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Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology

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DNA sequences from parts of the 12S, 16S and cytochrome *b* mitochondrial genes, which totalled 1049 aligned base pairs, were used to estimate the relationships of 49 species of Lacertidae, including representatives of 19 out of the 23 recognized genera and 23 species of the paraphyletic genus *Lacerta*. These data were used, together with morphological information, to estimate the relationships within the family. Molecular evidence corroborates the monophyletic status of many genera and species groups originally based on morphology. It indicates that *Psammodromus* forms a clade with *Gallotia*, which is the sister taxon of all other lacertids. These comprise three units: the primarily Afrotropical armatured group; the largely Oriental *Takydromus*; and the west Palaearctic *Lacerta* and its derivatives, *Podarcis* and *Algyroides*. Morphology also supports the first three assemblages, but suggests that they are derived from a paraphyletic *Lacerta*. Within *Lacerta* and its allies, DNA sequence analysis corroborates the affinity of some members of each of the subgenera *Lacerta* s. str. and *Timon*, and of the *L. saxicola* group. It also supports the relationship of *L. monticola*, *L. bonnali* and *L. horvathi*, and suggests that the *L. parva*–*L. fraasi* clade and *L. brandti* are not related to *Psammodromus*–*Gallotia*, as morphology indicates, but instead are associated respectively with the *L. danfordi* and *L. saxicola* groups. DNA sequence data provide additional evidence that the eastern Arabian '*Lacerta*' *jayakari* and '*L.*' *cyanura* are members of the armatured clade and also sister species. Our analysis supports an origin for present lacertids in west Eurasia. The armatured clade invaded Africa, probably in the mid-Miocene, spreading widely and evolving increasingly xeric-adapted forms, one lineage of which later moved back into the Palaearctic. '*Lacerta*' *jayakari* and '*L.*' *cyanura* are assigned to *Omanosaura*, Lutz and Mayer 1986. The name Gallotiinae Cano, Baez, Lopez-Jurado & Ortega, 1984 is available for the *Gallotia*–*Psammodromus* clade, Eremiainae Shcherbak 1975 for the armatured clade and Lacertinae for *Lacerta*, *Podarcis* and *Algyroides*. Two new subgenera of *Lacerta* are proposed here: *Caucasilacerta* for *L. saxicola* and its allies, and *Parvilacerta* for *L. parva* and *L. fraasi*.

Keywords: Lacertidae; 12S rRNA; 16S rRNA; cytochrome *b*; phylogeny

1. INTRODUCTION

Lacertid lizards comprise a clade of about 250 species that are found throughout Africa and most of Eurasia. They constitute the dominant reptile group in Europe and much work has been done on their ecology and behaviour in this region. In spite of this, a well-supported estimate of phylogeny is not available for the whole family, even though there is a perceived need for one to provide a historical dimension for non-systematic investigations of the group (Bauwens *et al*. 1995; Bauwens & Díaz-Uriarte 1997).

The monophyly of the lacertids is not in doubt, with Estes *et al*. (1989) defining ten morphological diagnostic synapomorphies. Firmly established within the Scincomorpha Camp 1923, the family's closest relatives are thought to be the Teioidea (Estes *et al*. 1989). Genera within the family are largely well-defined on the basis of morphology and in nearly all cases appear to be clades, the only exception being the large and admittedly paraphyletic *Lacerta*, within which some smaller clades are recognizable. The most recent estimate of phylogeny for the family based on morphology uses 112 binary characters derived from external features, skeleton, genitalia, nerves, other soft-anatomy and behaviour (Arnold 1989*a*). This hypothesis recognizes a clade including all Afrotropical species plus four genera that are found mainly in xeric areas of North Africa and non-tropical Asia (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*). Its members nearly always possess an armature, a complex supporting structure within the male intromittent organ or hemipenis, and the group is consequently informally known as the armatured clade. Morphology indicates substantial phylogenetic structure within this unit (Arnold 1989*a*,*b*, 1991).

However, morphology reveals little about the phylogeny of the remaining lacertids, which are nearly all anatomically quite primitive and occupy the Palaearctic

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and part of the Oriental regions. Although there are a number of well-defined genera and species groups, their interrelationships are largely unresolved.

Data from immunology (e.g. Lutz & Mayer 1984, 1985; Lutz *et al*. 1986; Busack & Maxson 1987; Mayer & Lutz 1989, 1990; Mayer & Benyr 1994) and protein electrophoresis (e.g. Guillaume & Lanza 1982; Capula 1994, 1997) have been used to investigate the relationships of lacertid genera and species groups, but results often conflict and also frequently differ from those derived from morphology. Mitochondrial DNA sequence data have been used to examine the relationships within some genera (Thorpe *et al*. 1994; Gonzalez *et al*. 1996; Fu *et al*. 1997; Harris *et al*. 1998*a*).

In an attempt to improve our knowledge of lacertid relationships, DNA sequence data, consisting of 1049 aligned nucleotide positions derived from three different mitochondrial genes, have been assembled for 49 species, and the resulting analysis compared with that based on morphology.

2. MATERIALS AND METHODS

Localities and sources of the lizards from which DNA was extracted are given in Harris (1997). Tissue samples were stored in 70% ethanol at 4 °C. Voucher specimens are deposited in the collection of the Natural History Museum, London. Total genomic DNA was extracted as per Kocher *et al*. (1989), followed by purification using phenol/chloroform extractions (Sambrook *et al*. 1989). The primers used in both amplification and sequencing were 12Sa and 12Sbs, cytochrome *b*1 and *b*2 (Kocher *et al*. 1989) and 16L and 16H (Hedges *et al*. 1991). These amplified regions were of approximately 400 base pairs (bp), 320 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. Both strands of the amplified DNA were sequenced on an Applied Biosystems Inc. 373A Automated DNA Sequencing System. Detailed procedures are given in Harris (1997).

Aligned regions of 326 bp of the 12S rRNA gene, 305 bp of the cytochrome *b* gene and 418 bp of the 16S rRNA gene were used in the analysis. The outgroups used were the teiid *Ameiva auberi*, and two xantusiids (Hedges *et al*. 1991). The sequences for 12S rRNA were aligned using the published outgroup sequences, and also *L. lepida* and *L. dugesii* (Hedges *et al*. 1991; Gonzalez *et al*. 1996). Sequences were also checked against secondary-structure models (Hickson *et al*. 1996). Two regions of 9 bp and 10 bp were removed from the analysis as they could not be aligned unambiguously. These were both in loop regions (between helices 36 and 38 and between 42 and 42′ respectively, as given by Hickson *et al*. (1996)) and involved length variations. Cytochrome *b* sequences were aligned against the published outgroups, and also *Psammodromus hispanicus* and *Gallotia galloti* (Hedges *et al*. 1991; Thorpe *et al*. 1994), and these contained no indels. 16S sequences were compared to the published outgroup sequences (Hedges & Bezy 1994) and were also aligned against a more limited secondary-structure model (Gutell 1993). A region of 89 bp of the 16S sequences could not be aligned unambiguously. These were mainly in a hypervariable region for which a secondary structure was also not obvious. Aligned sequences have been deposited in GenBank (accession numbers AF80268 to AF80388), and are also available on request from the corresponding author.

Unfortunately, not all of the extracted DNA samples could be amplified successfully with all three sets of primers using the polymerase chain reaction (PCR) method. *Eremias arguta*, *Takydromus septentrionalis*, *Mesalina adramitana*, *Mesalina guttulata*, *Adolfus africanus*, *Adolfus jacksoni*, *Heliobolus spekii*, *Lacerta monticola* and *Pedioplanis undata* failed to amplify with the cytochrome *b* primers. *Lacerta schreiberi* and *Psammodromus hispanicus* failed to amplify with the 12S primers.

3. PHYLOGENETIC ANALYSIS

(a) *Transition/transversion ratios*

True evolutionary relationships may be obscured in DNA sequence data sets if sites have become saturated by multiple substitutions (Swofford *et al*. 1996). To test for saturation, observed pairwise proportions of transitions and transversions in the separate 12S, 16S and separate coding positions from the cytochrome *b* sequence data sets were plotted against sequence divergences calculated using PAUP*4.0.d59. Only the alignable sequences were included, and comparisons were limited to 371 bp (294 alignable) of the 16S sequence to allow unbiased comparisons with the shorter published outgroup sequences. Both transitions and transversions in the 12S, 16S and first and second codon positions of cytochrome *b* sequences show an approximately linear relationship with distances (figure 1). However, third position sites of cytochrome *b* are almost certainly saturated by multiple substitutions, and would only add homoplasy if included in the data set. Therefore in the analysis of the whole lacertid family, only the first and second sites from the cytochrome *b* data were included.

(b) *Translation of cytochrome* b

All 41 partial cytochrome *b* sequences were translated using the standard vertebrate mtDNA translation. Thirty-six sites were parsimoniously informative. A maximum-parsimony (MP) analysis using the weighting implemented by Felsenstein (1993) in his PROTPARS program from the PHYLIP package found over 13 000 equally parsimonious trees, for which a strict consensus supported no relationships. Consequently they were not analysed further.

(c) *Combined analysis of mtDNA data sets*

Both MP and neighbour-joining (NJ; Saitou & Nei 1987) methods were used to estimate a phylogeny based on the three combined partial gene sequences, using PAUP*4.0.d63 (Swofford 1997). All alignable sequences were used in the analysis, except for the third positions of the cytochrome *b* data set. Support for nodes was estimated using the bootstrap technique (Felsenstein 1985; 1000 replicates; figure 2). For the MP analysis, trees were produced using heuristic searches with random stepwise additions (100 replications), TBR branch swapping, MULPARS option and zero length branches collapsed. Gaps were treated as a fifth character. All characters were weighted equally. This produced 27 equally parsimonious trees with 2224 steps (consistency index (CI) = 0.30, retention index (RI) = 0.44).

(d) *Relationships within* Lacerta *and its allies using maximum-likelihood (ML) analysis*

Analysis of mtDNA sequences suggests that this group is a clade (67% support on NJ analysis). Morphological

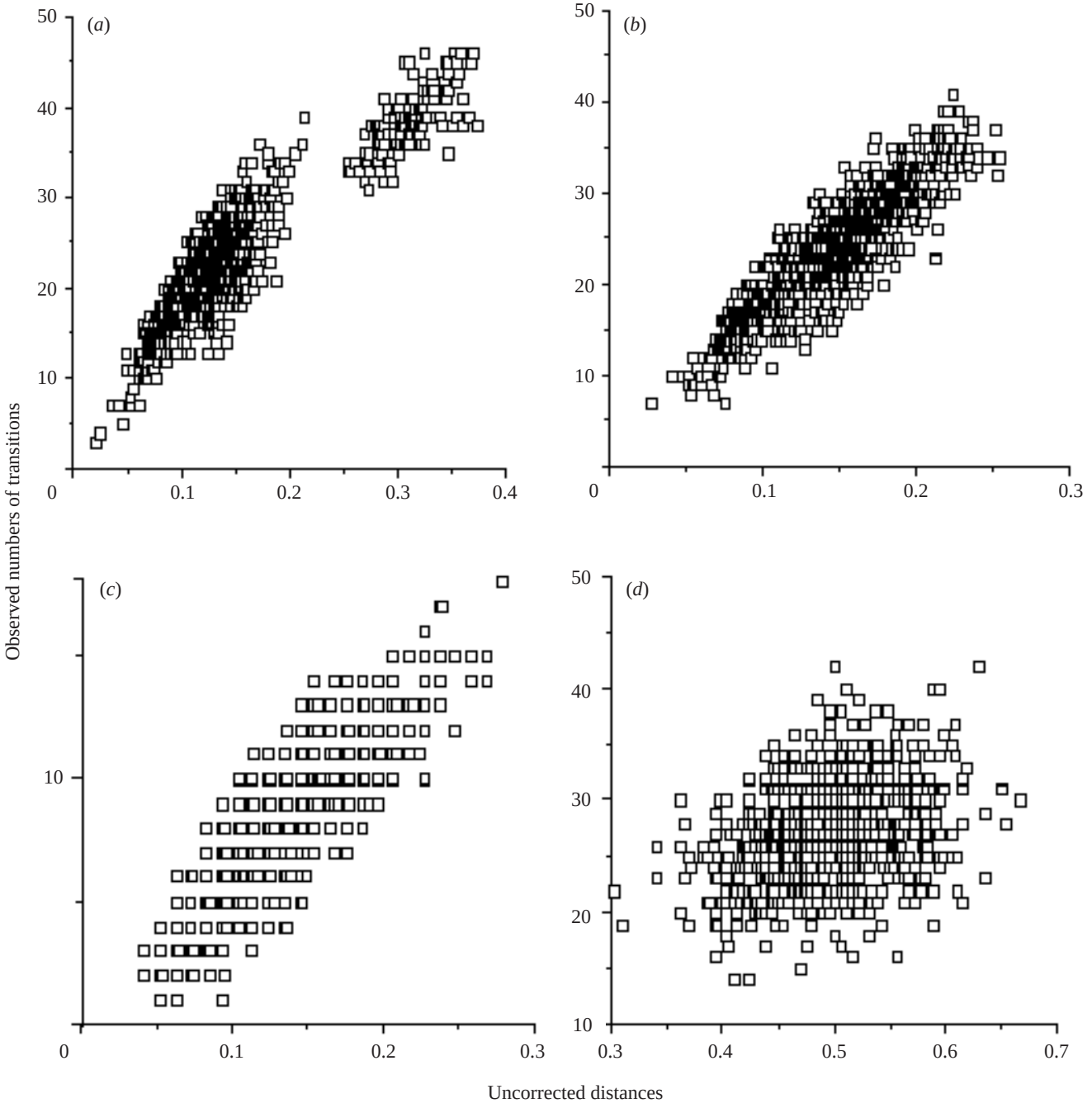

Figure 1. Observed numbers of transitions plotted against uncorrected distances for (*a*) partial 12S sequences, (*b*) partial 16S sequences, (*c*) partial cytochrome *b* position 1 sequences, and (*d*) partial cytochrome *b* position 3 sequences. Graphs for transversions (not shown) showed similar distributions, with only third positions of cytochrome *b* being nonlinear. The clear separation in the partial 12S sequences is between ingroup and outgroup taxa. Note that the scales are not the same.

characters give little information as to the relationships within this group; an MP reanalysis of the data from Arnold (1989*a*) gave bootstrap support over 50% only to a relationship between the *L. lepida* group (subgenus *Timon*) and the *L. agilis* group (subgenus *Lacerta* s. str.). Relationships within this probable clade were estimated using ML analysis. Only species with all three partial gene regions were included. *Psammodromus* and *Gallotia* were used to root the tree. *Takydromus smaragdinus* was included, as were *'L.' cyanura* and *'L.' jayakari*. Using PAUP*4.0.d59, a LogDet-corrected NJ tree was produced, and this was used to simultaneously estimate the optimal transition/transversion ratio, among-site rate variation and a discrete approximation to a gamma distribution (shape parameter estimated, with four rate categories (Yang 1996)). Using the HKY85 (Hasegawa *et al*. 1985) model, which allows for two substitution types (transition and transversion) and unequal base frequencies, and estimating the proportion of invariant sites using ML analysis, after ten heuristic searches a tree of log likelihood −5555.07 was produced (figure 3). A number of alternative hypothesized phylogenies were then tested against the ML trees, using the likelihood variance test of Kishino & Hasegawa (1989) (table 1). This included testing the assumption of a constant rate of evolution (a 'molecular clock'), which was rejected.

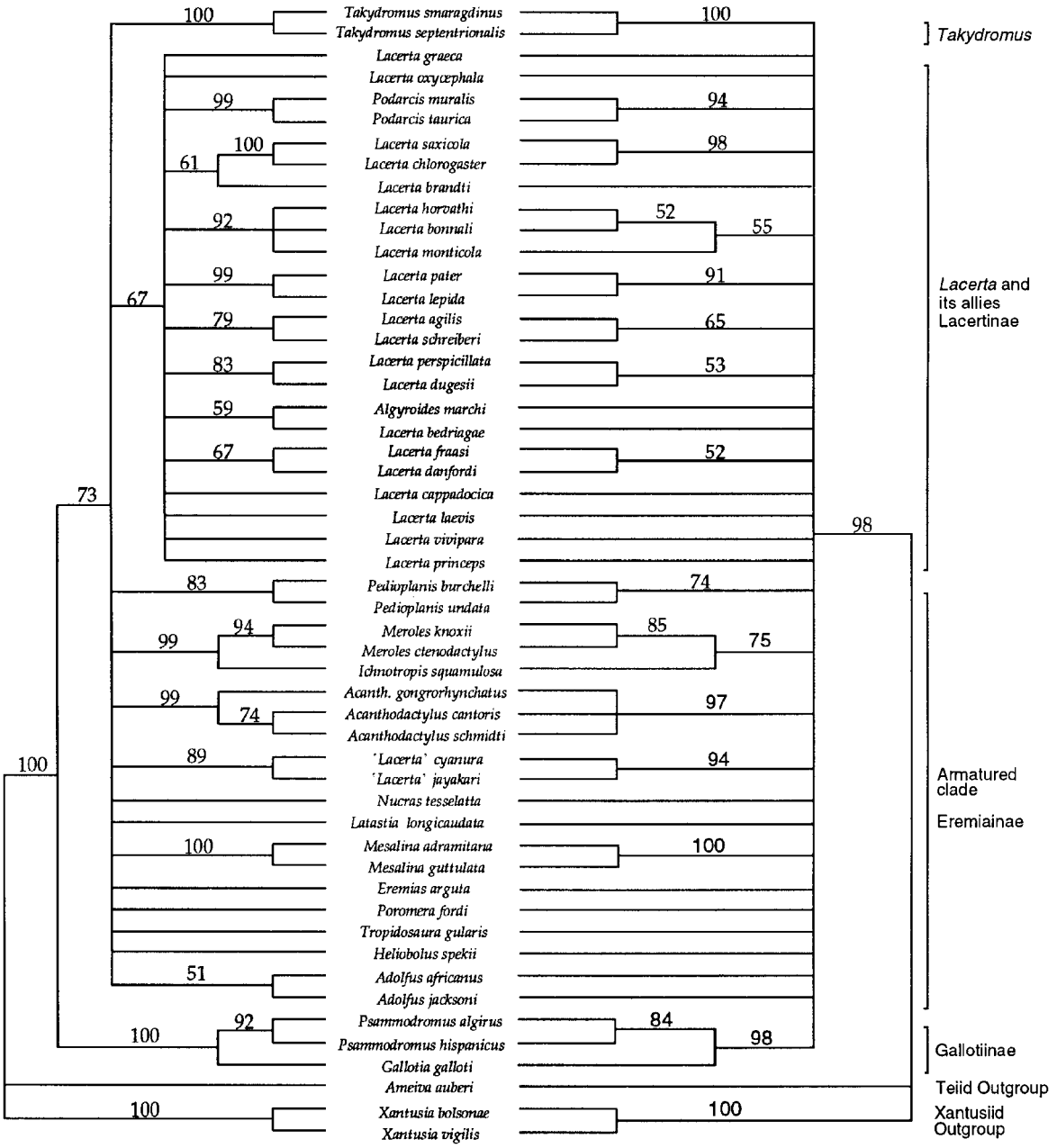

Figure 2. Fifty per cent bootstrap consensus trees (1000 replicates) of phylogenies derived from uncorrected NJ (left) and MP (right) analyses, using all three partial gene regions. Numbers above internal branches indicate bootstrap support. Trees were rooted using *Ameiva auberi*, *Xantusia bolsonae* and *Xantusia vigilis*. See text for details.

4. DISCUSSION

Where more than one species of a genus, or of a previously recognized unit within *Lacerta*, were included in the analysis, they group together, often with marked bootstrap support. The sequence data consequently corroborate many hypotheses about lacertid relationships made in the past on the basis of morphology. Cases include the following (the level of bootstrap support in the NJ tree is given in parentheses): *Psammodromus* (92), *Takydromus* (100, the two species represent the two main clades in this genus (Arnold 1997)), *Podarcis* (99), *Lacerta lepida* and *L. pater* (subgenus *Timon*, 99), *Lacerta agilis* and *L. schreiberi* (subgenus *Lacerta* s. str., 79), *Lacerta saxicola* and *L. chlorogaster* (*Lacerta saxicola* group, 100), *Meroles* (94), *Pedioplanis* (83), *Acanthodactylus* (99) and *Mesalina* (100).

DNA sequence analysis indicates that the most basal dichotomy in the Lacertidae separates a clade comprising the extreme west Palaearctic *Psammodromus* and *Gallotia* from all other lacertids (bootstrap support 73%). Within the latter unit there is a division into three main groups: (i) the armatured clade; (ii) the west Palaearctic *Lacerta* and its allies *Algyroides* and *Podarcis*; and (iii) the mainly Oriental genus *Takydromus*. The ML analysis of relationships within the *Lacerta* and its allies (figure 3) suggests that *Takydromus* is more closely related to *L. laevis* and *L. vivipara*, whereas the NJ analysis suggests it is basal to the whole clade. MP analysis also fails to resolve its position within the family, which is still therefore not fully resolved.

The *Psammodromus–Gallotia* and armatured clades and the unity of *Takydromus* are all supported by their morphology and behaviour (Arnold 1989*a*). Thus

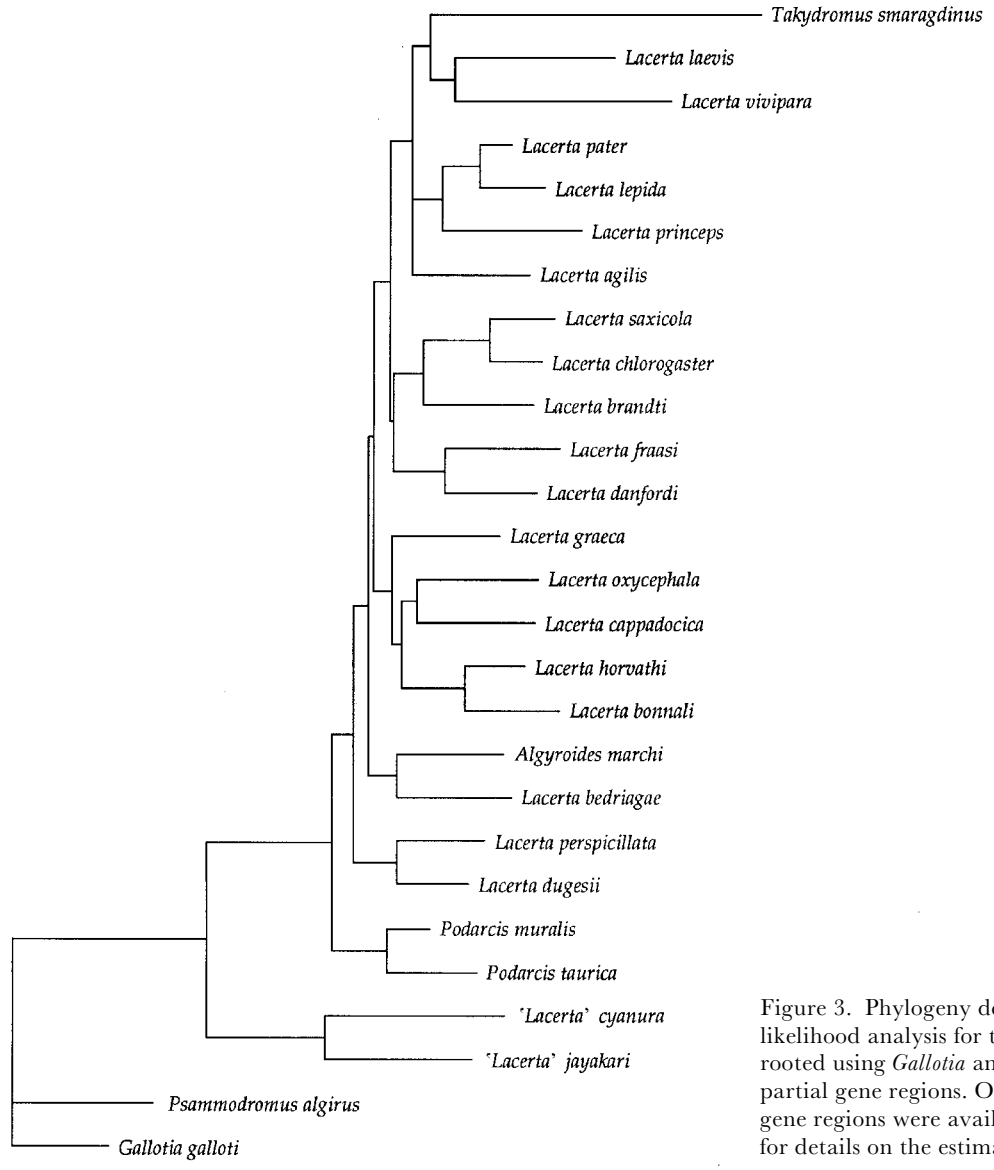

Figure 3. Phylogeny derived from a maximum-likelihood analysis for the '*Lacerta* and its allies' clade, rooted using *Gallotia* and *P. algirus* based on three partial gene regions. Only species for which all three gene regions were available were included. See text for details on the estimation of parameters.

Table 1. *Maximum-likelihood test (Kishino & Hasegawa 1989) of alternate tree topologies within* Lacerta *and its allies*

(Trees compared were the ML tree (number 1) based on DNA sequence data (figure 3), and the following alternative topologies: (2) *Lacerta fraasi* is sister species to *Gallotia/Psammodromus* clade; (3) *Podarcis* is sister species to *Lacerta dugesii/Lacerta perspicillata* clade: suggested by morphological characters; (4) *Takydromus* is sister species to the rest of the '*Lacerta* and its allies' clade; and (5) ML tree, under the constraint of a constant rate of evolution (a 'molecular clock'). In all cases the rest of the topology of relationships was identical to the ML tree. Trees (2) and (5) were significantly less likely than the ML tree.)

tree number	−ln likelihood	Δln likelihood	probability
1	5555.07	—	—
2	5605.46	50.4	0.000
3	5558.55	3.5	0.292
4	5561.48	6.4	0.312
5	5592.97	37.9	0.000

Psammodromus–Gallotia is characterized by the ability to squeak, large pointed papillae on the hemipenial lobes and a complex of other derived, but non-unique, features. In addition to the hemipenial armature, members of the armatured clade exhibit a derived condition of the ulnar nerve and most have an unlobed female genital sinus. *Takydromus* also has distinctive features (Arnold 1997). There is, however, no clear morphological evidence for the basal position of *Psammodromus–Gallotia*, or for the unity of *Lacerta* and its allies and, instead, the other three units are derived from this assemblage which appears as paraphyletic. However, the morphological evidence for the inter-relationships of these groups is very homoplastic and involves few characters. Immunological investigations of lacertid relationships are also interpreted as making *Psammodromus* and *Gallotia* a sister clade to the rest of the family (Mayr & Benyr 1994).

Although the total morphological data set does not support the unity of *Lacerta* and its allies, there are a number of apparently derived features that are especially common within it. These include the frequent interruption

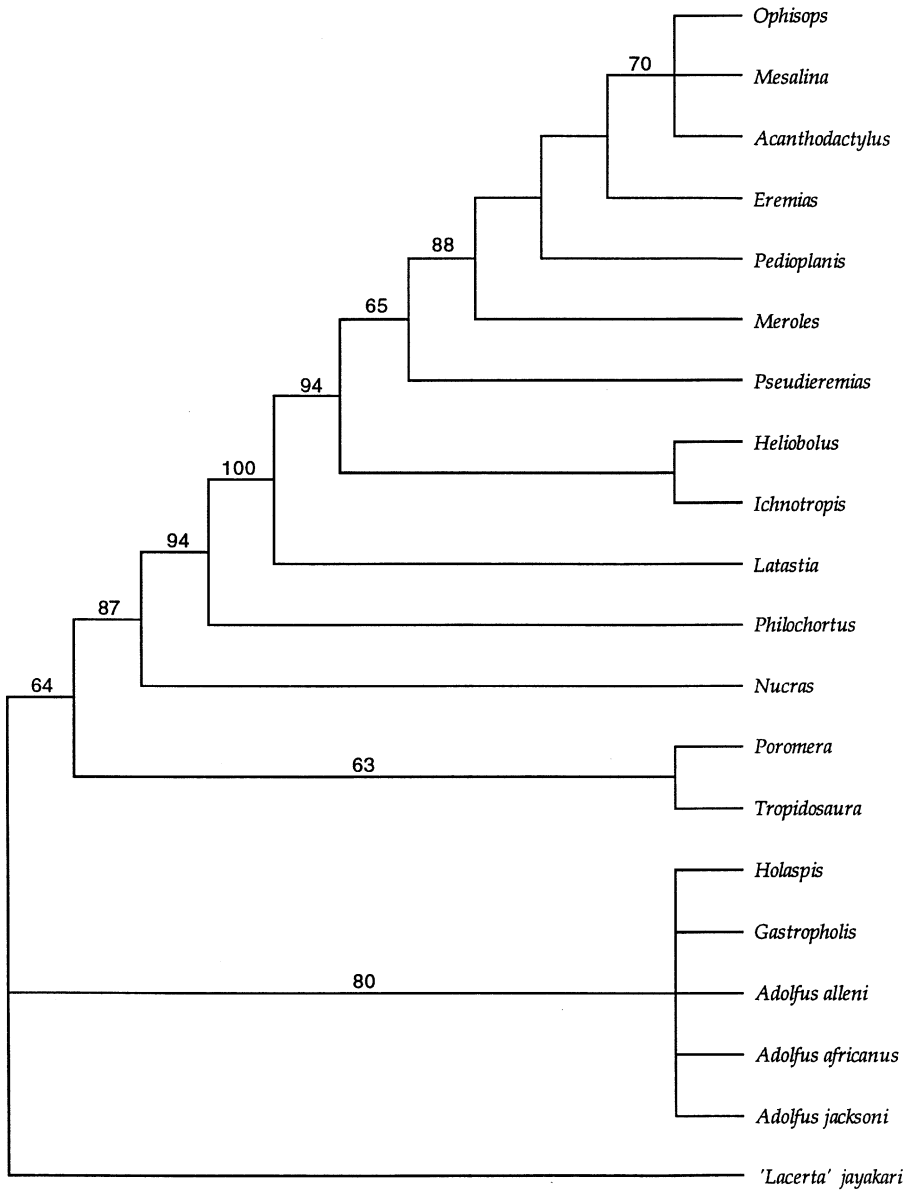

Figure 4. Strict consensus of 14 equally parsimonious trees (265 steps) based on morphological characters for the armatured clade. The tree was rooted using '*Lacerta*' *jayakari*. Numbers above nodes indicate bootstrap support (1000 replicates).

of the posterior border of the medial loop of the clavula and B-type pattern of caudal vertebrae (Arnold 1973; both also shared with '*Lacerta*' *jayakari* and '*L.*' *cyanura*, which are members of the armatured clade), parietal scales that primitively reach the edge of the squamosal but not of the postorbital bone, and the frequent presence of a masseteric scale (also present in some *Gallotia*).

An estimation of the relationships within the family, including only clades with at least 50% bootstrap support in any of the analyses based on DNA sequence or morphological data, or which are supported by both, are shown in figure 4. Within the family a number of relationships are hypothesized.

(a) *Relationships within the* Psammodromus–Gallotia *clade*

Psammodromus consists of two disparate units, the *P. hispanicus* group and *P. algirus*. The latter species shares a number of derived anatomical features with *Gallotia*, but total morphological data nonetheless indicates that *Psammodromus* is a clade (Arnold 1989). This is corroborated by present molecular evidence (figure 2, the NJ bootstrap support is 92%).

(b) *Relationships within* Lacerta *and its allies*

(i) Lacerta fraasi *and* L. parva

There is strong non-molecular evidence that these two species, found in Lebanon and the Asia Minor region, respectively, are sister taxa, for they share many derived morphological features (Peters 1962; Arnold 1973) and a derived karyotype (Odierna *et al.* 1995). Morphology also provides some indication that, together, they are most closely related to the *Psammodromus–Gallotia* clade (Arnold 1989*a*). But analysis of DNA sequence data (in which *L. fraasi* is included) suggests that this is significantly less likely than the ML tree (table 1), where *L. fraasi* is paired with *L. danfordi* (67% bootstrap support in the NJ tree). In addition to DNA sequence evidence that *Lacerta parva* and *L. fraasi* are related to *L. danfordi* (and presumably its close relatives *L. anatolica* and *L. oertzeni*), they have contiguous ranges and share a similar derived C pattern of caudal vertebrae, although this also occurs in *Psammodromus* and *Gallotia*. Although there is a substantial morphological similarity between *Lacerta parva* and the *Psammodromus hispanicus* group, both occur in similar habitats so convergence is a possibility.

(ii) L. brandtii

Morphology suggests that this species is the basal member of a clade that also includes *Lacerta parva*, *L. fraasi*, *Psammodromus* and *Gallotia*. In contrast, DNA sequence data support a more nested position, and indicate that it may be sister to the *Lacerta saxicola* group (the NJ bootstrap support is 61%).

(iii) *Relationships of* L. perspicillata, L. dugesii *and* Podarcis

The Moroccan *Lacerta perspicillata* and Madeiran *L. dugesii* are believed to be sister species, on the basis of morphological evidence, which also suggests that they are closely related to *Podarcis* (Arnold 1973). DNA sequence analysis supports the first of these relationships (figure 2), and although the association of *Podarcis* with the other species is not supported by the ML analysis (figure 3), its placement here is not significantly better-supported (table 1). Relationships of these lizards are considered further elsewhere (Harris *et al*. 1998*b*).

(iv) Algyroides

Morphology indicates that this European genus of four species is derived from a relatively small member of the paraphyletic genus *Lacerta* (Harris *et al*. 1998*c*). The relationship suggested by DNA sequence analysis to the Corsican–Sardinian *Lacerta bedriagae* is consequently possible, but the NJ bootstrap support (59%) is quite low and there are no known derived anatomical features corroborating this specific relationship. Interrelations among the four species of *Algyroides* have been assessed using 12S and 16S sequence and morphology (Harris *et al*. 1998*c*) giving the following result: *A. nigropunctatus* (*A. moreoticus* (*A. fitzingeri*, *A. marchi*)).

(v) Lacerta, *subgenera* Lacerta *s. str. and* Timon

Both of these subgenera of large west Palaearctic lacertids are supported by morphological features and by immunology (Mayr & Benyr 1994) but, whereas morphology indicates a close relationship between them (72% NJ bootstrap support), immunology contradicts this. As already noted, DNA sequence analysis associates the similar west Mediterranean representatives of *Timon*, *Lacerta lepida* and *L. pater* (a NJ bootstrap support of 99%), and two similar species of *Lacerta* s. str, *L. agilis* and *L. schreiberi* (the NJ bootstrap support is 79%). ML analysis includes another distinctive member of *Timon*, *L. princeps* of eastern Turkey, northern Iraq and western Iran in the former clade (figure 3).

(vi) *Archaeolacertas and their relatives*

Archaeolacertas are an informal and poorly delineated grouping of small-bodied west Palaearctic lacertids assigned to *Lacerta*. Many of their morphological characters are primitive, but they share a loose syndrome of cranial and external features, which vary greatly in the extent of their expression. Archaeolacertas are mainly found in rocky situations and often take refuge in fissures. Their distinctive features confer various advantages in crevice use and their development correlates strongly with the extent of this behaviour (Arnold 1973, 1998). Together with the fact that the features are ontogenetically easy to produce, this suggests that the features are very plastic and hence only weak indicators of a possible relationship (Arnold 1973, 1996).

As might be expected from this, DNA sequence analysis provides no robust evidence that archaeolacertas, as a whole, constitute a clade. There are, however, some species associations with strong bootstrap support.

DNA sequence analysis indicates that *L. bonnali* (Pyrenees), *L. monticola* (Iberia) and *L. horvathi* (Croatia, Slovenia, Austria and southern Germany) are closely related (a NJ bootstrap support of 92%). It is probable that *L. aranica* and *L. aurelioi*, which occur close to *L. bonnali* in the Pyrenees and share a derived karyotype with it (Odierna *et al*. 1996), should also be included in this clade. The same probably applies to *L. mosorensis* of Croatia, Bosnia and Montenegro, some populations of which are quite similar to *L. horvathi*.

Rock-dwelling lacertids in the Caucasus and surrounding regions, together with more disparate forms such as *L. praticola*, *L. derjugini* and *L. chlorogaster*, share some morphological features that are not common in other archaeolacertas. These include a single postnasal scale and a relatively high number of presacral vertebrae. Consequently, these lizards have been regarded as a distinct clade (Arnold 1989*a*). The two morphologically different forms, *Lacerta saxicola* and *L. chlorogaster*, subjected to DNA sequence analysis here, appear as each others' closest relatives among the included species (bootstrap support is 100%). Other mtDNA analyses also support this clade (Fu *et al*. 1997).

L. oxycephala, *L. graeca* and *L. cappadocica* are morphologically well differentiated, although they all have well developed, crevice-associated features of archaeolacertas. Protein electrophoresis suggests a close relationship between *L. oxycephala* of the central eastern Adriatic seaboard and *L. graeca* of southern Greece (Nei's distance 0.17 (Mayer & Tiedemann 1982)). Our ML analysis associates *L. oxycephala* with *L. cappodocica* of eastern Turkey, northern Iraq and adjoining Iran, but the lack of significant corroborating morphological evidence or bootstrap support in the NJ and MP analyses makes this association uncertain.

Other species regarded as archaeolacertas include the *L. bedriagae* and the *L. danfordi* group which, as noted, may be related to the non-archaeolacertas *Algyroides*, and the *L. fraasi*–*L. parva* clade, respectively.

(c) *Relationships within the armatured group*

Because analysis of morphological characters suggests that the armatured group is a clade, and mtDNA characters are ambiguous (the NJ analysis supports the group as a clade, but without 50% bootstrap support), relationships were assessed by reanalysing the morphological data set of Arnold (1989*a*). '*Lacerta*' *jayakari* was used to root the tree. A heuristic search with random stepwise additions (100 replications) found 14 equally parsimonious trees with 265 steps (CI = 0.52, RI = 0.66; figure 5).

As the phylogeny based on morphological characters for the armatured clade is generally much better supported than the mtDNA analysis, this is the main source of inference of relationships. There are, however, two exceptions.

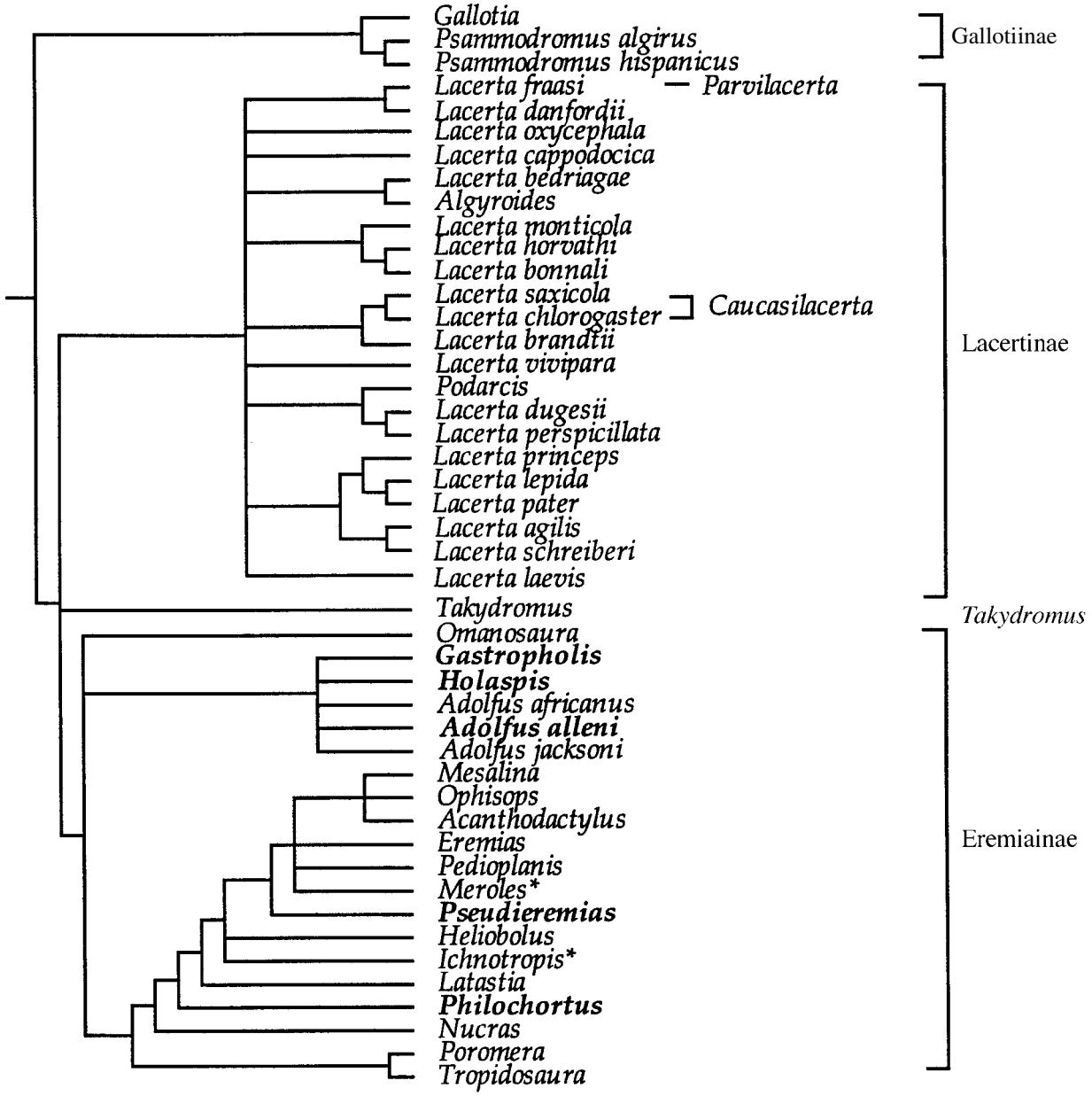

Figure 5. Our preferred phylogeny derived from separate morphological and mtDNA sequence characters. All nodes have either over 50% bootstrap support in the separate analyses, or have weaker support from both independent data sets. Where the two data sets are incongruent, alternative positions for taxa are marked. Taxa in bold were not available for the mtDNA analysis. *, mt DNA strongly associates *Meroles* with *Ichnotropis*. However, *Pseuderemias* was not included in this study.

(i) 'Lacerta' jayakari *and* 'Lacerta' cyanura *from eastern Arabia*

Although previously regarded as members of the genus *Lacerta*, morphology indicates that these two superficially very different species are basal members of the armatured clade, although there are no known unique derived anatomical features that indicate they are sister species. Molecular evidence corroborates membership of the armatured clade and also their sister taxa relationships. The name *Omanosaura* Lutz and Mayer, 1985 is available for these species and, as they do not appear to form a clade with other species assigned to *Lacerta*, it should be applied to them.

(ii) Ichnotropis *and* Meroles

Morphology suggests these southern African genera each arose independently from the main lineage of the armatured clade, but quite close together (figure 5). In contrast, the molecular evidence (which does not include the sequence from *Pseuderemias*) indicates that *Ichnotropis* and *Meroles* are sister taxa (bootstrap support 99%).

DNA sequence analysis also corroborates morphological evidence that the species of *Adolfus*, *A. africanus* and *A. jacksoni*, which were originally assigned to *Lacerta* and *Algyroides*, are indeed not members of these groups (Arnold 1989*b*) and that their resemblance to the European species that comprise these genera is superficial.

5. HISTORICAL BIOGEOGRAPHY

As with morphology, the pattern of lacertid relationships indicated by mtDNA sequence data agrees with the hypothesis that lacertids arose in Eurasia and that the armatured clade later dispersed into Africa, after this continent made contact with Eurasia in the mid-Miocene

(Arnold 1989*b*). This invasion was followed by spread across the continent, evolution of taxa increasingly adapted to xeric situations and then reinvasion of the Palaearctic and the drier parts of the Saharo–Sindian area by one lineage of these. The fact that both *Psammodromus–Gallotia* and *Lacerta* and its allies occur in the west Palaearctic makes it more likely that both the armatured clade and the Oriental *Takydromus* were derived from this area.

6. NOMENCLATURE

As already noted, *Omanosaura* Lutz & Mayer should be used for '*Lacerta*' *jayakari* and '*Lacerta*' *cynaura*. Several recently suggested nomenclatorial changes in the Lacertidae involve recognizing separate genera for members of the paraphyletic genus *Lacerta* (Mayer & Bischoff 1996). Of these, *Teira* Gray is probably not a clade if, as suggested, *Lacerta andreanszkyi* is included in it (Harris *et al*. 1998*b*), and *Zootoca* is monotypic and of uncertain position. *Lacerta* s. str. and *Timon* appear to be clades but their precise relationships are not totally resolved. Raising these units to generic status would involve changes in the binomials applied to the species concerned. Because many relationships within *Lacerta* s. lat. are still substantially uncertain and so likely to change in the future, these names could all be subject to further revision, creating instability in the nomenclature of well-known species. In these circumstances, it seems better to recognize subgenera of *Lacerta* rather than full genera, as these involve no necessity of changing binomials (Arnold 1989*a*). In addition to the subgenera already in use, we propose *Caucasilacerta* (type species *Lacerta saxicola*) for the *L. saxicola* group and *Parvilacerta* for *L. parva* and *L. fraasi*.

Formal names have already been created for some suprageneric groupings within the Lacertidae and these could be used for the main units within the family recognized here (figure 4). Thus *Gallotia* was placed in a separate family Gallotiidae Cano *et al*. 1984. Family rank is inappropriate for this genus (Arnold 1989*a*), but the name has been converted to subfamilial status as Gallotiinae for *Gallotia* and its close relative *Psammodromus* (see Mayr & Benyr 1994). Eremiainae Shcherbak, 1975 was originally applied to *Eremias* and some other advanced armatured genera, although this assemblage turns out to be paraphyletic (Arnold 1989*a*). However, the name can be used for the whole of the armatured clade. Lacertinae Linnaeus 1758 is then available for *Lacerta* and its allies, *Podarcis* and *Algyroides*, and possibly *Takydromus*.

7. CONCLUDING REMARKS

Available DNA sequence data provide evidence for some relationships within the Lacertidae that are not discernible from morphology and corroborate many more that are. On the other hand, morphology sometimes produces quite robust evidence for a relationship when the present molecular evidence does not, for instance in the armatured clade, and in the genus *Meroles* (Harris *et al*. 1998*a*). The two data sets consequently appear to be complimentary sources of phylogenetic inference. In the Lacertidae, direct and marked conflicts between comparatively robust hypotheses of relationship derived from molecules and morphology are relatively few.

The kind of ecological history a group has had appears to affect whether its phylogeny can be successfully reconstructed from morphological evidence (Arnold 1990). In general, lineages evolving along ecological continua towards increasingly specialized selective regimes have robust morphological estimates of phylogeny, partly because many new easily polarizable derived features tend to be produced. This phenomenon may account for the difference in quality of the morphological estimates of relationship in the Lacertinae and the Eremiainae. Members of the former have a generally narrow range of mesic spatial niches, whereas in the Eremiainae there has been an evolution from life modes involving a mixture of climbing and ground-dwelling in mesic habitats, to specialized ground-dwelling in increasingly xeric situations (Arnold 1989*a*).

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