Forum

Comments on the taxonomic value of (sub)genera within the family Lacertidae (Reptilia)

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Lacertids (Reptilia, Lacertidae) are some of the most studied lizards, especially in Europe where they make up nearly three-quarters of the lizard fauna. They have been used to assess the role of biological process in phylogenetics (Arnold, 1996), in assessing correlated evolution (Bauwens et al., 1995), and in estimating colonization patterns across islands (Thorpe et al., 1994). Relationships within lacertid lizards, however, have proved highly resistant to analyses based on morphological (Arnold, 1989), immunological (Mayer and Benyr, 1994) and DNA sequence data (Harris et al., 1998, 2001; Fu, 2000). Analysis of mitochondrial sequence data infers that *Gallotia* Boulenger 1916 and *Psammodromus* Fitzinger, 1826 (Gallotiinae) form a sister group to remaining lacertids, and this relationship has been supported by analysis of sequences from the nuclear gene C-*mos* (Harris et al., 2001). However, relationships within the subfamily Lacertinae have been weakly supported in all analyses, leading to the suggestion that rapid cladogenesis occurred so that further data will not resolve relationships (Fu, 2000).

In most situations lack of resolution within a clade has a limited effect on nomenclature, but in lacertids taxonomic difficulties arise because studies based on morphological and immunological data inferred that the genus *Lacerta* is paraphyletic (Arnold, 1989; Mayer and Benyr, 1994). Modern systematics attempts to reflect phylogeny, so paraphyletic genera are inappropriate. Following this principle several nomenclature changes have been suggested (Mayer and Bischoff, 1996) that involve recognizing separate genera for subgroups of *Lacerta*, specifically *Zootoca*, *Omanosaura*, *Timon* and *Teira*. Raising these units to generic status involves changes to the binomials applied to the species concerned. This procedure has caused much variation in the literature. For example, sequences from the endemic Madeiran lacertid lizard have been deposited on GenBank, the most important data bank for molecular studies, under *Podarcis*, *Teira* and *Lacerta dugesii*. Recent publication titles reflect this variation (e.g. Brehm et al., 2001; Galán and Vicente, 2002). This can easily lead to confusion among non-specialists. As has been stated before (e.g. Arnold, 2000), scientific names are not just used by taxonomists, but also by non-biologists such as lawyers, customs officers, doctors and hobbyists. Nomenclatural variation complicates the compilation of red books and other conservation lists. Harris et al. (1998) already recommended the use of subgenera within *Lacerta* for apparently monophyletic groups, specifically to avoid the necessity of binomial changes.

Since then two additional subgroups of *Lacerta* have been considered as full genera, *Darevskia* Arribas, 1997 and *Iberolacerta* Arribas, 1997. In cases where these subgroups are monophyletic, a case can be made for recognizing them as distinct genera. However two caveats should be applied. One is that the evidence for monophyly should be strong. If support is weak future evidence may contradict the grouping, thus requiring additional binomial changes. The second is that the new classification should maintain comparable levels of divergence within groups with the same taxonomic rank. In the case of *Lacerta* this means designating the largest well-supported monophyletic groups as genera — raising subsets of these to generic level will only give greater instability to the nomenclature. Here we consider all the recently proposed genera, and assess their utility in the context of their probable monophyly and support levels for the group.

Teira Gray, 1838

Three species are typically referred to *Teira* (Mayer and Bischoff, 1996): *T. dugesii* (Milne-Edwards, 1829), *T. perspicillata* (Duméril and Bibron, 1839) and *T. andreanskyi* (Werner, 1929). However other authors (e.g. Bons and Geniez, 1996) argue that *perspicillata* is distinct enough morphologically to warrant separation from *Teira* and placement in a monospecific genus, *Scelarcis* Fitzinger, 1843. Analysis of morphological characters makes *Teira* paraphyletic, with *T. andreanskyi* more closely related to *Podarcis* (Arnold, 1989). Harris and Arnold (1999) inferred a similar pattern of relationships derived from mtDNA sequences, while evidence from a different part of the mtDNA genome was equivocal (Oliverio et al., 2000). A much larger data set (not including *T. dugesii*) did not infer a sister taxon relationship between *T. perspicillata* and *T. andreanskyi* (Fu, 2000). All available evidence thus suggests this group is not a clade, unless *T. andreanskyi* is excluded. Nevertheless *T. perspicillata* and *T. dugesii* are well supported as sister taxa.

Zootoca Wagler, 1830

This monotypic genus containing only *Z. vivipara* (Jacquin, 1787). The phylogenetic position of this taxon is not well supported, with contradictory evidence from mtDNA and morphological characters (Arnold, 1989; Fu, 2000). Nevertheless, all of these analyses inferred that *Z. vivipara* was an internal branch within the paraphyletic *Lacerta*, and therefore its recognition as a full genus does not alter the paraphyly of *Lacerta*.

Omanosaura Lutz et al., 1986

This genus includes the species *O. jayakari* (Boulenger, 1887) and *O. cyanura* (Arnold, 1972). It was initially erected as a subgenus based on the genetic distance of *O. jayakari* from the rest of the collective genus *Lacerta* (Lutz et al., 1986), and later raised to full genus (Mayer and Bischoff, 1996). Based on mtDNA sequence data and morphology these two are sister taxa, and unlike all other "*Lacerta*" are members of the Eremiainae subfamily (Harris et al., 1998). Bootstrap support that the two species are sister taxa based on mtDNA sequence data is quite high (89% — Harris et al., 1998).

Timon Tschudi, 1836

Four species are included in this genus: *T. lepidus* (Daudin, 1802), *T. pater* (Lataste, 1880), *T. princeps* (Blandford, 1874) and *T. tangitanus* (Boulenger, 1887). They are supported as a clade by some derived morphological features (Arnold, 1989), by the presence of a derived karyotype (Rykena and Nettmann, 1986), and by mtDNA sequence data (Harris et al., 1998; Fu, 2000). These independent sources of evidence give strong support to the monophyly of the group. MtDNA sequence data and morphology suggest that the group is the sister taxon to the green lizards, *Lacerta* sensu stricto (Harris et al., 1998; Fu, 2000).

Iberolacerta Arribas, 1997

This genus contains several forms, the specific status of some of which are still debated (Pérez-Mellado, 1998; Salvador and Pleguezuelos, 2002), including *I. aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994), *I. bonnali* (Lantz, 1927), *I. cyreni* (Müller and Hellmich, 1937), *I. horvathi* (Mehély, 1904) and *I. monticola* (Boulenger,

1905). DNA sequence analysis indicates that *I. bonnali, I. monticola* and *I. horvathi* form a clade (92% bootstrap support, Harris et al., 1998), and since *I. aranica* and *I. aurelioi* occur close to *I. bonnali* in the Pyrenees and share a derived karyotype with it (Odierna et al., 1996) it is likely that this group is monophyletic. Morphological analyses also indicate that the group is monophyletic (Arribas, 1999).

Darevskia Arribas, 1997

Included in this genus are members of the "*saxicola* complex", *D. derjugini* (Nikolskij, 1898), *D. praticola* (Eversmann, 1834) and *D. chlorogaster* (Boulenger, 1908). Although no molecular studies have been performed including all accepted species, the included species have always formed well supported monophyletic groups (e.g. Fu et al., 1997; Murphy et al., 2000).

Archaeolacerta sensu novo Arribas 1999

Archaeolacerta Méhely 1909 was first used for Palearctic species showing morphological features associated with rocky habitats and crevice use, characters which also occur independently in other forms that use similar terrains (Arnold, 1989). *Archaeolacerta* sensu novo Arribas 1999 contains three species, *A. bedriagae* (Camenrano, 1885), the type species, *A. mosorensis* (Kolombatovic, 1886) and *A. oxycephala* (Duméril and Bibron, 1839). However neither morphological (Arnold, 1989) nor mtDNA sequence data (Harris et al., 1998) suggest that this is a monophyletic group.

Remaining *"Lacerta"*

Even if the above groups are all accepted as full genera there remain several species or species groups that would also need to be recognized as full genera to prevent *Lacerta* from being paraphyletic — *andreanskyi*, *fraasii/parva* (assigned to the subgenus *Parvilacerta*, Harris et al., 1998), *oxycephala*, *cappadocica* (which can be assigned to *Apathya* Méhely, 1909), *danfordi* group, *graeca* and the *laevis/kulzeri* group. Possibly future analyses will show that some of these forms are closely related and could be grouped into fewer genera, but at present there are no well supported units other than these groups that can be recognized. Recognition of monospecific genera, such as *Scelaris* or *Zootoca* does not improve the situation unless the other genera are part of a fully resolved phylogeny.

We suggest recognizing all the subgroups of *Lacerta* as subgenera, except *Omanosaura* that belongs to a phylogenetically distinct lineage, and is well supported as a clade. Of the previously proposed genera *andreanskyi* should be excluded from *Teira*, and *oxycephala* and *mosorensis* from *Archaeolacerta*. While *Timon*, *Iberolacerta* and *Darevskia* appear to be well supported monophyletic units on the evidence available so far, it seems prudent to use them as subgenera until relationships of the remaining *Lacerta* are better resolved, probably through the use of more molecular data. Two other groups form part of the Lacertinae, *Podarcis* Wagler, 1830 and *Algyroides* Bibron and Bory, 1833. While an argument could be made to similarly recognize these as subgenera, both are clearly monophyletic groups which are well established in the literature (Arnold, 1989; Harris and Arnold, 1999; Harris et al., 1999). We therefore recommend the continued use of these as full genera. In this way instability and confusion within the nomenclature will be minimized.

Acknowledgements. The authors are funded by grants from FCT, SFRH/BPD/5702/2001, SFRH/BPD/3596/2000, and POCTI/41912/BSE/2001.

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Received: June 17, 2002. Accepted: July 9, 2002.