed and maneuverability. This is especially the case of *Acanthodactylus* and *Eremias*.

Paraules clau: *Lacertidae*; diversitat morfològica; forma corporal; evolució ecològica.

Key words: *Lacertidae*; morphologic diversity; body morphology; ecological evolution.

INTRODUCTION

Lacertid lizards are a family of 250 species of squamate reptiles distributed across Eurasia and Africa. All the species are diurnal foragers and mainly insectivorous lizards, oviparous and heliothermic, with an typical squamate body plan with well developed extremities (Vitt & Pianka 2003). Molecular and morphologic evidences allows to define in lacertid lizards two subfamilies.

Gallotinae are mesic or xeric forms which are distributed in Canary Islands (endemic genus *Gallotia*) and western Mediterranean areas of Europe and Africa (*Psammodromus*) (Arnold 1989b; Fu 2000; Harris et al 1998).

Subfamily Lacertinae comprises the major number of species and diversity of ecology in the family and is divided in two main clades: Lacertini and Eremianidi. The former are basically Euroasiatic lizards with some north African representatives probably originated by a fast diversification (Fu 2000; Mayer & Pavlicev 2009). Within this clade *Takydromus* is endemic from the subtropical Asia, where they are the only lacertids present there (Arnold 1997). The other Lacertini are basically mesic forms of active foragers on ground, dense vegetation or rocks, from larger *Timon* and *Lacerta* to small *Podarcis*. This is a main European group, although some genus (*Timon*, *Podarcis* and *Scelarcis*) inhabits the Magrib area and other genus (i.e. *Phoenicolacerta* and *Anatololacerta*) reaches the Caucasus and the Middle East.

In contrasts, Eremianidi are a larger and older radiation of mainly xeric and mesic African lizards exhibiting a large diversity in terms of ecology and habitat. For example, they include rupicolous (*Australolacerta*), secretive dwellers (*Nucras*) o ground runners (*Ichnotropis*, *Pedioplanis* and *Meroles*). Based on the existence of many endemic and mesic genus in southern Africa (Branch 1998), probably this region has been the center for such species diversification. The other area exhibiting major species richness is the north of Africa, inhabited by xeric species belonging to the genus *Acanthodactylus* and *Mesalina*. Some species from this genus are also distributed in other arid areas in Iberian Peninsula and, from the Middle East to

India. In addition, a minor part of the species diversity in Eremianidi evolved in arid Asia (genus *Eremias* and *Ophisops*). Interestingly, a monophyletic clade of tropical species living in Equatorial Africa has been identified by molecular and morphologic studies, and is formed by the genus *Adolfus*, *Holaspis* and *Gastropholis* (Arnold 1989a; Mayer & Pavlicev 2009).

Although the body plan of lacertids is in general very conservative, some morphologic diversity may be constated, probably developed as a result of adaptation to wide variety of habitats (Arnold 1998-2004). Morphologic convergence seems to be plausible in this family due to their extensive geographic range and large number of species, living in radically different environments, as tropical or coniferous forest, mesic mediterranean scrub, savanna or deserts in north of Africa.

The main goal of this work is to evaluate the ecological diversification in lacertid lizards in relation to their body shape. I want to test whose of this factors influences the diversity of body shape in this family. Then, I reconstructed their ecological diversification across a phylogenetic tree. I also explore the basic patterns of body shape in lacertid lizards by means of the analysis of multivariate morphologic data using a comparative approach. Finally, I examine for covariation among the habitats in lacertids and their morphologic diversity in order to determine the existence of ecomorphs.

MATERIAL AND METHODS

The monograph of lacertid lizards from Albert Boulenger (1917) is the most comprehensive morphologic study of this family. For each species, they include raw data on eight linear morphometric measurements taken from preserved individuals from the British Museum of Natural History collections. Although Boulenger did not presented methodological details about how measurements were performed, it is likely that all were homologous and had the same error. The large number of species analyzed allows a unique opportunity to perform a large scale analysis of morphological evolution in lacertid lizards and test their correlation with the species ecology. Due to their poor ecologic relevance, a variable (the length from the snout to the forelimb length) was excluded. Then, I selected following seven variables: snout-vent length, head length, width and dept, fore and hindlimb length, and tail length. Data on this latter variable were only recorder by Boulenger from specimens with entire and non regenerated tails. Although lacertid lizards exhibit some degree of sexual dimorphism (see for i.e. Braña 1996) it is assumable that interespecific differences on body shape are most important than intraspecific (sexual) ones. Then, I pooled data from males and females to calculate mean values for each variable. The final dataset includes mean values of morphometric variables from 132 taxa of 129 lacertid species (Appendix I) representing almost all the lineages of this family. Statistical analyses were carried out on log₁₀ transformed variables.

In order to test for differences in body shape among the diversity of ecologies, I selected only taxa clearly assignable to the following categories, based on the available bibliography (see Appendix I for species information). Obviously this is a limited approach to the diversity of ecologies and habits in lacertids, but some simplification is needed to reconstruct their evolution and analyze correlation with morphology. Ground and vegetation dwellers includes species actively foraging at moderate speed on compact substrate with limited ability to climb in vertical surfaces. Fast runners are species that run faster, in open areas with scarce vegetation and almost never climbs into vegetation. Vegetation climbers comprises species usually climbing in flimsy or lower vegetation. Arboreal climbers are adapted to efficiently moves on trees and rarely dwell in litter. Arboreal gliders comprises only one representative of extremely specialized tree climbers, the genus *Holaspis* (Arnold 2002) exhibiting a remarkable ability to glide among trees. Ground and rocky climbers includes lacertids moving on rocky surfaces with some ground activity. Most specialized forms, extremely linked to rocky walls or boulders that use crevices as a refuge (for example *Hellenolacerta* or *Archaeolacerta*) are considered fissuricolous rocky climbers. Cryptozoic species belongs exclusively to the African genus *Nucras* and lives underneath dense vegetation cover, logs or rocks (Branch 1998). Grass dwellers moves in some extend into grasses or other kinds dense vegetation. Finally, most lacertids can be considered generalized forms capable of run at moderate speed, with some ability climb on rocky or vegetal surfaces.

Reconstruction of ecological diversification through the evolutionary history of lacertids was performed using parsimony, considering those categories as unordered states and equally weighting all the transitional changes. Parsimony analysis was carried out on a phylogeny of the family (see below) using Mesquite 2.72 (Maddison & Maddison 2010). Because biological data often lacks of statistic independence, comparative methods should be used taking into account phylogenetic relationship among species (Harvey & Pagel 1991). I choose the Felsenstein's method of independent contrast to analyze morphometric data (Felsenstein 1985). A lacertid tree was constructed based on phylogenies obtained by analysis of molecular and information on escalation, myology and osteology (Arnold 1989a; Arnold 1989b; Arnold 1991; Arnold et al 2007; Fu 2000; Fu et al 1999; Harris et al. 1998a, Harris et al. 1998b; Harris & Arnold, 2000; Hipsely et al 2009; Kapli et al 2008; Lamb & Bauer 2003; Lin et al 2002; Makokha et al 2007; Mayer & Pavlicev (2007-2009); Ota et al 2002; Figure 1). Although molecular data was proved more useful to reconstruct the evolution of this family than morphology, some lineages as the Equatorial clade (*Holaspis*, *Gastropholis* and *Adolfus*) lacks of complete molecular datasets. The tree have many politomies reflecting the severe difficulties to define the relationships among the members of the lacertinae subfamily (Arnold et al 2007; Fu 2000; Mayer & Pavlicev 2009). Thus, these politomies were considered as "hard politomies" in the analysis, reflecting an explosive diversification of lacertid lizards. Assumptions for independent contrasts were checked using correlations among absolute values of standardized contrasts and the square root of the branch length.

Initial branch length set to one, results in significant correlations, that became not significant after the transformation using the Nee method (Purvis 1995).

Bivariate allometry among the seven linear measurements were analyzed using Pearson parametric correlation, ordinary least-square (OLS), major axis (MA) and reduced major axis (RMA) regression through the origin (Harvey & Pagel 1991) on independent contrasts. Patterns of covariation among the variables were analyzed by means of evolutionary principal components (EPC) on raw data, using Mesquite 2.72 (Dyreson & Maddison 2006). This method extracts factors that maximize evolutionary change rather than simply ordinating variation. Ancestral states are reconstructed on the lacertid phylogeny using squared-change parsimony and then cryptanalysis is performed on vectors of change along each branch. Thus, while conventional PCA ignores phylogenetic inertia, EPC accounts for this effect and represents a valid comparative methodology for ordination analyses. However, patterns of covariation among morphometric variables are in many cases masked by the strong correlation of them with body size (Gould 1966). To control for this effect, OLS regression on each dependent variable was performed on raw species data using SVL as an independent variable. Residuals from OLS regression can be considered as variables measuring the free size variation and EPC was also performed on those new variables.

RESULTS

Parsimony analysis reconstructs unambiguously the common ancestor of living lacertids as ground dwelling or generalized form (Fig. 2). Living Eremianidi seems to be evolved from a fast runner species, based on the parsimony reconstruction on this node. At least four independent transitions to ground and vegetation dwelling species evolved in this tribe: *Pedioplanis*, *Meroles*, *Adolfus* and *Ophisops*. Vegetation climbers and truly arboreal forms evolved independently in the Equatorial African clade (*Holaspis* and *Gastropholis*) and the subtropical Asian *Takydromus*. In this latter genus, the ground dweller *Takydromus amurensis* seems to be re-evolved to this condition from a semiarboreal ancestor. Grass dwellers are rare in lacertid lizards, evolving four times in *Zootoca*, *Lacerta agilis*, *Tropidosaura* and *Darevskia praticola*. The ancestral ecology of Lacertini was ambiguously reconstructed as fissuricolous or generalized dweller and climber.

Analyses of allometric relationships among SVL and the other morphometric variables based on independent contrasts shows strong and positive covariation (Table 1). Residual (free-size) variables obtained through OLS regression of independent contrast are in most cases positively correlated. Coefficients of correlation indicates strong covariation among limb proportions, and lack of covariation among cephalic traits and tail length (Table 2). The former are correlated among them, while the latter variable covaries with limb variables.

EPCA of species dataset including all the variables accounts for the 94.3% of total variability for the two first principal components. The first one can be considered as a typical size component because all the variables are positively scored (Table 3). The second one reveals the major trends on body shape diversity by opposition among scores of tail and limb variables, and on the other hand of SVL and head variables. Species scores (Fig. 3) in 1st EPC show a gradient of body sizes from smaller species (*Psammodromus*, *Ophisops* and *Adolfus*) and larger species on the opposite. Second EPC allows little ecological discrimination, only noticeable in the case of arboreal climbers which have long tails in absolute values.

Residual variables representing free-size measurements for species dataset were obtained from significant OLS regressions (Table 4). The two first two components extracted by EPCA performed with residual variables accounts for the 77.7% of total variability. First principal component is polarized by limb and tail variables, with large positive scores in opposition to cephalic variables (Table 3). In second principal component, tail length is strongly and positively scored in contrast to limb and head variables. Scores of the species in two first EPCA reveals the basic ecomorphic structure in Lacertidae (Fig. 4). Gradual transition to arboreality in *Takydromus* and specialized in *Gastropholis* are defined by their extremely long tails and long limbs respect to their body size. The only exception the arboreal lizards of genus *Holaspis*, are phylogenetically close to *Gastropholis*, but short limbed and tailed. Species with relative short limbs and long tails belongs to two different ecological categories: grass dwellers (*Tropidosaura*, *Zootoca* and *Darevskia praticola*), cryptozoic species (*Nucras delalandi* and *N. holubi*). Most fast runner species (*Acanthodactylus*, *Meroles* and *Eremias*) are characterized by relatively larger fore and hindlimbs. Although in all the lacertid species forelimbs are even shorter than hindlimbs, in arboreal species this difference is small, while in fast runners is larger.

DISCUSSION

Despite their stable body plan in comparison to elongated or limbless squamates, the analysis of few linear morphometric variables in lacertids lizards reveals a pattern of body shape related to the main species ecology. Vanhooydonck & Van Damme (1999) failed to found ecomorphic structure in this family and suggest that the lack of a well resolved phylogeny was the main cause. This study, found a pattern of covariation among lacertid morphology and ecology despite the large number of polytomies in the phylogenetic tree. Probably the problems encountered by Vanhooydonck & Van Damme (1999) may be due to their scarce sampling in relation to the habitat diversity in lacertids.

Body size (SVL) appear in the analysis as the first variable on ecological importance in lacertids ranging from some phylogenetically independent lineages of small species (for example *Ophisops* or *Adolfus*) to large *Timon*, *Lacerta* or *Omanosaura*. This capacity of evolution on body size is the final product of the influence of several

factors as dietary niche segregation, intrapopulation competence or predatory effects on survivorship. Insular populations of lacertids reflect at intraspecific level such determinants promoting changes on body size (Barahona et al. 2006).

Probably, the adaptation to arboreality in tropical forests represents the most dramatic changes experienced on the ancestral lacertid morphology. Morphometric analysis performed indicates body shape convergence among Asian *Takydromus* (with the only exception of the grass dweller *T. amurensis*) and African *Gastropholis*. Both genus exhibit proportional longer tails in relation to body size and relatively longer forelimbs respect to hindlimbs. It is likely that such features enhanced the ability to climb in vertical surfaces generated by the extensive forest cover, like trunks or branches. Arnold (1998) finds the same pattern in this genus on its analysis of lacertid limb proportions using conventional statistics. Remarkably, the arboreal *Holaspis* lacks of longer tail. This species was secondary adapted to gliding in the African equatorial forests through a primary adaptation to moves into crevices (Arnold 2002). Other gliding squamates are also short tailed species as in the case of *Draco* agamids or the geckos of genus *Ptychozoon*. This suggests that longer tails could be a serious handicap to stabilize the body position in the air, during gliding. Species that forages in wide open spaces and with a few isolated patches of vegetation needs to develop faster locomotion to elude predators and extreme higher temperatures. In response to this environmental pressures species inhabiting steppes or deserts (for example the genus *Mesalina*, *Acanthodactylus* and *Eremias*) developed relative longer hindlimbs (Arnold 2002). Although they are a phylogenetic diverse group, lacertids foraging into dense vegetation matrix presents comparatively shorter limbs. Finally, species that actively forages into dense vegetation matrices as for example herbs or small bushes trends to cluster in multivariate analysis. Representatives of this short limbed and long tailed lizards belongs to different clades and habitats use. This latter case of morphologic convergence is well represented by *Takydromus amurensis*, *Lacerta agilis*, *Darevskia praticola*, *Zootoca vivipara* or *Tropidosaura montana*.

The results of this study are very limited and therefore is a tentative approach to ecomorphic analysis in lacertids. For example ancestral, reconstructions of ecology on the Lacertini and Eremianidi nodes are ambiguous due to large number of politomies in the phylogeny. Another problem is the lack of data on relevant biometric variables as trunk or digit length. A more detailed picture of morphologic diversification in this family may be obtained by increasing the number of morphometric measurements and improving the resolution of Lacertid tree.

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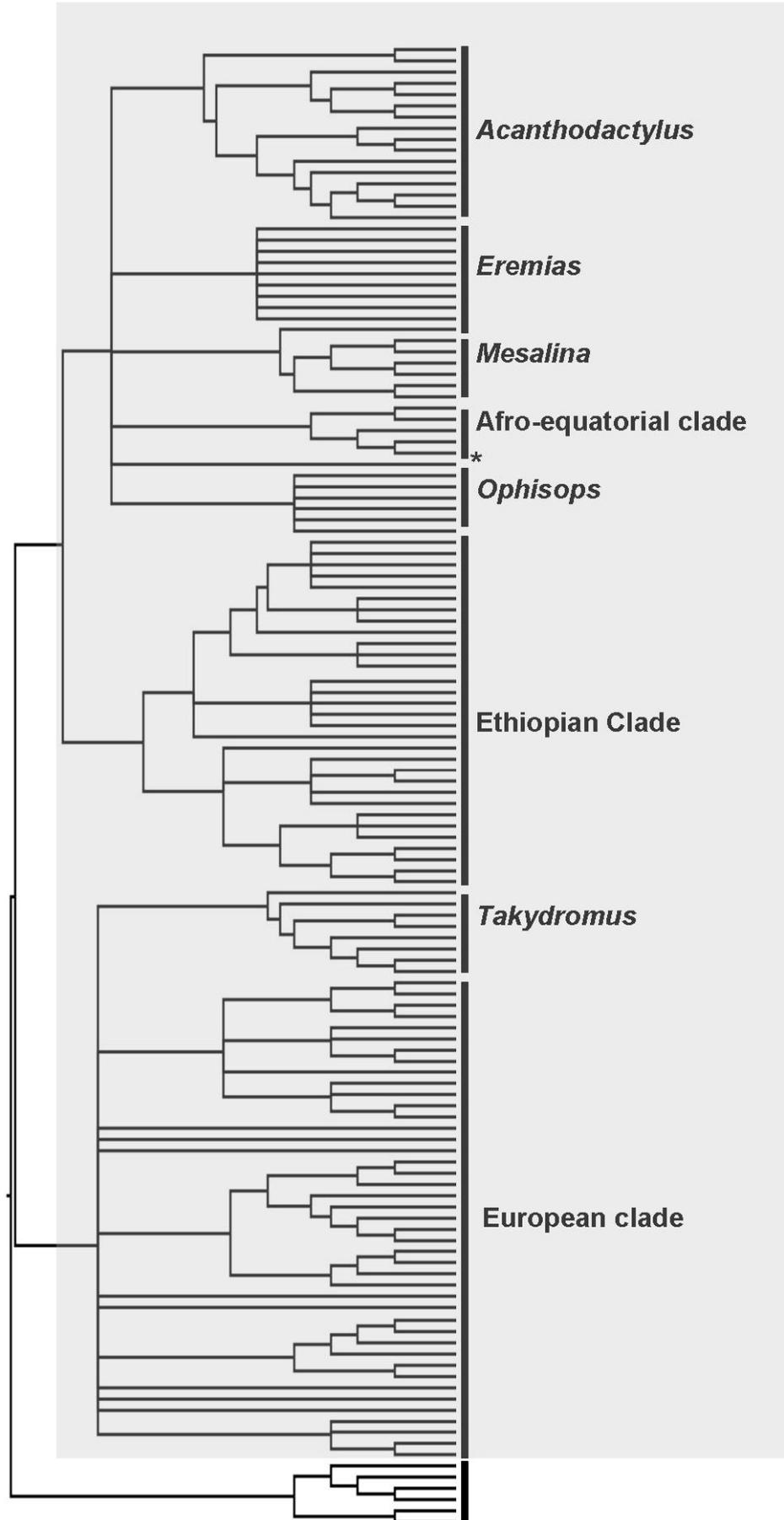
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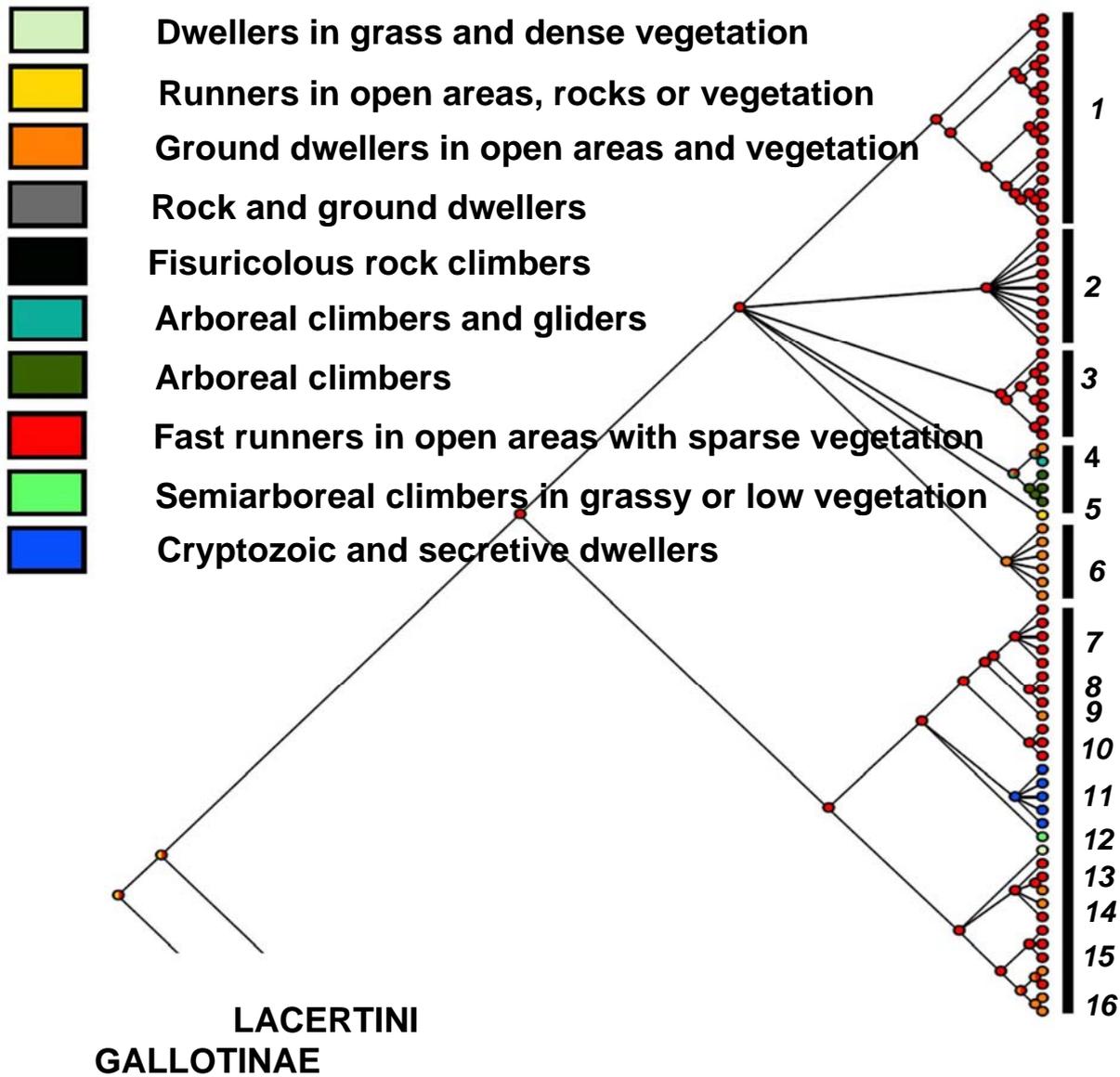
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Fig. 1 (see page 38). Lacertid tree based on anatomical and molecular evidences. *Gallotinae* are basal and includes the genus *Psammmodromus* and *Gallotia*. The other subfamily, *Lacertinae* is formed by two monophyletic clades: *Lacertini* and *Eremianidi*. The former is constituted by the tropical Asian genus *Takydromus* and a mainly European clade, which reach Middle East, north of China and Magrib (Arnold et al., 2007). Chitin the *Eremianidi*, the Ethiopian clade is formed by the genus *Australolacerta*, *Meroles*, *Pedioplanis*, *Tropidosaura*, *Poromera*, *Nucras*, *Latastia*, *Ichnotropis*, *Philochortus*, *Heliobolus* and *Pseudoeremias*. Based on molecular results (Mayer & Pavlicev, 2007) the Equatorial African clade (*Holaspis*, *Gastropholis* and *Adolfus*) is nested within the xeric *Eremianidi* group that includes *Omanosaura* (marked with *).



Fig.1.





1. *Acanthodactylus*
2. *Eremias*
3. *Mesalina*
4. Afro-Equatorial clade
5. *Omanosaura*
6. *Ophisops*
7. *Pseudoeremias*
8. *Heliobolus*

9. *Philochortus*
10. *Latastia*
11. *Nucras*
12. *Poromera*
13. *Tropidosaura*
14. *Pedioplanis*
15. *Ichnotropis*
16. *Meroles*

Fig. 2a. Most parsimony reconstruction of the ecological diversification in lacertid lizards.

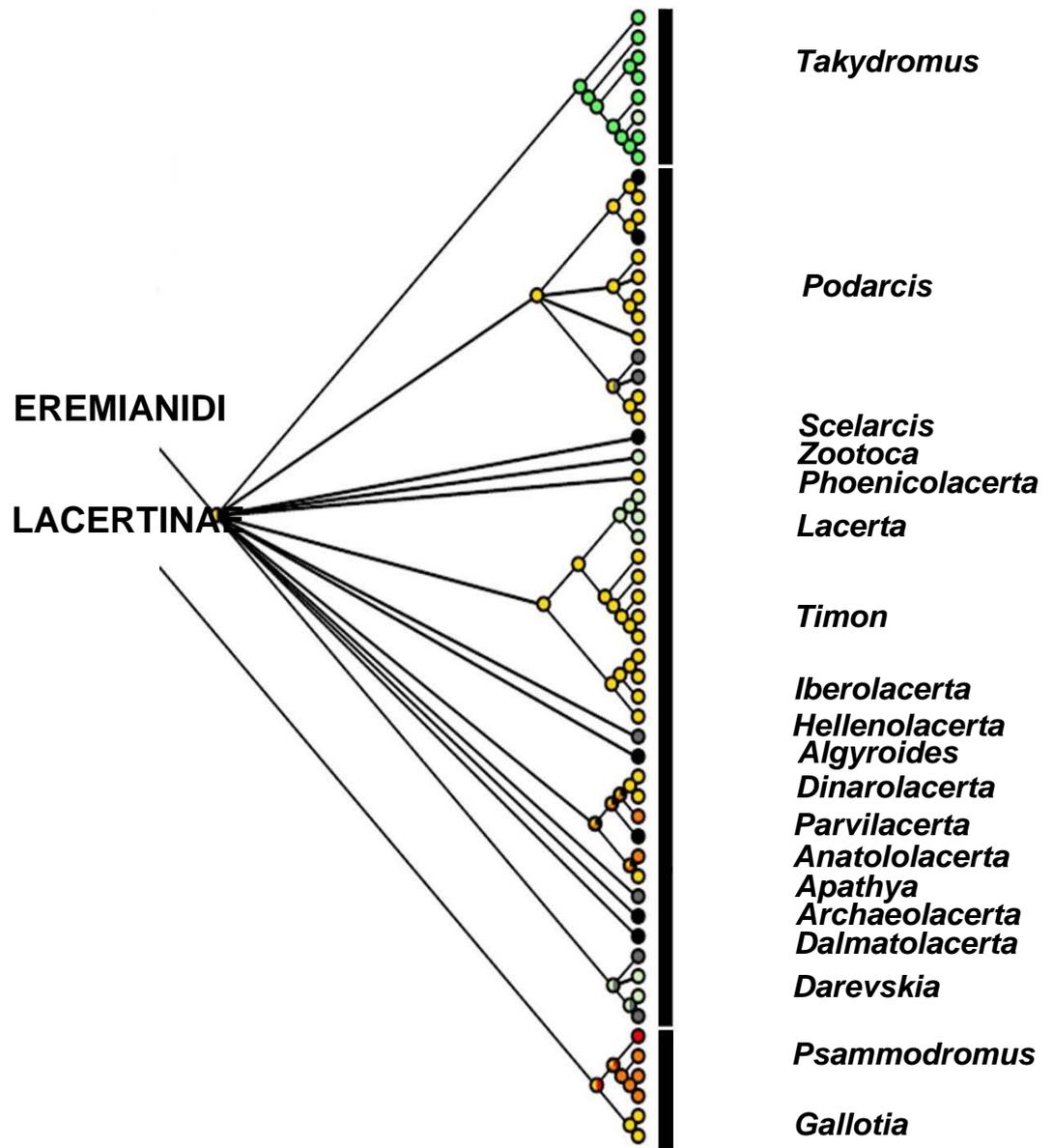


Fig. 2b. Most parsimony reconstruction of the ecological diversification in lacertid lizards.

Fig. 3.

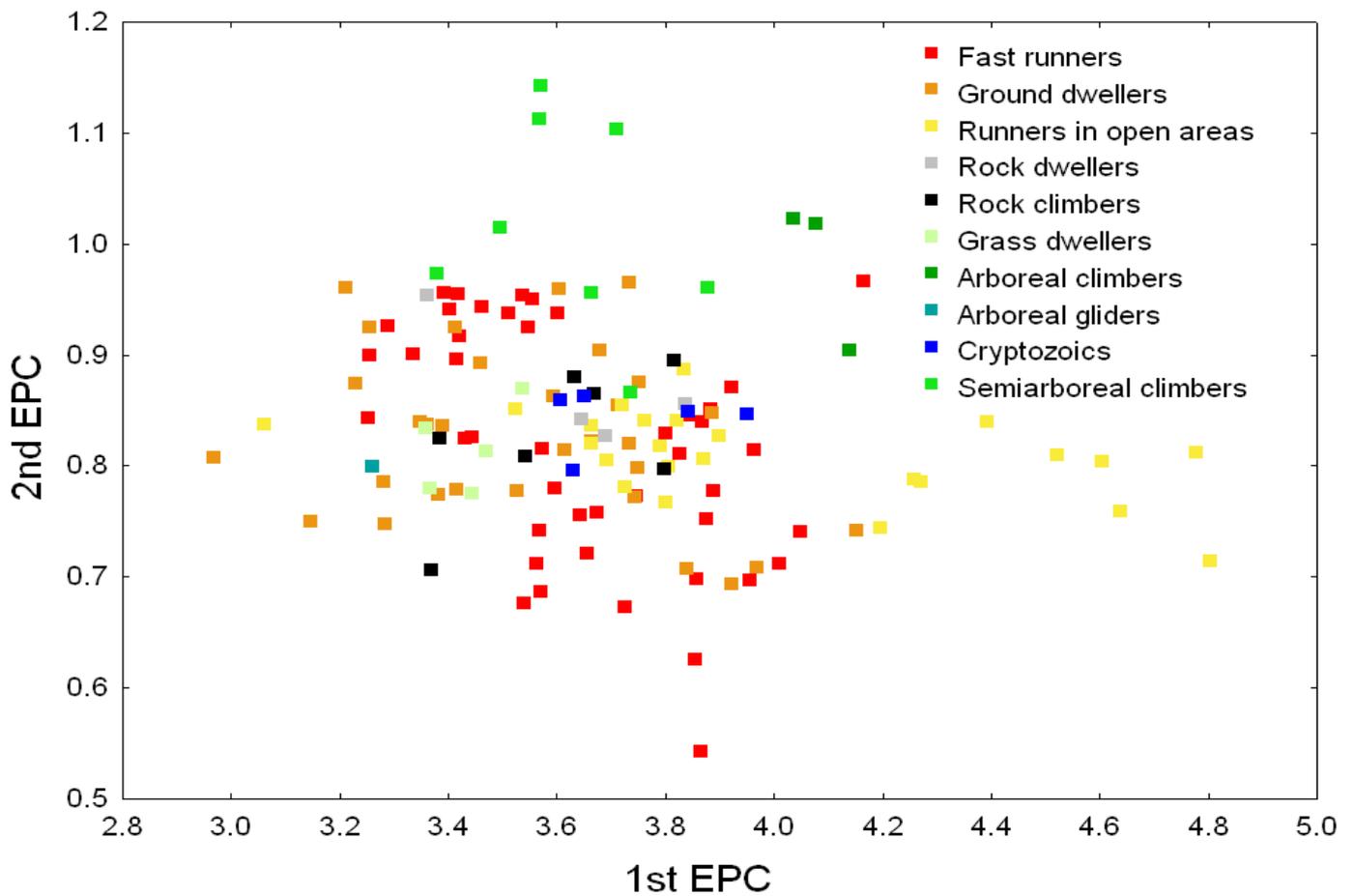


Fig. 3. Scatterplot of 132 lacertid lizards categorized by their main ecology in the two first evolutionary principal components obtained from raw variables. Larger lacertids (*Lacerta* sensu stricto, *Timon* and *Omanosaura*) are shown enclosed in discontinuous line.

Fig. 4.

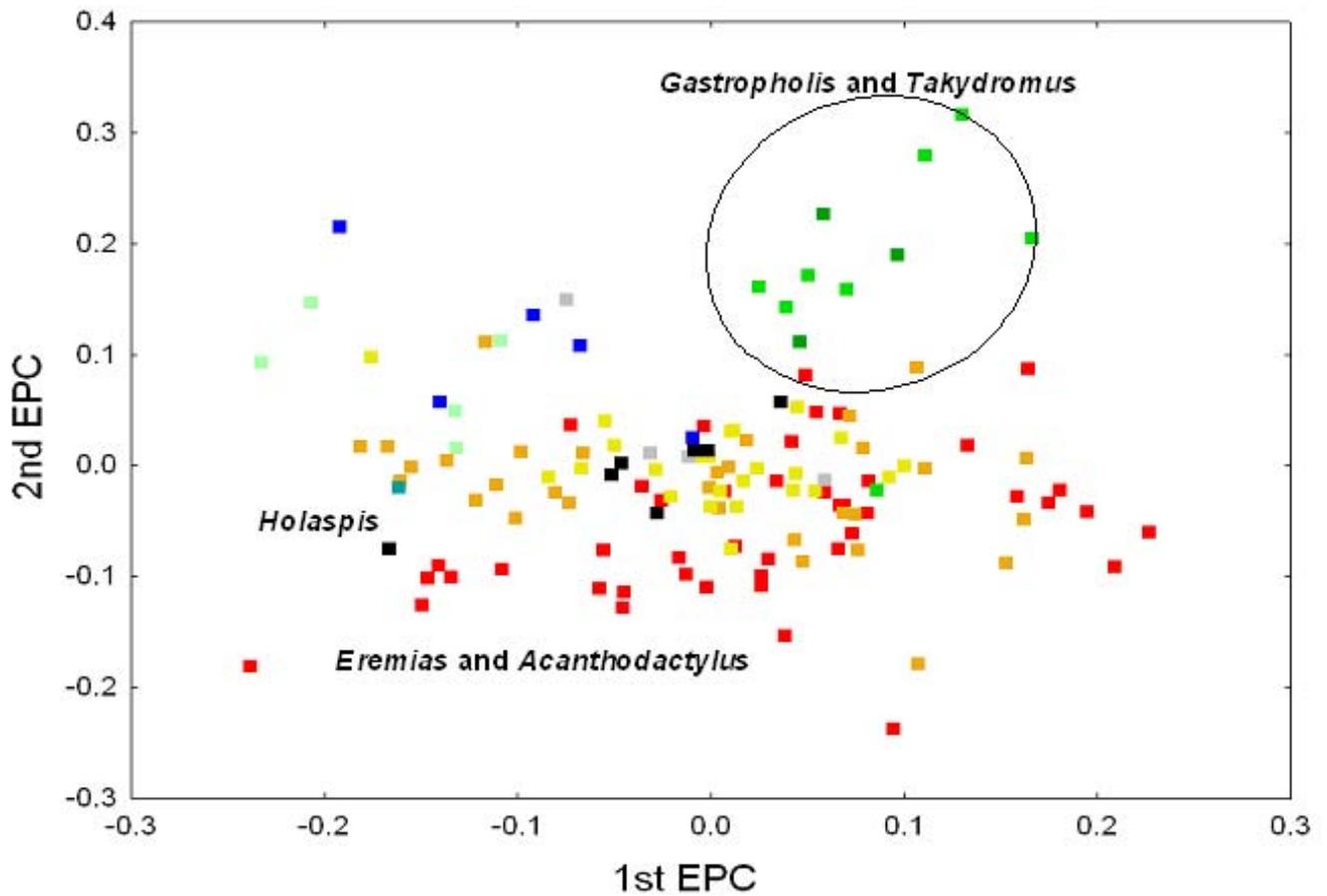


Fig. 4. Scatterplot of 132 lacertid lizards categorized by their main ecology in the two first evolutionary principal components from size-free variables. Ecological categories are shown as in Figure 3.

Variable	R	RMA	MA	OLS
Head length	0.958	1.065	1.068	1.021
Head width	0.935	1.136	1.146	1.063
Head depth	0.913	1.260	1.287	1.151
Forelimb length	0.936	1.075	1.080	1.006
Hindlimb length	0.874	1.168	1.194	1.021
Tail length	0.812	1.361	1.458	1.106

Table 1. Summary of regression analysis forced through the origin on 131 independent contrasts: R, correlation coefficient, RMA, slope for reduced major axis regression; MA, slope for major axis regression and OLS, slope for ordinary least square regression. All parameters significant at $P < 0.01$.

Variable	Head length	Head width	Head depth	Forelimb length	Hindlimb length	Tail length
Head length	-	0.517	0.181	0.658	0.650	0.146
Head width	<0.0001	-	0.382	0.423	0.373	-0.133
Head depth	0.039	<0.0001	-	-0.034	-0.054	-0.081
Forelimb length	<0.0001	<0.0001	0.703	-	0.765	0.350
Hindlimb length	<0.0001	<0.0001	0.541	<0.0001	-	0.366
Tail length	0.096	0.129	0.358	<0.0001	<0.0001	-

Table 2. Matrix of parametric correlation of size-free variables obtained by the OLS regression forced through the origin on independent contrasts. Correlation coefficients above the diagonal (significant correlations in black) and P values below.

Variable	1st EPC	2nd EPC	1st EPC	2nd EPC
	raw variables	raw variables	free-size variables	free-size variables
SVL	0.340	-0.138	-	-
Head length	0.364	-0.099	0.184	-0.227
Head width	0.376	-0.345	0.046	-0.373
Head depth	0.406	-0.421	-0.075	-0.145
Forelimb length	0.365	0.012	0.516	-0.391
Hindlimb length	0.382	0.135	0.516	-0.391
Tail length	0.405	0.809	0.652	0.693
% of total variability	88.0	6.2	52.1	25.6

Table 3. Coefficients of the morphometric measurements of 132 lacertid species in the first two evolutionary components for raw and free-size variables. This latter are residuals obtained from OLS regression on body size of species data.

Variable	Slope ± EE	T(130)	P	Intercept ± EE	T	P	R ²
Head length	1.003 ± 0.201	49.851	<0.0001	-0.623 ± 0.036	-17.219	<0.0001	0.950
Head width	1.065 ± 0.028	36.776	<0.0001	-0.923 ± 0.052	-17.714	<0.0001	0.912
Head depth	1.179 ± 0.032	35.991	<0.0001	-1.241 ± 0.058	-21.071	<0.0001	0.908
Forelimb length	0.955 ± 0.026	35.970	<0.0001	-0.381 ± 0.047	-7.987	<0.0001	0.908
Hindlimb length	0.879 ± 0.047	18.672	<0.0001	-0.040 ± 0.087	-0.482	0.630	0.728
Tail length	0.924 ± 0.065	14.053	<0.0001	0.425 ± 0.118	3.590	0.0004	0.603

Table 4. Summary of regression analysis of allometric relationships among SVL (OLS regression) and dependent variables for 132 lacertid lizards.

Appendix I.- Taxa of Lacertid lizards analyzed in this study and their ecologic characterization.

Species	Ecology
<i>Acanthodactylus aureus</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus bedriagai</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus blanci</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus blanfordi</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus boskianus</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus boueti</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus cantoris</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus erythrurus belli</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus e. erythrurus</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus grandis</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus longipes</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus micropholis</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus pardalis</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus schreiberi schreiberi</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus schreiberi syriacus</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus scutellatus</i>	Fast runner in open areas with scarce vegetation
<i>Acanthodactylus tristami</i>	Fast runner in open areas with scarce vegetation
<i>Adolfus africanus</i>	Ground dweller in open areas and vegetation
<i>Algyroides fitzingeri</i>	Ground dweller in open areas and vegetation
<i>Algyroides moeroticus</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Algyroides nigropunctatus</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Anatololacerta danfordii</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Apathya cappadocica</i>	Rock and ground dweller
<i>Archaeolacerta bedriagai</i>	Fissuricolous rocky climber
<i>Dalmatolacerta oxycephala</i>	Fissuricolous rocky climber
<i>Darevskia chlorogaster</i>	Rock and ground dweller
<i>Darevskia derjugini</i>	Dweller in grass and dense vegetation
<i>Darevskia portchinski</i>	Rock and ground dweller
<i>Darevskia praticola</i>	Dweller in grass and dense vegetation
<i>Dinarolacerta mosorensis</i>	Fissuricolous rocky climber
<i>Eremias argus</i>	Fast runner in open areas with scarce vegetation
<i>Eremias arguta</i>	Fast runner in open areas with scarce vegetation

<i>Eremias fasciata</i>	Fast runner in open areas with scarce vegetation
<i>Eremias lineolata</i>	Fast runner in open areas with scarce vegetation
<i>Eremias multiocellata</i>	Fast runner in open areas with scarce vegetation
<i>Eremias persica</i>	Fast runner in open areas with scarce vegetation
<i>Eremias scripta</i>	Fast runner in open areas with scarce vegetation
<i>Eremias velox</i>	Fast runner in open areas with scarce vegetation
<i>Eremias vermiculata</i>	Fast runner in open areas with scarce vegetation
<i>Gallotia atlantica</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Gallotia caesaris</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Gastropholis echinata</i>	Arboreal climber
<i>Gastropholis tropidopholis</i>	Arboreal climber
<i>Gastropholis vitatta</i>	Arboreal climber
<i>Heliobolus lugubris</i>	Fast runner in open areas with scarce vegetation
<i>Heliobolus nitida</i>	Fast runner in open areas with scarce vegetation
<i>Heliobolus spekii</i>	Fast runner in open areas with scarce vegetation
<i>Hellenolacerta graeca</i>	Fissuricolous rocky climber
<i>Holaspis guentheri</i>	Arboreal climber and glider
<i>Iberolacerta horvathi</i>	Rock and ground dweller
<i>Ichnotropis bivittatus</i>	Fast runner in open areas with scarce vegetation
<i>Ichnotropis capensis</i>	Fast runner in open areas with scarce vegetation
<i>Ichnotropis squamulosa</i>	Ground dweller in open areas and vegetation
<i>Lacerta agilis agilis</i>	Dweller in grass and dense vegetation
<i>Lacerta agilis chersonensis</i>	Dweller in grass and dense vegetation
<i>Lacerta agilis exigua</i>	Dweller in grass and dense vegetation
<i>Lacerta bilineata</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Lacerta schreiberi</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Lacerta strigata</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Lacerta trilineata</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Lacerta viridis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Latastia boscai</i>	Fast runner in open areas with scarce vegetation
<i>Latastia johnstonii</i>	Fast runner in open areas with scarce vegetation
<i>Latastia longicaudata</i>	Fast runner in open areas with scarce vegetation
<i>Meroles ctenodactylus</i>	Ground dweller in open areas and vegetation
<i>Meroles cuneirostris</i>	Fast runner in open areas with scarce vegetation
<i>Meroles knoxii</i>	Ground dweller in open areas and vegetation
<i>Meroles suborbitalis</i>	Ground dweller in open areas and vegetation

<i>Mesalina adramitana</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina balfouri</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina brevirostris</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina guttulata</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina martini</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina olivieri</i>	Fast runner in open areas with scarce vegetation
<i>Mesalina rubropunctata</i>	Fast runner in open areas with scarce vegetation
<i>Nucras delalandi</i>	Cryptozoic and secretive dweller
<i>Nucras holubi</i>	Cryptozoic and secretive dweller
<i>Nucras intertexta</i>	Cryptozoic and secretive dweller
<i>Nucras tessellata</i>	Cryptozoic and secretive dweller
<i>Nucras emini</i>	Cryptozoic and secretive dweller
<i>Omanosaura jayakari</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Ophisops beddomei</i>	Ground dweller in open areas and vegetation
<i>Ophisops elegans</i>	Ground dweller in open areas and vegetation
<i>Ophisops jerdonii</i>	Ground dweller in open areas and vegetation
<i>Ophisops leschenaulti</i>	Ground dweller in open areas and vegetation
<i>Ophisops microlepis</i>	Ground dweller in open areas and vegetation
<i>Ophisops occidentalis</i>	Ground dweller in open areas and vegetation
<i>Parvilacerta parva</i>	Ground dweller in open areas and vegetation
<i>Pedioplanis benguelensis</i>	Fast runner in open areas with scarce vegetation
<i>Pedioplanis burchelli</i>	Ground dweller in open areas and vegetation
<i>Pedioplanis lineocellata</i>	Ground dweller in open areas and vegetation
<i>Pedioplanis namaquensis</i>	Fast runner in open areas with scarce vegetation
<i>Pedioplanis undulata</i>	Fast runner in open areas with scarce vegetation
<i>Philochortus spinalis</i>	Ground dweller in open areas and vegetation
<i>Phoenicolacerta laevis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis bocagei</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis carbonelli</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis erhardii</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis filfolensis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis liolepis</i>	Fissuricolous rocky climber
<i>Podarcis lilfordi</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis melisellensis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis muralis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis peloponnesiaca</i>	Generalized runners and climbers in vegetation, rocks and open areas

<i>Podarcis pityusiensis</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis taurica</i>	Ground dweller in open areas and vegetation
<i>Podarcis tiliguerta</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Podarcis vaucheri</i>	Fissuricolous rocky climber
<i>Poromera fordii</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Psammodromus algirus</i>	Fast runner in open areas with scarce vegetation
<i>Psammodromus blanci</i>	Ground dweller in open areas and vegetation
<i>Psammodromus hispanicus</i>	Ground dweller in open areas and vegetation
<i>Psammodromus microdactylus</i>	Ground dweller in open areas and vegetation
<i>Pseuderemias brenneri</i>	Fast runner in open areas with scarce vegetation
<i>Pseuderemias erythrostica</i>	Fast runner in open areas with scarce vegetation
<i>Pseuderemias mucronata</i>	Fast runner in open areas with scarce vegetation
<i>Pseuderemias smithii</i>	Fast runner in open areas with scarce vegetation
<i>Pseuderemias striata</i>	Fast runner in open areas with scarce vegetation
<i>Scelarcis perspicillata</i>	Fissuricolous rocky climber
<i>Takydromus amurensis</i>	Dweller in grass and dense vegetation
<i>Takydromus dorsalis</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus formosanus</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus sauteri</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus septentrionalis</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus sexlineatus</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus smaragdinus</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Takydromus tachydromoides</i>	Semi-arboreal in flimsy, grassy and lower vegetation
<i>Teira dugesii</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Timon lepidus</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Timon pater</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Timon princeps</i>	Generalized runners and climbers in vegetation, rocks and open areas
<i>Tropidosaura montana</i>	Dweller in grass and dense vegetation
<i>Zootoca vivipara</i>	Dweller in grass and dense vegetation
