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Phylogenetic relationships of the European lacertid genera *Archaeolacerta* and *Iberolacerta* and their relationships to some other 'Archaeolacertae' (*sensu lato*) from Near East, derived from mitochondrial DNA sequences

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Abstract

Parts of the mitochondrial genes coding for 12SrRNA and 16SrRNA (together about 960 bp) were sequenced for all Mediterranean species of 'Mountain lizards' of the genera *Archaeolacerta* (*sensu lato*) and *Iberolacerta*. All subspecies of the Iberian species *Iberolacerta cyreni* and *I. monticola* were included in this study. In addition, samples of *Apathya cappadocica* and *Darevskia rudis* were analysed to elucidate the relationships of the European 'Mountain lizards' to their possible relatives in the Near East. Maximum parsimony and neighbour joining analyses lead to the following major conclusions: (i) the monophyly of the genus *Iberolacerta* is very well supported; (ii) *Archaeolacerta bedriagae* (the type species of the genus) is most basal with respect to the ingroup taxa. If we accept *Iberolacerta* as a genus, *Archaeolacerta* becames paraphyletic. Therefore, we propose to restrict *Archaeolacerta* to the type species and to treat *A. mosorensis* and *A. oxycephala* provisionally as members of the collective genus *Lacerta*; (iii) within the genus *Iberolacerta* three groups were found: a Pyrenean group, an Iberian group and *I. horvathi*. The relationships among these groups remain unresolved; and (iv) the Peña de Francia lizards, described originally as a subspecies of *I. cyreni*, are in fact more closely related to *I. monticola*.

Key words: *Lacertidae – Iberolacerta – Archaeolacerta – Darevskia – Apathya – Podarcis – Lacerta* – phylogeny – mitochondrial rRNA sequences

Introduction

The systematics and taxonomy of small lacertids belonging to the so-called '*Lacerta* part II' (*sensu* Arnold 1973) is far from being resolved. Some species groups previously assigned to *Lacerta* Linnaeus 1758 (s.l.) are now grouped in different genera or subgenera, depending on the authors' points of view. A complete and more stable taxonomy of the whole group is still not accomplished. These taxonomic units are: *Apathya* Mehely 1907, *Archaeolacerta* Mertens 1921, *Darevskia* Arribas 1997, *Iberolacerta* Arribas 1997, *Gallotia* Boulenger 1916, *Omanosaura* Lutz, Bischoff and Mayer 1986, *Parvilacerta* Harris, Arnold and Thomas 1998, *Podarcis* Wagler 1830, *Teira* Gray 1838, *Timon* Tschudi 1836 and *Zootoca* Wagler 1830. Apart from these more or less well defined groups, a heterogeneous assemblage of species still remains in the collective genus *Lacerta*.

Today the European Mountain lizards ('Archaeolacertae') are assigned to the genera *Darevskia, Archaeolacerta* and *Iberolacerta* (Arribas 1997a, 1999b). '*Lacerta*' *graeca*, a saxicolous species with unresolved relationships but frequently ascribed to this group, remains without clear generic assignment.

Archaeolacerta was originally defined by Mertens (1921) as a subgenus of *Lacerta* (type species: *L. bedriagae*) for Mehely's (1907, 1909) 'Archaeolacertae', a plethora of small Palaearctic species in which the skull is depressed and only slightly ossified, with fenestrated supraocular osteoderms and frequently without pterygoid teeth. In the last decades the name was repeatedly used at the generic level for different groups of Mountain lizards (first used by Lanza et al. 1977). In the most recent reviews, Arribas (1997a, 1999b) restricted *Archaeolacerta* to the Tyrrhenic species *A. bedriagae*, and tentatively to the balcanic *A. mosorensis* and *A. oxycephala*, but emphasized the necessity of more detailed studies in order to ascertain the degree of relationship between the Tyrrhenic and the two Balcanic species.

The genus *Iberolacerta* (see Arribas 1997a, 1999b) includes the following taxa: *Iberolacerta aranica* (Arribas 1993 a,b), *I. aurelioi* (Arribas 1994), *I. bonnali* (Lantz 1927), *I. monticola* (Boulenger 1905) (ssp. *monticola* s.str. and *cantabrica* Mertens 1928) and *I. cyreni* (Müller and Hellmich 1937) (with ssp. *cyreni* s.str., *castiliana* Arribas 1996 and *martinezricai* Arribas 1996), and additionally the east-Alpine and Dinaric species *I. horvathi* (Mehely 1904). This genus is a group of small sized and moderately saxicolous lizards. Their colourations and patterns are typical for the members of the Eurasian radiation (vertebral stripes, costal bands, etc). Bellies are usually spotted in various degrees. Within the Eurasian radiation of lacertids (*sensu* Mayer and Benyr 1994) a characteristic of *Iberolacerta* is the lack of microchromosomes (karyotype composed only of 36 macrochromosomes or less, as some species show Robertsonian fusions of acrocentric chromosomes resulting in biarmed ones). Also, in contrast to other small lacertid genera from the same area, females have greater snout–vent length than males. The number of vertebrae in males is mostly 26, and ranges from 27 to 29 in females (Arribas 1997a, 1998, 1999b).

The intrageneric relationships of *Iberolacerta* have been studied from two different data sets: morphologic, osteologic and karyotypic (Arribas 1997a, 1999b) and allozyme studies (Mayer and Arribas 1996 as well as Almeida et al. 2002).

In this paper we present partial DNA sequences of the mitochondrial genes coding for the 12SrRNA and 16SrRNA of European 'Mountain lizards' – with special consideration of the members of the genus *Iberolacerta* – to clarify the phylogeny of this group.

Materials and methods

Localities and abbrevations of the lizard samples investigated are listed in table 1. *Podarcis muralis* was used as outgroup.

DNA from tissue samples (liver, heart or tail tips) was extracted and purified using a phenol-chloroform standard protocol (Sambrook et al. 1989). For sequence comparisons we amplified sections of the mitochondrial genes coding for 12SrRNA und 16SrRNA which produce a 12S fragment of about 460-bp and a 16S fragment of about 900-bp length (primer see Table 2). polymerase chain reaction (PCR)

Table 1. Investigated samples: taxa, localities and GenBank accession numbers

Taxon	Locality	GenBank accession numbers	
		12s-rRNA	16s-rRNA
Iberolacerta monticola monticola	Estrela, Beira Alta, Portugal	AF440589	AF440604
I. m. cantabrica	Paderne, La Coruña, Spain	AF440591	AF440606
I. m. cantabrica	Puerto de Vegarada, León, Spain	AF440590	AF440605
I. cyreni cyreni	Guadarrama, Segovia-Madrid, Spain	AF440592	AF440607
I. c. castiliana	Gredos, Avila, Spain	AF440593	AF440608
I. c. martinezricai	Peña de Francia, Salamanca, Spain	AF440594	AF440609
I. aurelioi	Ordino, Andorra	AF440595	AF440610
I. aranica	Armeros, Lleida, Spain	AF440596	AF440611
	Port de Orlà, Lleida, Spain	AF440597	AF440612
I. bonnali	Monte Perdido, Huesca, Spain	AF440598	AF440613
I. horvathi	Carnian Alps, Carinthia, Austria	AJ238186	AF149943
Archaeolacerta bedriagae	Col de Vergio, Corse	AF440599	AF440614
A. mosorensis	unknown locality in former Yugoslavia	AF440600	AF440615
A. oxycephala	Hvar, Croatia	AF440601	AF440616
'*Lacerta*' *graeca*	Lira, Lakonia, Greece	AF440602	AF440617
Apathya cappadocica	Al Barah, Syria	AF145444	AF149946
Darevskia rudis	Chernali valley, Adjaria, Georgia	AJ238180	AF149938
Podarcis muralis	Baden, Austria	AF440603	AF440618

Table 2. Primers used for PCR and sequencing. (1) Knight and Mindell (1993); (2) Titus and Frost (1996); (3) Kocher et al. (1989), modified; (4) Reeder (1995), modified; (5) Knight and Mindell (1993), modified

Primer	Sequence	Used for	Reference
L-1091	5′-aaactgggattagatccccactat-3′	PCR	(1)
H-1298	5′-gctacaccttgacctgacgt-3′	Sequencing	(2)
L-1318	5′-acgtcaggtcaaggtgtagc-3′	Sequencing	Inverse H-1298
H-1478	5′-agggatgacgggcggtgtgt-3′	Sequencing	(3)
H-1557	5′-gtacacttaccttgttacgactt-3′	PCR	(1)
L-2190	5′-gtgggcctaaaagcagccac-3‘	PCR	(4)
L-2510	5′-cgcctgtttaccaaaaacat-3′	Sequencing	(5)
H-3056	5′-ccggtctgaactcagatcacg-3′	PCR	(4)

products separated on agarose gel were purified using QIAquick® spin columns (QIAGEN®, Qiagen Inc., Valencia, California, USA). and reamplified with the same primers. Sequencing of approx. 500 bp of the 16S gene and approx. 460 bp of the 12S gene was performed by the sequence service of MWG-Biotech (Ebersberg, Germany).

The alignment of the concatenated 12S and 16S sequences (ranging from 953 to 969 bp) was performed with CLUSTAL X (Thompson et al. 1997) and corrected by eye. A total of 15–20 bp of each sequence which could not be aligned unambiguously were excluded from the analysis resulting in a final alignment length of 958 positions (including gaps) (the alignment can be viewed under 'Sequences' at our website at http://www.nhm-wien.ac.at/NHM/1Zoo/first_zoological_department/web/chemsyst/cuhp_25e.html). The neighbour joining tree (NJ, p-distances) was calculated by CLUSTAL X, the maximum parsimony (MP) dendrograms (Heuristic Search, gaps treated as fifth character state) and the MP majority rule consensus tree were produced using PAUP® version 4.0b3a (Swofford 1998) program package. The trees were rooted using *P. muralis* as an outgroup.

Results

Maximum parsimony analysis resulted in 45 equivalent most parsimonious trees with a length of 639 steps, 279 sites are variable, the number of informative characters is 166, and the consistency index is 0.615. The NJ tree is given in Fig. 1, the MP 50% majority rule consensus tree in Fig. 2.

The main lineages of the trees (Figs 1 and 2) namely (1) *Iberolacerta* (perhaps including *Archaeolacerta mosorensis*), (2) *Darevskia* (*D. rudis*), (3) a group with the three otherwise well differentiated taxa *Archaeolacerta oxycephala*, *Apathya cappadocica* and '*L.*' *graeca*, and (4) *Archaeolacerta bedriagae*, are deeply rooted.

Differences between MP and NJ are found with respect to the position of *I. horvathi*, the branching order of the Pyrenean group (*I. aranica*, *I. aurelioi* and *I. bonnali*) as well as within the *A. cappadocica*–*A. oxycephala*–'*Lacerta*' *graeca* group.

The clade representing *Iberolacerta* as presently defined is well supported by both tree constructing methods (100% of the MP trees, bootstrap values of 97% in the NJ tree). The

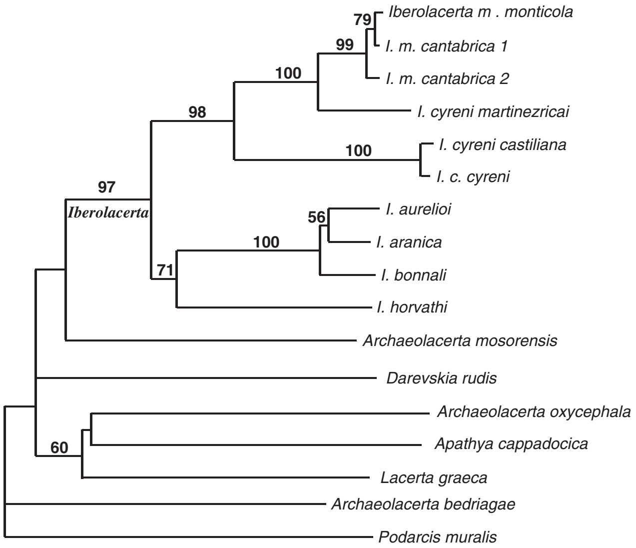

Fig. 1. Neighbour joining (NJ) tree, bootstrap values above 50% (2000 bootstrap resamplings) are given above branches

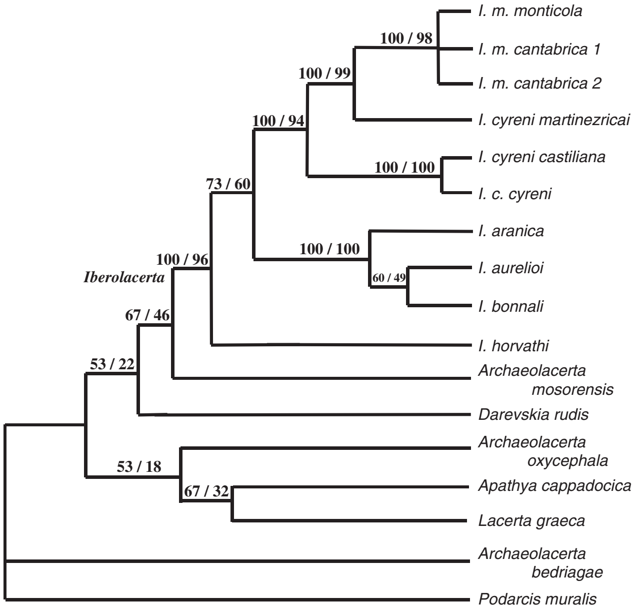

Fig. 2. Maximum parsimony (MP) 50% majority rule consensus tree of 45 equally parsimonious trees. Numbers represent frequencies of each node (left) and percentage of 2000 bootstrap replicates (right)

relationships between *I. horvathi* and the Ibero-Pyrenean species are not clearly resolved. Whereas in the MP dendrogram *I. horvathi* appears as the sister group of all the remaining *Iberolacerta* (supported by 73% of the 45 most parsimonious trees), in the NJ tree it is the sister species of the Pyrenean group (bootstrap value 71%).

With respect to the Iberian species, we found nearly identical sequences in the three *I. monticola* samples studied, belonging to the type subspecies (Serra de Estrela) as well as to *I. m. cantabrica* from Puerto de Vegarada (Cantabrian Mts.) and La Coruña province (sea level populations). The sequences obtained from the samples of the two subspecies of *I. cyreni*, namely *I. c. cyreni* from Guadarrama and *I. c. castiliana* from Gredos, are very similar (0.6% sequence difference) and well differentiated from *I. monticola* (approx. 6.5%). But surprisingly, *I. cyreni martinezricai* does not group with *I. cyreni* but with *I. monticola* (100% in both trees).

Both samples of *I. aranica* (from Armeros and Port de Orlá) have shown identical sequences. The Pyrenean group is clearly monophyletic, but the relationships among the three species are not clear. Whereas *I. aurelioi* and *I. bonnali* group in the MP tree, *I. aranica* and *I. aurelioi* are sister species in the NJ dendrogram. The low support of the respective nodes in both trees implies an unresolved trichotomy of these three species.

All other relationships are not well resolved. Nevertheless, in both cladograms *A. mosorensis* appears as the taxon most closely related to the *Iberolacerta* clade, and *Apathya cappadocica*, *A. oxycephala* and '*L.*' *graeca* form a group, although these groupings are only weakly supported. Finally, *Archaeolacerta bedriagae* and *Darevskia rudis* belong to clearly different lineages.

Discussion

The position of *I. horvathi* is uncertain with respect to other *Iberolacerta* species. In the MP cladogram it appears as the sister species of the whole Ibero-Pyrenean species group, a relationship corroborated by allozyme analysis (Mayer and Arribas 1996; Almeida et al. 2002). In contrast, in the NJ tree *I. horvathi* is the sister species of the Pyrenean clade only. The results of Harris et al. (1998) and Harris (1999) based on shorter sequences gave equivalent topologies with the same tree constructing methods. In a study of a fair number of taxa from the Eurasian radiation of lacertids based on morphology, osteology and karyology, Arribas (1997a, 1999b) found *I. horvathi* as sister species of the Pyrenean group. However, if the analysis was restricted to *Iberolacerta* species only, *I. horvathi* changed position as sister species of either the Iberian group or of the Pyrenean group, thus giving rise to an unresolved trichotomy in the consensus tree. In any case, in the present mtDNA analyses *I. horvathi* was never closely related to the Iberian group (*I. cyreni* and *I. monticola*). Therefore the designation of a subgenus *Pyrenesaura* Arribas 1999 is not meaningful as it would leave *Iberolacerta* s.str. (as presently defined) as a paraphyletic group.

The DNA sequence similarities between *I. m. monticola* and *I. m. cantabrica* is in accordance with karyological (Odierna et al. 1996), allozymic (Mayer and Arribas 1996; Almeida et al. 2002) and morphological results (Arribas 1996). Except for differing frequencies of contact of some head scales, no other morphological differences between these taxa were found. The present range of *I. monticola* is more or less continuous along the Cantabrian Mountains and Galicia, with a southern exclave in the Serra da Estrela. These two groups of populations represent the two subspecies currently recognized (e.g. Salvador 1984; Barbadillo 1987; Perez-Mellado et al. 1993; Arribas 1996; Perez-Mellado 1997, 1998). The discovery of lowland populations from the Galician coast (Galan 1982, 1991, 1999; Elvira and Vigal 1982) raises new questions about the ecological needs and the biogeography of this species, so far considered as a mountain species.

Both lowland and highland populations originated likely in the course of a retreat towards more fresh and wetter conditions as a consequence of the progressive temperature rise during the Holocene. In the Estrela and Cantabrian mountain ranges the populations moved to the heights whereas in the Galician lowlands they retreated to wet and shady gorges (covered by relic autochtonous deciduous forests which are considered to be an stable habitat from the Tertiary up to the present), as well as to coastal cliffs in areas with high precipitations (see for instance Arribas 1996). Populations from Cantabrian Mountains show a wide ecological valence. They may have retreated to the mountains before the postglacial temperature rise, but lowland populations still persist, especially in the west of Asturias (see Arribas 1996). Even some Cantabrian populations (as from Sierra de la Cabrera Baja and Sanabria area) are morphologically more similar to Portuguese specimens than to those from the main Cantabrian range (O. Arribas, unpublished data). Thus we assume that the present distribution was established postglacially and the subspecific distinction is not justified.

Iberolacerta cyreni is quite different from *I. monticola*. The Guadarrama and Gredos populations are presently allopatric and considered different subspecies of *I. cyreni* based on scalation characters (Arribas 1996). But the two populations seem to be poorly differentiated and may also be the result of a Holocene retreat to higher altitudes and the subsequent isolation of these populations. Both populations share the same karyotypic characteristics of *I. cyreni* [chromosome number and morphology, Nuclear Organizer Region of Karotype (NOR) position [Odierna et al. 1996)] and no differences in osteology were found (Arribas 1997a, 1998).

The Peña de Francia lizards, originally described as *I. c. martinezricai*, represent a very well differentiated taxon which is with certainty more closely related to *I. monticola* than to *I. cyreni*. The ancestors of *I. cyreni* and *I. monticola* possibly split off from Upper Miocene whereas *I. m. martinezricai* probably separated at the beginning of the Pliopleistocene Cooling and represents a remain of a formerly greater *I. monticola* distribution.

The Pyrenean species constitute a monophyletic group. The sequence differences (about 2%) among the Pyrenean taxa are the smallest found so far for lacertid species corroborating the hypothesis of a Pleistocenic differentiation (Arribas 1997a, 1999a,b, 2000, 2001). The clear morphological, osteological, karyological and allozymic differences (Mayer and Arribas 1996; Odierna et al. 1996; Arribas 1997a,b, 1998, 1999a, 2000, 2001) support their specific distinctiveness. Low sequence divergence indicates a relatively recent and rapid burst of speciation. Thus, differences in karyotype, bones, allozymes and morphology have been aquired and fixed within a short time, probably due to extremely small population sizes during critical periods of the Pyrenean Quaternary. Harsh and hostile habitat conditions both during glacial and interglacial periods could have led to isolation and bottleneck effects as well as to local extinction and recolonization waves during the differentiation of these species. These events should have favored the evolution and fixation of karyotypic and ostelogical differences, as well as the changes in morphology.

In our study, the phylogenetic relationships of the three Pyrenean species remains uncertain. Nevertheless, the relationship implied by the MP tree corroborates hypotheses from karyotypic and osteological characters (Arribas 1997a, 1999b). *I. aranica* has the anterodistal process of the postfrontal and the anteromedial of postorbitary well developed, whereas the latter is absent in *I. bonnali* and both are not present in *I. aurelioi* (Arribas 1997a, 1998, 1999a, 1999b, 2000). In addition, *I. aranica* possesses a ZW sex chromosome system (almost universal in Lacertids, see for instance Olmo et al. 1987; Odierna et al. 1993) in a karyotype comprising 26 chromosomes in both males and females. In contrast, *I. aurelioi* and *I. bonnali* share the Z_1Z_2W sex chromosome system, but *I. aurelioi* has 26 chromosomes in males and 25 in females, whereas the respective numbers in *I. bonnali* are 24 and 23 (Odierna et al. 1996; Arribas 1997a,b, 1999a,b, 2000, 2001). We can assume that the karyotype of *I. aranica* represents the ancestral chromosome set in this group and that the karyotypes of *I. aurelioi* and *I. bonnali* would have derived from it successively. Therefore, *I. aranica* seems to be the sister species of the clade of *I. bonnali* and *I. aurelioi* (Arribas 1997a, 1999b), a hypothesis also suggested by allozyme electrophoresis (Mayer and Arribas 1996).

Concerning the remaining species included in the analysis, *Archaeolacerta*, as recently redefined (Arribas 1997a, 1999b), represents a polyphyletic assemblage with the Tyrrhenian paleoendemic type species *A. bedriagae* as the most basal taxon in our trees. Furthermore, both trees group '*L.*' *graeca* and *A. oxycephala* with *A. cappadocica*. Even though this clade is only weakly supported, our results tentatively imply closer relationships among these species. Further studies will be necessary to clarify if these three species form a monophyletic group to be classified as the genus *Apathya*, which so far includes only *A. cappadocica*. Our results are in accordance with earlier, similar suggestions by Harris et al. (1998) and Harris (1999).

The relationships of *A. mosorensis* are particularly interesting. In our analyses it is the sister group to the *Iberolacerta* clade, a very interesting result although only weakly supported. Further research must clarify whether *A. mosorensis* in fact represents a sister group to *Iberolacerta* or holds a more remote position itself. If *A. mosorensis* lacks microchromosomes (*Iberolacerta* autapomorphy) is hitherto unknown.

Taxonomic implications

We propose the following taxonomic alterations: (1) the genus *Archaeolacerta* should be restricted to the type species *A. bedriagae*. (2) The species *mosorensis, oxycephala* and *graeca* should remain provisionally in the collective genus *Lacerta*. To express the fact that there is no closer relationship between them and the real members of the genus (the green lizards) we propose a spelling between quote marks (e.g., '*Lacerta*' *mosorensis*). (3) The Peña de Francia lizards, originally described as *I. cyreni martinezricai*, could be treated provisionally as a subspecies of *I. monticola: I. monticola martinezricai*. (4) *I. monticola cantabrica* is a synonym of *I. monticola monticola*. (5) *I. cyreni cyreni* and*I. cyreni castiliana* should not be given subspecific status and unified as *I. cyreni*.

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Zusammenfassung

Die phylogenetischen Beziehungen der europäischen Lacertiden der Gattung Archaeolacerta und Iberolacerta und ihre Verwandtschaft zu anderen "Archaeolacertae" aus dem nahem Osten, basierend auf mitochondrialen DNA-Sequenzen

Wir sequenzierten Teilabschnitte der Gene für 12SrRNA und 16SrRNA (zusammen ungefähr 960 Basenpaare) von allen europäischen 'Gebirgseidechsen' der Gattungen *Archaeolacerta* (sensu lato) und *Iberolacerta*. Alle Subspezies der iberischen Arten *Iberolacerta cyreni* und *I. monticola* wurden in die Studie aufgenommen. Zusätzlich wurden Proben von *Apathya cappadocica* und *Darevskia rudis* untersucht, um die phylogenetischen Beziehungen der europäischen 'Gebirgseidechsen' zu ihren möglichen Verwandten im Nahen Osten aufzuklären. Maximum Parsimony und Neighbor Joining Analysen führten zu folgenden wesentlichen Ergebnissen: i) Die Monophylie der Gattung *Iberolacerta* ist gut abgesichert. ii) *Archaeolacerta bedriagae* (die species typica der Gattung) hat eine basale Position innerhalb der Gruppe der 'Gebirgseidechsen'. Daher schlagen wir vor, *Archaeolacerta* auf die species typica zu restringieren und *A. mosorensis* und *A. oxycephala* provisorisch in der Sammelgattung *Lacerta* zu belassen. iii) Die Gattung *Iberolacerta* zerfällt in drei Gruppen: eine Pyrenäen-Gruppe, eine iberische Gruppe und *I. horvathi.* Die Beziehungen zwischen diesen Gruppen konnten nicht aufgeklärt werden. iv) Die Eidechsen von Peña de Francia, ursprünglich als Subspezies von *I. cyreni* beschrieben, sind tatsächlich näher mit *I. monticola* verwandt.

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