A phylogeny of the European lizard genus *Algyroides* (Reptilia: Lacertidae) based on DNA sequences, with comments on the evolution of the group

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Abstract
The four species of *Algyroides* Bibron & Bory, 1833 form part of the relatively plesiomorphic Palaearctic clade of lacertids comprising *Lacerta* and its allies. An estimate of phylogeny based on DNA sequence from parts of the 12S and 16S rRNA mitochondrial genes confirms the monophyly of the genus already suggested by several morphological features. The molecular data also indicates that relationships within the clade are: (*A. nigropunctatus* (*A. moreoticus* (*A. fitzingeri*, *A. marchi*))); this agrees with an estimate of phylogeny based on morphology that assumes the taxon ancestral to *Algyroides* was relatively robust in body form, and not strongly adapted to using crevices. Initial morphological evolution within *Algyroides* appears to involve adaptation to crypsis in woodland habitats. The most plesiomorphic form (*A. nigropunctatus*) is likely to have originally climbed extensively on tree boles and branches and there may have been two subsequent independent shifts to increased use of litter and vegetation matrices with related anatomical changes (*A. moreoticus*, *A. fitzingeri*), and one to increased use of crevices (*A. marchi*). Some members of *Algyroides* are strikingly similar in superficial morphology to particular species of the equatorial African genus *Adolfus*. This resemblance results from a combination of many shared primitive features plus a few independently acquired derived ones that are likely to give performance advantage in the relatively similar structural niches that these forms occupy. This study provides evidence that: (1) the use of a combination of molecular and morphological data may sometimes allow the estimation of ancestral anatomical features when these are otherwise unknown; (2) process considerations may permit a choice to be made in cases of character evolution where tree topology means that equally parsimonious alternatives exist; such decisions about character evolution may allow ecological shifts to be similarly assessed; (3) parallel evolution in ecological analogues may involve relatively few characters.

Key words: lizards, *Algyroides*, DNA sequence, evolution

INTRODUCTION

*Algyroides* Bibron & Bory, 1833 is a small clade of four well-differentiated species of lacertid lizards with largely disjunct distributions in southern Europe (Fig. 1), that may be originally associated with woodland habitats (Arnold, 1973, 1987). The genus is part of a large Palaearctic clade of mainly primitive lacertids that includes most present members of the paraphyletic genus *Lacerta* and the wall lizards *Podarcis* (Harris, Arnold & Thomas, 1998a); it will be referred to here as *Lacerta* and its allies†. Detailed affinities within this assemblage have not been firmly resolved (Arnold, 1989a; Mayr & Benyr, 1994; Harris, 1997), although mtDNA sequence provides restricted evidence that *Algyroides* is the sister group of *Lacerta bedriagae* (Harris et al., 1998a). Within *Algyroides*, morphological features that might give information about relationships are few with considerable conflict in their distributions, and because of the uncertainties about relationships within the *Lacerta* and its allies, it is not possible to designate the most appropriate outgroups for phylogenetic analysis of the genus with any certainty.

To resolve relationships within *Algyroides* and confirm its monophyly, a phylogenetic analysis was conducted using DNA sequences derived from sections of two mitochondrial genes. These were then combined with morphological information and employed to assess changes in anatomy and ecology and the general evolution of the genus and to examine parallelism.

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† This assemblage does not include *Lacerta jayakari* and *Lacerta cyanura* which are most appropriately placed in a separate genus, *Omanosaura* Lutz & Mayer 1986 (Harris et al., 1998a).
between members of *Algyroides* and those of the central African genus *Adolfus*, that show considerable superficial resemblance to each other.

**EVIDENCE FOR CLADE STATUS OF *ALGYROIDES* AND INTERRELATIONSHIPS WITHIN THE GENUS DERIVED FROM MORPHOLOGY**

The morphological characters mentioned in the text are discussed elsewhere (Arnold, 1973, 1989a, b)

A number of derived morphological features which, in combination, define *Algyroides* as a clade are likely to have been present in the immediate common ancestor of the genus (Table 1, characters 1–6). Characters varying interspecifically within *Algyroides* are also listed in Table 1, and their distributions shown in Table 2. To establish a hypothesis of relationships, these data were analysed by maximum parsimony, with exhaustive searches, using the program PAUP 3.1.1 (Swofford, 1993); the single multistate character (number 7) was treated as ordered.

Several of the morphological features that vary within *Algyroides* also vary in the rest of the clade made up of *Lacerta* and its allies, including characters 8, 9, 10, 11, 20 and 25. As the closest outgroups of *Algyroides* within this assemblage are not known for certain, this variation means that the immediate ancestor of *Algyroides* could have had a range of different character states. Which ones are assumed affects the supposed pattern of relationships produced within *Algyroides*. At one extreme, the tree can be rooted using a hypothetical ancestor in which characters 8, 9, 10 and 11 are scored as 1, and character 20 as 0. In this case the ancestor would resemble some of the delicately built and flattened *Lacerta* species in the Palaearctic group that live on rocky surfaces and frequently use crevices as refuges, such as *Lacerta oxycephala*. Four most parsimonious trees are produced using such an ancestor, and the strict consensus tree derived from these is uninformative. If, on the other hand, alternative states are entered for these characters, the hypothetical ancestor resembles a more robustly built *Lacerta* without marked crevice-using specializations, such as *Lacerta laevis*. In this case, a single most parsimonious tree is produced (Fig. 3). This latter version of events is more parsimonious overall, given the lack of knowledge about detailed relationships within the clade made up of *Lacerta* and its allies, as most 0 states are more likely to be primitive in the ancestor of this assemblage.

**EVIDENCE FOR RELATIONSHIPS FROM ALBUMIN IMMUNOLOGY**

Two possible phylogenies for the species of *Algyroides* have been suggested on the basis of albumin evolution assessed by immunological means (Mayer & Lutz, 1990). One is that the relationships are: *A. fitzingeri* (*A. marchi* (*A. nigropunctatus, A. moreoticus*)). The alternative is similar except that *A. marchi* is excluded and appears to be most closely related to a putative clade comprising *Podarcis* and *Lacerta graeca*. The latter arrangement would make *Algyroides* polyphyletic, something that conflicts strongly with the morphological evidence that the genus is a clade.

**EVIDENCE FOR RELATIONSHIPS FROM MITOCHONDRIAL DNA SEQUENCES**

Given the problems of choosing appropriate outgroups for *Algyroides* when assessing the morphological
evidence of relationships, and the conflicting results from immunological studies of albumin, additional data are necessary to resolve the relationships of the species of *Algyroides*. These data are provided in this paper by investigation of mitochondrial DNA (mtDNA) sequences. Portions of two mitochondrial genes, 12S rRNA and 16S rRNA were sequenced for all four species of *Algyroides*, for two species of wall lizards, *Podarcis muralis* and *Podarcis taurica*, and for the more distantly related *Gallotia galloti* (Arnold, 1989a; Mayr & Benyr, 1994); the later three species provide appropriate outgroups.

**MATERIALS AND METHODS FOR DNA ANALYSIS**

Localities and sources of the lizards from which DNA was extracted are given in the Appendix. Tissue samples consisted of tail tips, stored in 70% ethanol at 4°C. Voucher specimens are deposited in the collection of the Natural History Museum, London.

**Laboratory procedures**

Total genomic DNA was extracted from 1 or 2 mm³...
pieces of tail tissue. The material was finely diced and digested with proteinase K (Kocher et al., 1989). Purification was by phenol/chloroform extractions (Sambrook, Fritsch & Maniatis, 1989), followed by centrifugal dialysis through a Centricon 30000 MW membrane (Amicon). Polymerase chain reaction (PCR) primers used in both the amplification and the sequencing were 12Sa and 12Sb (Kocher et al., 1989) and 16L and 16H (Hedges, Bezy & Maxson, 1991). These amplified regions were some 400 bp and 450 bp, respectively.

Thermocycling consisted of 30 cycles of 93 °C for 30 s, 55 °C for 1 min and 72 °C for 1 min, followed by a single cycle at 72 °C for 10 min. PCR products were checked by electrophoresis on a 2% agarose gel, and sizes of amplified products were estimated using a molecular weight marker. Successful PCR bands were cut out and purified using a QIAEX II kit (Quiagen). The DNA was then dialysed through a Microcon 30000 MW membrane (Amicon) twice with double-distilled water and the volume made up to 10 μl; 2 μl of this was then sequenced on an Applied Biosystems Model 373A DNA Sequencing System, using a PRISM Ready Reaction DyeDeoxy Terminator Cycle Sequencing kit. Centrisep spin columns (Princeton Separations Inc.) were used for excess dye extraction. More detailed procedures are given by Harris (1997).

Alignment

12S rRNA sequences were aligned by eye and compared to homologous sequences of Lacerta lepida and Lacerta dugesii (Gonzalez et al., 1996) and Meroles. They were also aligned against secondary structure models (Neefs et al., 1990; Hickson et al., 1996). 16S rRNA sequences were similarly aligned using Meroles, other lacertids (Harris, 1997), various xantusiid lizards (Hedges & Bezy, 1994) and a more limited secondary structure model (Gutell, 1993). The resulting alignments contained 315 and 398 sites, respectively. A total of 36 sites that could not be aligned convincingly because they were hypervariable were removed from the analysis. The alignment used is available on request from the corresponding author. Sequences have been deposited in Genbank (Accession numbers AF080306, AF019648–019650 and AF111174–111177).
Intraspecific variation

In all species a single individual was sequenced, as the partial gene regions used have very low intraspecific variation in lacertids. Where individuals of the same species of lacertid have been sequenced independently in different laboratories, differences have been minimal and largely confined to the hypervariable regions removed in this analysis (e.g. *L. lepida* and *G. galloti*; Gonzalez *et al*., 1996; Harris, 1997).

Phylogenetic analysis

Phylogenetic analyses were performed using PAUP* 4.0.d52 (Swofford, 1998), employing the 3 main methods of inferring phylogenies, namely parsimony, distance methods and maximum likelihood. Branch lengths, transition/transversion ratios (TS/TV) and among-site rate variation have all been shown to influence phylogenetic analysis (Hillis, Moritz & Mable, 1996; Yang, 1996) and were all consequently taken into account in the analysis.

PAUP* was also used to calculate base composition across the combined sequences. If base composition differs substantially between lineages, systematic error can be introduced into any analysis that incorrectly assume the same equilibrium base frequencies across lineages (Hillis *et al*., 1996). In fact, base composition in *Algyroides* is typical of vertebrate mitochondria, and almost identical to that of other lacertids for this region (average occurrences in the light strand A 34%, G 20%, C 24%, T 22%; Kocher *et al*., 1989; Harris, 1997). Base composition biases within *Algyroides* and the outgroups were tested using the approach proposed by Rzhetsky & Nei (1995). Frequencies did not vary significantly between species ($I = 23.91$, $P > 0.05$).

RESULTS

Initially a maximum parsimony analysis was carried out on the combined 12S and 16S data sets. These contained a total of 677 characters after unalignable ones were excluded, of which 489 were invariant and 91 were uninformative under parsimony criteria. An exhaustive search with all characters weighted equally resulted in one most parsimonious tree (Fig. 4). Support for nodes was estimated by bootstrapping (Felsenstein, 1985). Bootstrap support is particularly strong for the monophyly of *Algyroides* (93%) and for the sister-relationships of *A. fitzingeri* and *A. marchi* (100%). It is less robust for the relationship of *A. moreoticus* to the latter two species (59%). Maximum parsimony analyses were also carried out on the separate 12S and 16S data sets, and bootstrapped 50% majority rule trees produced. These differed from the combined tree only in that the tree derived from 12S data alone was not as fully resolved, thereby justifying the use of an approach in which the two gene regions were combined (Hillis *et al*., 1996).

A neighbour joining analysis was also carried out, using LogDet (Steel, 1994) corrected distances, a method that does not require stationarity of nucleotide frequencies, the assumption of which can misleadingly group sequences of similar nucleotide frequencies regardless of true evolutionary relationships (Hasegawa & Hashimoto, 1993; Gu & Li, 1996). This analysis gave the same topology as maximum parsimony.

A maximum likelihood analysis was then performed on the combined data sets. The optimal TS/TV ratio was estimated using PAUP* 4.0.d52 (Swofford, 1997) to be 3.10. Among-site rate variation was estimated using a discrete approximation to the gamma distribution (shape parameter 1.132, with four rate categories; Yang, 1996). Gaps were treated as missing data. Employing the HKY85 model (Hasegawa *et al*., 1985), which allows for two substitution types and unequal base frequencies, and estimating the proportion of invariant

![Fig. 4. Maximum-likelihood tree (log-likelihood −2243) based on the combined 12S and 16S partial gene sequences. The maximum parsimony tree has an identical topology. Numbers above internal branches are branch lengths for the maximum likelihood tree, and reflect numbers of nucleotide substitutions per site. Bootstrap (500 replicates) percentages for the maximum parsimony tree are given below the internal branches. For details of models used see text.](image)
sites (0.607) using maximum likelihood, a single tree of log likelihood $-2243$ was produced (Fig. 4).

Previous studies have shown that relationships may be obscured by saturation of sites by multiple substitutions, transitions being likely to become saturated before transversions (see Hillis et al., 1996). Because of this, pairwise proportions of transitions and transversions in the combined sequences were plotted against LogDet corrected sequence divergence calculated using PAUP* 4.0.d52 (Swofford, 1996). They show an approximately linear relationship (Fig. 5), indicating that sites are unlikely to have been saturated by multiple substitutions.

The combined sequences were analysed further using the ‘split-decomposition method’ (Bandelt & Dress, 1992a), employing the program Splitstree 1.0 (Huson & Wetzl, 1994). In a typical phylogenetic analysis, data are forced to fit a tree topology. The split-decomposition method however allows for conflicting alternative groupings, exhibiting networks of relationships including the more tentative ones that will be overridden on a single tree topology (Bandelt & Dress, 1992b). All alignable positions were used in the analysis, and the Logdet correction applied. The topology of the network (Fig. 6) indicates strong support for the relationships shown, which are identical to those produced by the approaches already discussed.

To check if there was any significant differences between the estimates of phylogeny derived from the albumin evolution data set and that from the mtDNA data set, the topology of the tree for the DNA characters was constrained to the topology of the albumin evolution estimates. The log likelihoods for these hypothesized relationships, using the same model of evolution as the maximum likelihood estimate, were $-2269$ (in the estimate derived from albumin evolution in which Algyroides is a clade) and $-2276$ (in the estimate in which A. marchi is more closely related to Podarcis and Lacerta graeca than to other Algyroides). Both of these estimates of phylogeny are significantly less well supported than the unconstrained maximum likelihood tree, according to the likelihood variance test of Kishino & Hasegawa (1989) (Table 3), calculated using PAUP.

**PHYLOGENETIC CONCLUSIONS**

Molecular and morphological data both support the monophyly of Algyroides. The DNA phylogeny corroborates the tree based on morphology in which a robustly built ancestor without marked crevice specializations, similar to Lacerta laevis, is assumed. Such an assumption does not necessarily mean that Lacerta laevis itself is the sister taxon of Algyroides, and DNA sequence data provides no evidence for this (Harris et al., 1998a). The long branch length of Gallotia on the maximum likelihood and splitstree analyses (Figs 4 & 6) is consistent with this genus being more distantly related to Algyroides than Podarcis. This conclusion is also supported by evidence from morphological (Arnold, 1989a) and karyological (Olimo, Odierna & Capriglione, 1993) data.

In contrast to the similar tree topologies produced from DNA sequence and morphological data, albumin immunology suggests different relationships among the species of Algyroides, and the possibility of a polyphyletic origin for the genus (Mayer & Lutz, 1990). As two of these three apparently independent sources of phylogenetic evidence corroborate each other closely, it

Table 3. Maximum-likelihood tests (Kishino & Hasegawa, 1989) of alternative tree topologies for Algyroides lizards

<table>
<thead>
<tr>
<th>Tree topology</th>
<th>Log likelihood</th>
<th>$\Delta$ Log likelihood</th>
<th>sd</th>
<th>$P^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNA sequence (ML)</td>
<td>$-2243$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albumin evolution (1)</td>
<td>$-2269$</td>
<td>26</td>
<td>9.0</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Albumin evolution (2)</td>
<td>$-2276$</td>
<td>33</td>
<td>11.2</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

$^a$ Trees compared were the maximum-likelihood tree based on DNA sequence data (Fig. 3), and alternative hypotheses based on albumin evolution data (1, monophyletic Algyroides; 2, polyphyletic Algyroides).

$^b$ $P$ is the probability of getting a more extreme $t$-value under the null hypothesis of no difference between trees. Both these hypotheses are significantly worse than the maximum likelihood tree.
is likely that it is the hypotheses of relationships based on immunology that are wrong. In the immunological tree all the internal branches are extremely short, so slight variation in the rates of albumin evolution, or imprecision in the techniques used to assess them, could result in errors in the estimation of relationships. Unfortunately, with immunological data it is not possible to gauge the degree of statistical support for particular internal branches. This contrasts with the situation with DNA sequences where the bootstrap technique (Felsenstein, 1985) permits such tests to be made. As already noted, these tests indicate that most relationships derived from DNA sequence receive statistical support that is often strong, with bootstrap figures of from 59% to 100% (Fig. 4). The split-tree analysis of sequence data also suggests little homoplasy, with a 77% data fit and a clear single tree topology, indicating that no other relationship is strongly supported by the DNA data (Fig. 6).

**DISTINCTIVE FEATURES OF THE SPECIES OF ALGYROIDES**

The four species of Algyroides are well defined and easily distinguished from each other. The phylogeny supported here allows autapomorphic features to be recognised with some certainty and, with the exception of A. nigropunctatus, two to five morphological autapomorphies are assignable to each species. These are listed below; figures in parentheses refer to Table 1.

*Algyroides moreoticus*: sternal fontanelle sometimes weakly heart-shaped (13); often a single postnasal scale (14); micro-ornamentation of dorsal scales with the raised posterior borders of oberhautchen cells denticulated (19); sexual dichromatism (23); males often with narrow light dorsolateral streaks (24).

*Algyroides fitzingeri*: very small size (7); more long postternal ribs (12); mean number of presacral vertebrae in males particularly high; tail robust (22).

Molecular phylogeny of *Algyroides* lizards

**Fig. 6.** Split-decomposition network of the LogDet corrected distances between species of *Algyroides*, *Podarcis* and *Gallotia*. Only alignable positions were included in the analysis. The tree-like topology of the network indicates strong support for these relationships.

**Fig. 7.** Phylogeny for the Central African *Adolfus* and their relatives (from Arnold, 1989b), showing principal changes in morphology that also occur in *Algyroides* (see Fig. 3). Black rectangles: characters supporting monophyly of *Algyroides*. Numbers refer to Table 1.
**EVOLUTION WITHIN ALGYROIDES**

**Character evolution (Fig. 3)**

Combined morphological and molecular considerations suggest that *Algyroides* is derived from a member of the Palaearctic assemblage of lacertids comprising *Lacerta* and its allies which had features likely to be primitive for this group, including a robust skull with complete suprocular osteoderms and small dorsal scales. *Algyroides nigropunctatus*, which constitutes the most basal branch of the main lineage of the genus, is in many ways the most plesiomorphic form. It is about the same size as most other members of the clade consisting of *Lacerta* and its allies and, although it has enlarged keeled scales, these do not overlap very extensively posteriorly and are found only on the dorsum and not on the flanks, where small scales are retained.

The remaining three species of *Algyroides* are characterized by relatively small size (7(1)), a derived condition. *Algyroides fitzingeri* and *A. marchi* share several other features that are congruent with the phylogeny of *Algyroides* accepted here, including a weakly ossified skull (8) with fenestrated supraocular osteoderms (9) and absence of pterygoid teeth (10); these are also the only species to sometimes possess a dark vertebral streak or row of spots (21). The phylogeny indicates that weak keeling of the large dorsal scales (18R) of *A. marchi* is secondary and not an intermediate stage in the development of strong keeling.

Some derived features are not congruent with the phylogeny, including a possible increase in the number of presacral vertebrae in females (11), development of large scales on the flanks (16), dorsal and lateral scales lanceolate and more overlapping (17) and an increase in the overlap of ventral scales (20). These features occur in both *A. moreoticus* and *A. fitzingeri* and could result from a single origin on the main lineage of the genus, followed by reversal in the ancestor of *A. marchi*. Just as parsimoniously, in terms of number of steps on the tree, they may have developed independently and in parallel in the two species. The latter alternative is preferred for the following reasons:

1. The features concerned appear to evolve quite easily. Within the Lacertidae, characters 16, 17 and 20, and sometimes 11, have appeared together several times, in *Psammodromus*, *Adolfus alleni*, *Tropidosaura*, *Ichnotropis* and *Ophisops* (Arnold, 1989a) and do not appear to have reversed in the groups.

2. The evolution of the features is concurrent on the phylogenies of these taxa with occupation of spatial niches in which they are likely to confer performance advantage (see below). There is consequently likely to be strong selection for these features in such environments.

3. There are no residual signs in *A. marchi* that the lineage leading to it ever possessed the features under consideration.

**Changes in niche**

As noted, the species of *Algyroides* all seem to have been originally associated with woodland and woodland-edge habitats (Arnold, 1987), so this is likely to have been the ancestral environment of the genus. Although heliothermic, they tend to occur in relatively cool places and often close to shade; *Algyroides* may also operate at rather lower temperatures than syntopic *Lacerta* and *Podarcis* (Arnold, 1973, 1987). If *Algyroides* is indeed derived from a form morphologically similar to *Lacerta laevis*, its ancestor is likely to have been like this species in being partly scansorial on continuous surfaces such as those of rocks and occasionally trees (Zinner, 1967). A shift to increased use of tree boles and branches, and of fallen timber, would then produce the kind of spatial niche found in the most basal species, *A. nigropunctatus*.

The three more derived smaller species often occur close to water or moisture, and a shift to these conditions presumably occurred on the common lineage leading to them. One of these species, *A. marchi*, often climbs on continuous surfaces, like *A. nigropunctatus*, but makes greater use of narrow crevices than this species and probably other members of the genus too (Arnold, 1987; Rubio & Carrascal, 1994). *Algyroides moreoticus* and *A. fitzingeri* are found more frequently in vegetation matrixes such as brushwood and litter. Because of the particular topology of the phylogeny it is not possible to decide, just on the basis of the distribution of structural niche types on this, whether it is more parsimonious to assume the shift to greater use of matrix situations occurred once or twice. However, as already noted, there are reasons for thinking that some derived morphological features, found in the two *Algyroides* species that occur in matrix situations, have developed in parallel. As the derived morphological features are likely to confer a performance advantage in these environments and were therefore probably promoted by natural selection in them, a double origin of occupation of the environments themselves seems most feasible. Although no detailed comparison of ecology and behaviour has been made, the marked morphological differences between *A. moreoticus* and *A. fitzingeri* suggest that have different structural niches and life modes while similar are not identical.

The marked differences in body size in the species of *Algyroides* suggest they probably eat different sizes of prey, with a shift to smaller food items eaten by smaller species that is most marked in *A. fitzingeri*.
Possible performance advantages of character shift

The development in the immediate ancestor of *Algyroides* of large keeled dorsal scales with a complex micro-ornamentation that reduces shine, and sombre dorsal coloration, may have enhanced crypsis in woodland and woodland-edge habitats by producing a rough, rather dull surface. Such features have also evolved independently in *Adolfus* and *Takydromus*, which both include species that occur in these environments (Arnold, 1989b). It is uncertain what may have caused the reduction in body size in the three more derived members of *Algyroides*. The morphological parallels between *A. fitzingeri* and *A. moreoticus* may be functionally connected with a greater occupation of vegetation matrices such as litter and brushwood. In these habitats, large flank scales and an increased overlap of most body scales provides enhanced mechanical protection for the body in spiky situations (Arnold, 1973), and an increase in the number of presacral vertebrae may promote flexibility, facilitating movement through the often complex twisting interstices of the environments concerned.

The reduction in the strength of dorsal scale keeling in *A. marchi* may be functionally connected with the way this species uses narrow crevices more than other *Algyroides* species. A smooth flexible surface is advantageous to maintain position and facilitate movement in crevices (Arnold, 1973) and is provided by the weakly keeled scales. The fact there is not a reversal to the primitive relatively small scales found in most crevice-dwelling lacertids suggests that large scales may be just as effective in this situation or that they are retained as a result of phylogenetic constraint.

BIOGEOGRAPHY OF *ALGYROIDES*

The phylogeny of the extant species of *Algyroides* suggests their immediate ancestor may have had an eastern distribution and that there was dispersal to the west. Alternatively there may have been a sequence of vicariance events that began in the east.

The disjunct distribution of the species of *Algyroides*, each with small individual ranges, is similar to that of rock lizards in Europe. As their name suggests, these are mainly saxicolous members of *Lacerta* that have sometimes been placed in their own subgenus, *Archeolacerta* Mertens 1921, although there is no evidence that they form a clade (Harris et al., 1998a). European rock lizards include *Lacerta bedriagae*, *L. monticola*, *L. bontali*, *L. aurelioi*, *L. aranica*, *L. horvathi*, *L. mosorensis*, *L. oxycephala* and *L. graeca*. In both the European Rock lizards and in *Algyroides*, species are well defined morphologically and often represent long external branches in molecular phylogenies, suggesting that they have been separated from each other for a long time. These features contrast with the situation in the far more widely distributed wall lizards *Podarcis*, which suggests the possibility that a long-established European lizard fauna comprising members of *Lacerta* and *Algyroides* may have been largely displaced by the recent expansion of *Podarcis* (Arnold, 1981). Certainly the species of rock lizards and of *Algyroides* tend to have narrow niches in the presence of species of *Podarcis* that may be in competition with them. For instance, *A. nigropunctatus*, which climbs considerably, is quite restricted in its habitat on the east Adriatic mainland in areas where it occurs with partly scansional *Podarcis muralis*, being absent for instance from urban environments. In contrast, it is found in a wide range of situations on Corfu where no climbing *Podarcis* occurs (Arnold, 1987).

PARALLEL EVOLUTION WITH THE CENTRAL AFRICAN *ADOLFUS* CLADE

Some tropical African lizards, now placed in the genus *Adolfus*, were assigned to *Algyroides* (Boulenger, 1906, 1920; Loveridge, 1957). These are *Adolfus africanaus*, *Adolfus vaurenselli* and *Adolfus alleni*. It was later shown that they differed substantially from *Algyroides* (Arnold, 1973) and they were consequently placed in the Equatorial African clade of the Lacertidae (Arnold, 1989a, b). Derived features in which the members of *Adolfus* differ from *Algyroides* include: medial loop of clavicle never interrupted posteriorly, basal autotomic caudal vertebrae always with simple transverse processes; hemipenis with a well-developed armature and complexly folded lobes (Arnold, 1986); course of ulnar nerve ‘varanide’ or intermediate between the ‘lacertide’ and ‘varanide’ conditions (Julien & Renous-Lécureu, 1972). In addition there are six features that define the Equatorial African clade (see Arnold, 1989a, b for details). Relationships of the species of *Adolfus* and their near relatives are shown in Fig. 7.

The resemblance between *Algyroides nigropunctatus* and *Adolfus africanaus* is particularly striking. However, phylogenetic analysis shows that most of this results from primitive shared characters, although there are a few, sometimes very distinctive, features that have been independently derived in the two species. These include: a distinctive micro-ornamentation pattern on the dorsal body scales (Table 1, character 2); large scales on the dorsum (3) that are blunt, and strongly keeled (18); few enlarged dorsal scales between the hind legs (4); a low number of presacral vertebrae (5); sombre dorsal coloration (6).

There are also marked resemblances between *Adolfus alleni* and *Algyroides moreoticus* and *Algyroides fitzingeri*. Apart from large and strongly keeled dorsal scales (3, 18), derived similarities include a probable increase in the number of presacral vertebrae, especially in females (11), large lateral body scales (16), dorsal and lateral body scales lanceolate and imbricate (17) and ventral scales with marked posterior overlap (20). In addition, the presence of narrow light dorsolateral...
streaks in at least some individuals (24) is shared with A. moreoticus, while a larger proportion of long presacral ribs in both sexes (12), the occasional presence of a dark vertebral streak or series of spots (21) and the possession of a robust tail (22) are shared with A. fitzingeri.

More restricted parallels occur between Holaspis guentheri, a highly modified member of the Adolfus clade (Arnold, 1989b), and Algyroides marchi. Both have ossification of the skull reduced (8), fenestrated supraocular osteoderms (9) and ancestral keeling on dorsal scales reduced or, in the case of Holaspis, absent (18R).

The members of the equatorial clade nearly all climb quite extensively and are associated with forest and forest-edge situations, so this is likely to have been their ancestral life-mode, as it appears to have been in Algyroides. Within the general forest environment, Adolfus africanus and Algyroides nigropunctatus both climb on tree boles and branches and fallen timber, although they also spend some time on the ground (Arnold, 1987, 1989b). Adolfus alleni is exceptional in that the phylogeny indicates it has shifted from forest situations into montane environments above the tree line, where it lives in and around dense clumps of low vegetation (Arnold, 1989b). It consequently resembles Algyroides moreoticus and Algyroides fitzingeri in using vegetation matrices and litter. Holaspis guentheri and Algyroides marchi also have ecological similarities, both climbing extensively and using narrow crevices, especially for refuges (Arnold, 1987, 1989b).

At least some of the derived resemblances occurring in Algyroides and the Adolfus clade may consequently have arisen as a result of adaptation to the structurally similar habitats they occupy. Possible performance advantages of some of these features that could have resulted in their being favoured by natural selection have already been discussed.

Not only do Algyroides and the Adolfus clade show significant parallels in the structural niches they have occupied and their morphological evolution, but they are both likely to have been derived from ancestors that were superficially similar in their gross morphology. As has already been suggested, a robust scansorial ancestor similar to Lacerta laevis is likely for Algyroides, and the most basal member of the Adolfus clade, A. jacksoni, is externally very like a robust Lacerta.

Concluding remarks

The use of both morphology and mtDNA sequence to estimate the phylogeny of Algyroides reveals a number of points of broader interest.

1. The DNA evidence corroborates a particular morphological estimate of phylogeny in which an ancestor with specified anatomical features is assumed but not known. Molecular evidence thus allows something to be said about the morphology of the precursor of a clade that is not derivable from morphological evidence alone. This is another case where combining morphological and molecular approaches to phylogeny reconstruction provides more insight into evolution than using either one or the other exclusively.

2. Where both morphology and molecules indicate a topology in which it is equally parsimonious to assume that some anatomical characters may have either arisen once and then reversed, or alternatively arisen twice and not changed, considerations of biological process (Arnold, 1996) may allow a choice to be made between these two possibilities. In Algyroides the ease with which such features seem likely to evolve – based on the existence of parallel cases in other groups, evidence that there may be strong selection for them, and the lack of evidence for previous presence of the features in some lineages where they might otherwise be expected – suggests that parallelism has occurred rather than reversal. Once a case for parallelism in the evolution of derived morphological features has been made, this can be used to assess the number of shifts into the environments where these attributes confer performance advantage.

3. Comparisons of evolution in Algyroides and Adolfus demonstrate that, where ancestral forms are similar, striking parallelism may occur in analogous environments, although the number of characters involved is quite small compared to similarity resulting from primitive resemblance.

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REFERENCES


Appendix. Data for specimens used for DNA extraction

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Source</th>
<th>Dates</th>
</tr>
</thead>
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<tr>
<td><em>Algyroides fitzingeri</em></td>
<td>Sardinia</td>
<td>H. in den Bosch</td>
<td>Received November 1995</td>
</tr>
<tr>
<td><em>Algyroides marchi</em></td>
<td>Sierra de Cazorla, Spain</td>
<td>H. in den Bosch</td>
<td>Hatched 1989</td>
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<tr>
<td><em>Algyroides moreoticus</em></td>
<td>Greece</td>
<td>H. in den Bosch</td>
<td>Received October 1996</td>
</tr>
<tr>
<td><em>Algyroides nigropunctatus</em></td>
<td>Aghios Stefanos, Corfu</td>
<td>E. N. Arnold</td>
<td>Collected August 1991</td>
</tr>
<tr>
<td><em>Gallotia galloti</em></td>
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<td>H. in den Bosch</td>
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<tr>
<td><em>Podarcis muralis</em></td>
<td>Near Cannes, France</td>
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<tr>
<td><em>Podarcis taurica</em></td>
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