African Journal of Herpetology,
Vol. 60, No. 1, April 2011, 60–69

Short communication

Phylogenetic position of the southern rock lizard *Australolacerta australis* within the Lacertidae radiation

DANIELE SALVI[1]*, PIERLUIGI BOMBI[2] & LEONARDO VIGNOLI[3]

[1]*CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Vairão, Portugal;* [2]*SPACEnvironment, Via Maria Giudice 23, 00135 Rome, Italy;* [3]*Dipartimento di Biologia Ambientale, Roma Tre University, Rome, Italy*

Abstract.—The southern rock lizard *Australolacerta australis* is a rock-dwelling lizard endemic to South Africa. The phylogenetic relationships of this species with other lacertid lizards are still not clear and have never been assessed in any phylogeny of Lacertidae using DNA sequence data. In this study we employed 3 044 base pairs from mitochondrial cytochrome *b*, 12S and 16S rRNA genes to investigate the phylogenetic position and the evolutionary history of *A. australis*. We performed phylogenetic analyses under the assumptions of Maximum Likelihood and Bayesian inference and estimated the timing of the cladogenic events related to *A. australis* by using a relaxed molecular clock method. Our phylogenetic reconstruction clearly placed *A. australis* within the southern African branch of the tribe Eremiadini including genera *Tropidosaura*, *Meroles*, and *Pedioplanis*. The former genus constitutes with *A. australis* a clade endemic to southernmost mountains of Africa. The radiation of this southern African clade is estimated to have occurred during the Mid Miocene (14.7–11.5 Mya), and it was likely due to the climate changes that occurred in the South African region at that time.

Key words.—Lacertidae, *Australolacerta australis*, Eremiadini, phylogeny, southern Africa, mtDNA

Lacertids are some of the most studied lizards and several estimates of their phylogeny have been made by means of morphological (Arnold 1986, 1989), immunological (Mayer & Benyr 1994), and genetic data (Fu 1998, 2000; Harris *et al.* 1998a; Mayer & Pavličev 2007). Molecular phylogenies of the whole family (Harris *et al.* 1998a; Fu 2000; Mayer & Pavličev 2007) clearly distinguish the subfamilies Gallotiinae (including the genera *Gallotia* and *Psammodromus*) and Lacertinae (including the remaining genera) in which two other groups may be recognised: the African (the armatured) clade and the Eurasian clade which are considered as tribes (Eremiadini and Lacertini respectively; Arnold *et al.* 2007) or subfamilies (Eremiadinae and Lacertinae respectively; Harris *et al.* 1998a; Pavličev & Mayer 2009). Although African lacertids show the highest diversity in the southern African region (Arnold 1989), to date only the genera *Meroles* and *Pedioplanis* have been investigated using molecular data (Harris *et al.* 1998b; Lamb & Baur 2003, Makokha *et al.* 2007) and their evolutionary history been clarified. Interestingly, the evolutionary history of both *Meroles* (Lamb & Bauer 2003) and *Pedioplanis*

---

*Corresponding author. Email: salvi@uniroma3.it

ISSN 2156-4574 print/ISSN 2153-3660 online

DOI: 10.1080/21564574.2010.547609
http://www.informaworld.com

(Makokha *et al.* 2007), as well as of other lizards (Lamb *et al.* 2003; Bauer & Lamb 2005), has been associated with the habitat changes driven by climate aridification that occurred in South Africa during the Mid-Miocene (Siesser 1978, 1980).

The southern rock lizard, *Australolacerta australis* (Hewitt 1926) is a rock-dwelling lizard restricted to the Cederberg Mountains (Western Cape, South Africa) and a few other neighbouring areas (Fig. 1). Among African lizards, this is one of the most poorly known species. It was assigned by Hewitt (1926) to the Palaearctic genus *Lacerta* (subgenus *Podarcis*), producing a zoogeographic and systematic dilemma which remained unresolved since no further specimens were available for examination after the single female collected in 1926 by Lightfoot from Matroosberg, near Ceres (Western Cape Province, South Africa). In addition, for some years even the

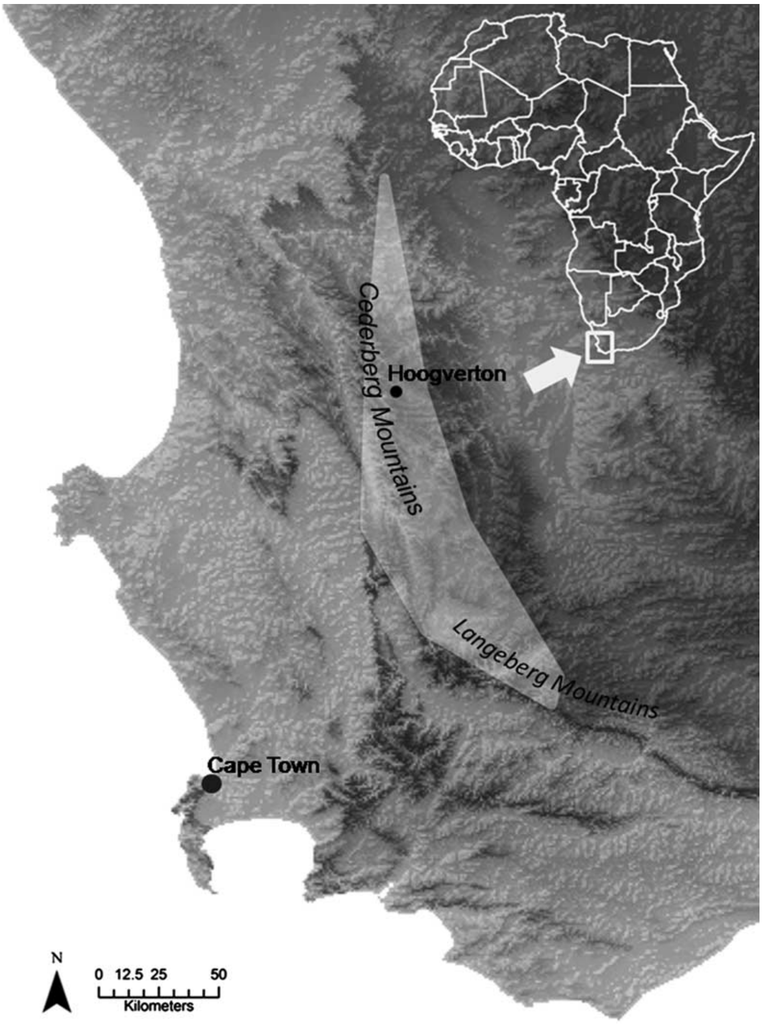

Figure 1. Sampling location and distribution (light shaded area) of *Australolacerta australis.* The range of the species is based on records from the specimens preserved in the herpetological collection of the Stellenbosch University and used in Bombi *et al.* (2006).

type disappeared. A few years later, another unexpected lizard was found in the Soutpansberg (Limpopo Province, South Africa) and described as *Lacerta (Podarcis) rupicola* by FitzSimons (1933). The description of both southern and Soutpansberg rock lizards remained the only studies about these species for nearly half a century, until new specimens were found in the Cederberg (Haacke 1982; De Villiers *et al.* 1983; Mouton *et al.* 1987) and Soutpansberg areas respectively. *Australolacerta australis* has been included only in the studies of morphology (Arnold 1989) and albumin immunology (Mayer & Benyr 1994) but has never been assessed in any phylogeny of Lacertidae using DNA sequence data. In a morphological study, Arnold (1973) suggested a close relationship between *A. rupicola* and *Tropidosaura* but stated the position of *A. australis* as unknown since no specimens were available at that time. Later, Arnold (1989) formalised the genus *Lacerta* as polyphyletic and placed *A. rupicola* and *A. australis* in the present genus, suggesting a possibly basal, although unclear, position within the Ethiopian assemblage. Using albumin immunology in the assessment of relationship of the family Lacertidae, Mayer & Benyr (1994) tentatively placed *A. australis* as sister to *Meroles* although the data they used actually failed to resolve the relationship of *A. australis.*

We employed mitochondrial DNA markers to test (1) whether *A. australis* has a close phylogenetic relationship to other African genera as suggested by albumin immunology (Mayer & Benyr 1994) and by morphology (Arnold 1983, 1989), and (2) whether the paleogeographic and paleoclimatic events that occurred in the South African region have played a role in the evolution of *A. australis* as they likely did for other South African lizards. Thus, the aims of this paper are to investigate the phylogenetic relationship of *A. australis* relative to lacertid lizards, and to place the main events of the evolutionary history of *A. australis* in a relative time frame in order to elucidate historical and ecological factors underlying the evolution of this species.

Tail tips from two *A. australis* specimens from Hoogverton (Cederberg Mountains, Western Cape, South Africa; see Fig. 1) were obtained in the field and stored in pure ethanol. Total DNA was extracted from tail muscle following standard phenol/chloroform methods (Hillis *et al.* 1996). Total DNA was used as template for the polymerase chain reaction (PCR). Primers used for PCR and sequencing are those used in Fu (2000) with some modifications (L717, H1478, H1497 and H2568 for 12S gene; H1497, H2568, L2510-modified [5′-TCAACTGTTTACCAAAAA CAT-3′] and H3060 for 16S gene; L15153, H15488-modified [5′-TTGCGGGTGA GAAGTTTTCTGGGTC-3′], and H15915 for cytochrome *b* gene). Both heavy and light strands were sequenced by an automated sequencer (Hitachi 3100 Genetic Analyzer), at the ENEA laboratories (La Casaccia, Rome).

A total of 3 044 base pairs of DNA sequences from mitochondrial cytochrome *b*, tRNA$^{\mathrm{Thr}}$, 12S rRNA, tRNA$^{\mathrm{Val}}$ and 16S rRNA genes (715 bp, 31bp, 864 bp, 72 bp, and 1362 bp respectively) were obtained from two specimens of *A. australis* (accession numbers FR751395–FR751398). The sequences from 33 species from 24 genera representing the main lineages of the family Lacertidae (mostly from Fu 2000) were obtained from GenBank (accession numbers AF206173, AF206529-AF206542, AF206544-AF206547, AF206587-AF206599, AF206601-AF206605, AF206607-AF206616, FJ 460597, NC008328, NC011764, U69834, U88603). Following Towsend *et al.* (2004) the species *Neusticurus* sp. (Teioidea) and *Blanus cinereus*

(Amphisbaenidae) were used as outgroups (accession numbers AF206528, AF206584, EU443257).

Sequences were aligned using ClustalX (version 1.8, Thompson *et al.* 1997) and then adjusted by hand. Ambiguous alignment within ribosomal sequences were selected by the software Geneblock (following a relaxed selection of blocks [Talavera & Castresana 2007]) and removed from the analysis.

Two dataset were used in phylogenetic analysis, one including 12S and 16S gene sequences from 35 taxa (12S-16S dataset) and another one including 12S, 16S and cytochrome *b* gene sequences limited to 28 taxa (12S-16S-cyt*b* dataset). Each dataset was partitioned by gene fragment and congruence between these partitions were tested using 1 000 replicates of the partition homogeneity test in PAUP* (v. 4.0b10, Swofford 2002). Phylogenetic analyses were performed under the assumptions of Maximum Likelihood (ML) and Bayesian inference (BA) employing partition-specific nucleotide substitution models and parameters estimated separately for each partition during the phylogenetic reconstruction.

ML reconstruction was performed in Treefinder version October 2008 (Jobb 2008). We selected the best-fitting model of nucleotide substitution for each gene partition independently using the corrected Akaike Information Criterion in the model proposal function of Treefinder and performed searches under the selected models. The GTR + G model was selected for the 12S and 16S partitions, and TIM for the cytochrome *b* partition (each model with rate parameters optimisation and empirical estimation of frequency parameters). We evaluated support for the nodes with 1 000 replicates of the Expected-Likelihood Weights applied to Local Rearrangements of tree topology (LR-ELW; Strimmer & Rambaut 2002). Bayesian searches were done in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). The optimal models of nucleotide evolution for the Bayesian analysis were selected using jModelTest 0.1.1 (Posada 2008) under the Akaike Information Criterion as the GTR + I + G model for the 12S and 16S partitions and the Tvm + G model for the cytochrome *b* partition. Bayesian analysis started with a randomly generated tree and was run for 10^7 generations sampling one tree each 1 000 generations. Stationarity was considered to be reached when the average standard deviation of split frequencies shown in MrBayes was less than 0.01 (Ronquist & Huelsenbeck 2003) and confirmed by plotting log-likelihood scores and tree lengths against generation number using the software Tracer 1.4 (Rambaut & Drummond 2007). The first 2 500 trees (25%) were discarded as burn-in and the remaining trees were used to assess posterior probabilities (BPP) for nodal support. To assess the timing of the cladogenic event which originated *A. australis* we used a molecular clock for the complete dataset (12s + 16S + cyt*b*) with the Local Rate Deformation Method (LRDM) in Treefinder. Because we wanted to estimate the divergence time for *A. australis*, as suggested by Jobb (2008) tree calibration was applied to a selected part of the tree including the branches of interest and the taxa used for calibration constraints. Primary calibration points for the tree are not available either from biogeographical or fossil data. Instead, we used four secondary calibration points derived from previous studies: the age of split of *Podarcis* species at 5.1 million years ago (Mya), the split of *Lacerta* species at 9.1 Mya, the split between *Psammodromus* and *Gallotia* at 12.8 Mya, and the timing of Lacertine radiation from 13.5 to 16 Mya (Carranza *et al.* 2004; Arnold *et al.* 2007; Pavličev & Mayer 2009). In order to estimate confidence intervals of divergence time, we used the resampling of edge lengths by ML bootstrap analyses under a fixed topology (1 000 replicates), and the resampling of calibration times from the calibration time intervals (100 time replicates).

After alignment and removal of ambiguously-aligned sites, 2 206 characters remained of the 12S-16S dataset (89%), of which 1362 were variable. The 12S-16S-cyt-*b* dataset comprised 2 990 characters, of which 1815 were variable. Partition homogeneity tests revealed congruence between the gene partitions ($P > 0.05$) both in the 12S-16S dataset and in the 12S-16S-cyt-*b* dataset. The comparison between the phylogenies from ML and BI analyses based on the two datasets together with nodal support are shown in Fig. 2. Overall, the ML and BA trees inferred from both the 12S-16S and the 12S-16S-cyt*b* datasets were largely congruent. *Australolacerta australis* fell inside the African clade (LR-ELW $\geq$ 94, BPP = 100) and in particular within a strictly-southern-African clade including this species and *Tropidosaura gularis* (LR-ELW $\geq$ 83, BPP = 99). This clade, endemic to southernmost mountains of Africa, grouped into a well supported southern African assemblage also including the genera *Meroles* and *Pedioplanis* (LR-ELW $\geq$ 83, BPP $\geq$ 99). The Sub-Saharan genera *Nucras*, *Heliobolus* and *Latastia*, mostly distributed in East Africa, grouped in a well supported clade (LR-ELW $\geq$ 99, BPP $\geq$ 100, although the 12S-16S-cyt*b* dataset does not include the genus *Nucras*) which was the sister group to the southern African clade (LR-ELW $\geq$ 89, BPP = 100). The remaining Palaearctic and equatorial African genera of the Eremiadini (*Acanthodactylus*, *Eremias*, *Adolfus*, *Ophisops*, *Atlantolacerta*) constituted an assemblage basal to the southern African clade with poorly resolved relationships. As expected the subfamilies Gallotiinae and Lacertinae, and the tribes Eremiadini and Lacertini received high support in all the analyses (LR-ELW $\geq$ 90, BPP = 100). With the exception of the genus *Adolfus*, the monophyly of all genera with multiple representatives (*Meroles*, *Eremias*, *Lacerta*, *Timon* and *Podarcis*) was verified by all the analyses (LR-ELW and BPP = 100).

The chronogram (Fig. 3) shows time estimates for the cladogenic events related to *A. australis* from the LRDM molecular clock analysis. This analysis placed the major cladogenic events concerning the East African and southern African clades during the Mid-Miocene (14.6–7.8 Mya). The split between the Sub-Saharan and the southern African clades is estimated to have occurred 14.6 Mya (confidence interval, CI: 16.7–12.5 Mya), the divergences among genera of the southern African clade 13.1 Mya (CI: 14.7–11.5 Mya), and the split between *A. australis* and *T. gularis* 9.3 Mya (CI: 10.8–7.8 Mya).

Our phylogenetic reconstruction clearly places *A. australis* within the strictly-African branch of the tribe Eremiadini. *Australolacerta australis* is the sister species to *Tropidosaura gularis* with which it constitutes a clade endemic to the southernmost mountains of Africa. All the phylogenetic trees strongly support the sister taxon relationship of *A. australis* and *T. gularis* corroborating the hypotheses of a close relationship between this two genera based on morphological traits (Arnold 1973). Congruent with their geographical distribution, the other two southern African genera *Meroles* and *Pedioplanis* constitute a well supported clade with *A. australis* and *T. gularis*, although it is not possible to disentangle which genus, of *Meroles* and *Pedioplanis*, is the sister genus to the *A. australis* + *T. gularis* clade. The close relationship among *Pedioplanis*, *Meroles* and *Tropidosaura* is congruent with previous allozyme, mtDNA, and nuclear DNA phylogenies (Mayer & Berger-Dell'mour 1988; Harris *et al.* 1998b; Fu 2000; Mayer & Pavličev 2007; see also

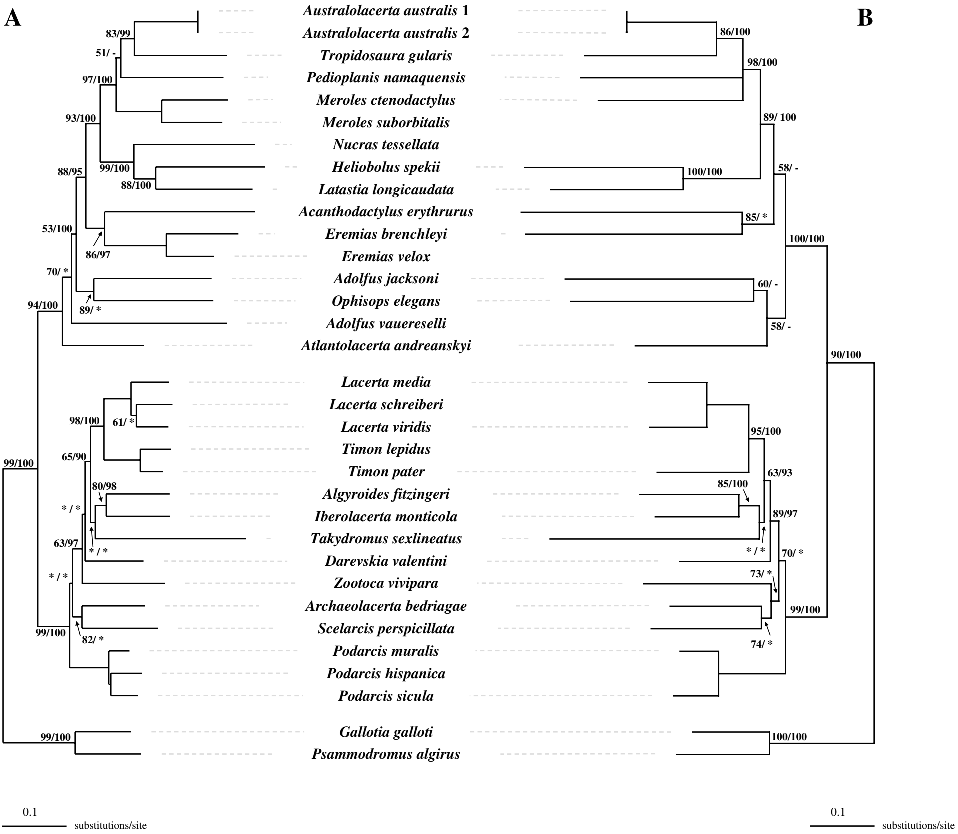

Figure 2. Maximum likelihood phylogenetic trees based on the 12S-16S combined dataset (A) and the 12S-16S-cyt*b* dataset (B). Phylogenetic trees are rooted using the species *Neusticurus* sp. (Teioidea) and *Blanus cinereus* (Amphisbaenidae) as outgroups (not shown). Statistical support for major nodes are indicated above the branches of tree topology as Expected-Likelihood Weights applied to Local Rearrangements (LR-ELW) for Maximum Likelihood analysis (ML) and Bayesian posterior probability (BPP) for Bayesian analysis (BA) (LR-ELW / BPP; * = LR-ELW < 50 or BPP < 90; – = node not recovered in the analysis). All the clades formed by congeneric species were supported by LR-ELW and BPP = 100 (not shown).

Arnold *et al.* 2007). Conversely, Makokha *et al.* (2007) estimated that *Pedioplanis* is the sister taxon to the East African genera *Heliobolus* and *Nucras.* Such differences in phylogenetic estimates are likely due to the different taxon sampling between these studies as well as to the outgroup choice. Indeed, Makokha *et al.* (2007), in assessing the relationships among the genera *Pedioplanis*, *Meroles*, *Heliobolus*, and *Nucras*, rooted the phylogenetic tree using *Australolacerta* which would actually belong to the same group of *Meroles* and *Pedioplanis.* Nevertheless, these authors were mostly focused on the relationship within the genus *Pedioplanis.*

The comparison between our sequence data of *A. australis* and those generated by Makokha *et al.* (2007) is possible only for a 16S gene fragment (500 bp) and revealed a high genetic differentiation (3.0–3.4%, uncorrected pairwise distances)

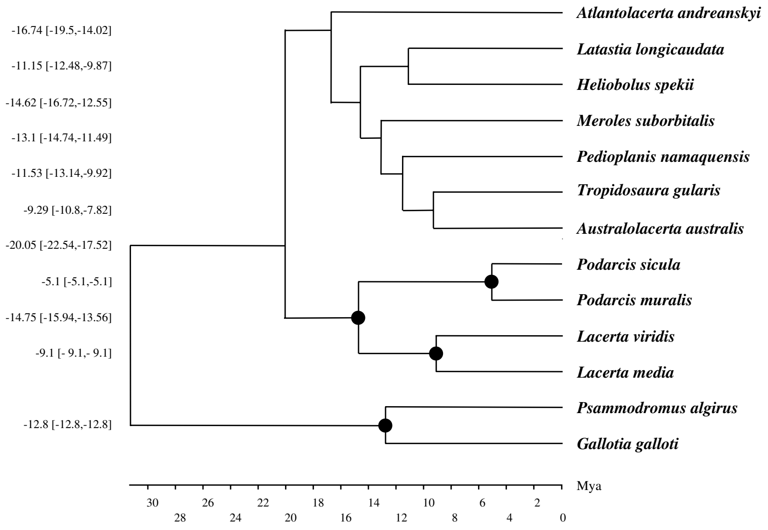

Figure 3. Chronogram with time estimates for the cladogenic events related to East African and southern African clades from the LRDM molecular clock analysis based on the 12s + 16S + cyt*b* dataset. The timing of Lacertine radiation (from 13.5 to 16 Mya) and the ages of split of *Podarcis*, *Lacerta*, and between *Psammodromus* and *Gallotia* (at 5.1 Mya, 9.1 Mya, and 12.8 Mya, respectively) were used as calibration points and the respective nodes are marked by black circles in the tree. Values in the left column indicates divergence times and 95% confidence limits (square brackets).

between specimens from the Cederberg area and those from the southernmost areas of the species' range, about 115–150 km away from Hoogverton (Zuurberg Private Nature Reserve, Naudesberg-Langeberg, and Goedemoed-Langeberg). These values are considerably high for conspecific specimens and similar to the corresponding distance detected between well-recognised lizard species included, among others, in the genera *Pedioplanis*, *Mesalina*, and *Podarcis* (see Makokha *et al.* 2007; Kapli *et al.* 2008; and Poulakakis *et al.* 2005, respectively). This would suggest that *A. australis* is probably a polytypic species or even a species complex, and highlights the need for further investigation on the pattern of genetic variation of this species.

The divergence time estimates suggested that the cladogenic event between the East African and the southern African clades, as well among genera within them, occurred during the Mid-Miocene (16.7–12.5 Mya). More specifically, the radiation of the southern African clade is estimated to have occurred 14.7–11.5 Mya. Given that primary calibration points for the dating procedure are not available, and the intrinsic inaccuracy of divergence time estimates based on molecular data (e.g. Heads 2005), our estimates should be considered coarse approximations aimed at placing the main events of *A. australis*' evolutionary history in a relative time frame rather than at providing exact dating. Based on these temporal hypotheses, the main evolutionary events related to *A. australis* took place during a period of great climatic instability in South Africa. Thus, as suggested also for other lacertids (Lamb *et al.* 2003; Lamb & Bauer 2003; Bauer & Lamb 2005; Makokha *et al.* 2007), the climate changes that occurred in South African region during the Mid-Miocene could have played an important role in the evolution of *A. australis* and *T. gularis*, which remained confined in mountain areas. In South Africa climate changed during the Miocene in relation to the glaciation history and the palaeogeographic evolution of Antarctica (Woodruff *et al.* 1981; Zachos *et al.* 2001; De Conto & Pollard 2003). During the early and middle Miocene, climate was more mesic than current conditions (Udeze & Oboh-Ikuenobe 2005). The increase in Antarctic glaciation from 14 Mya (Woodruff *et al.* 1981; Zachos *et al.* 2001), associated with a strengthening of the South Atlantic high-pressure cell (Shi *et al.* 2001), initiated a trend towards the modern seasonally arid conditions in the Cape Floristic Region (Linder 2005). The separation of Antarctica from South America made possible the development of a cold circum-Antarctic (Benguela) current around 14–11 Mya (Siesser 1978, 1980), which concurred to make the South African climate colder and to start the aridification process in the Cape region. Such aridification played a crucial role in the transformation (initiated 26 Mya) of sub-tropical forest to the fynbos vegetation of today (Richardson *et al.* 2001). In South Africa, the mentioned Miocene palaeoclimatic changes had a stronger effect in determining the principal radiation events in lizards (see Daniels *et al.* 2004 and references therein), than the following Plio-Pleistocenic glaciations. Indeed, in the Austral Hemisphere these glaciations were much less severe than in the Boreal Hemisphere (Moritz *et al.* 2000; Glor *et al.* 2001).

In conclusion, *Australolacerta australis* belongs to the southern African radiation of the Eremiadini, which is likely associated with the climatic changes occurred in this region during the Mid-Miocene. *Tropidosaura* rather than *Meroles* is the sister genus to *Australolacerta*. Further morphological and molecular analyses will be needed to assess the apparently huge differentiation within *A. australis* as has been evidenced by 16S rRNA data.

ACKNOWLEDGEMENTS

We are grateful to Le Fras Mouton, Mandi Alblas and all of the Survey of Cederberg Amphibians and Reptiles for Conservation and Ecotourism (SCARCE) project staff for the logistic support and to Donny Malherba (Cederberg Wilderness Area) for the permit of collecting within the natural reserve. We wish to thank Marco A. Bologna, Monica Pitzalis, Marco Oliverio, Chiara Settanni and D. James Harris who in various ways gave help to this study. This research was partially funded by the project 'Zoogeography of Mediterranean–southern African disjunct distributions by a multimethod approach' (Ministero dell'Istruzione, dell'Università e della Ricerca, n. 2004057217; coordinated by Marco A. Bologna).

REFERENCES

Arnold, E.N. 1973. Relationships of the Palaeartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). Bull. Nat. Hist. Mus. Zool. 29: 289–366.

Arnold, E.N. 1986. The hemipenis of lacertid lizards (Reptilia: Lacertidae): structure, variation and systematic implications. J. Nat. Hist. 20: 1221–1257.

Arnold, E.N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bull. Nat. Hist. Mus. Zool. 55: 209–257.

ARNOLD, E.N., O. ARRIBAS & S. CARRANZA. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa 1430: 1–86.

BAUER, A.M. & T. LAMB. 2005. Phylogenetic relationships of southern African geckos in the *Pachydactylus* group (Squamata: Gekkonidae). Afr. J. Herp. 54: 105–129.

BOMBI, P., D. SALVI, L. VIGNOLI & P. LE F.N. MOUTON. 2006. Distribution of *Australolacerta australis*: from known to potential range through a bioclimatic analysis. Atti del 6° congresso nazionale Societas Herpetologica Italica. Roma, Museo Civico di Zoologia, 27 September–1 October. Edizioni Belvedere, Latina: 133–138.

CARRANZA, S., E.N. ARNOLD & F. AMAT. 2004. DNA phylogeny of Lacerta (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? Syst. Biodiv. 2: 57–77.

DANIELS, S.R., P. LE F.N. MOUTON & D.A. DU TOIT. 2004. Molecular data suggest that melanistic ectotherms at the south-western tip of Africa are the products of Miocene climatic events: evidence from cordylid lizards. J. Zool. 263: 373–383.

DECONTO, R.M. & D. POLLARD. 2003. Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO_2. Nature 421: 245–249.

DE VILLIERS, A.L., E. BAARD & W.R. BRANCH. 1983. '*Lacerta*' *australis*: additional material. J. Herpetol Assoc. Afr. 29: 13–14.

FITZSIMONS, V.F.M. 1933. Descriptions of five new lizards from the Transvaal and Southern Rhodesia. Ann. Transvaal Mus. 15: 273–280.

FU, J. 1998. Toward the phylogeny of the family Lacertidae: implications from Mitochondrial DNA 12S and 16S gene sequences (Reptilia: Squamata). Mol. Phylogenet. Evol. 9: 118–130.

FU, J. 2000. Toward the phylogeny of the family Lacertidae – Why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol. J. Linn. Soc. 71: 203–217.

GLOR, R.E., L.T. VITT & A. LARSON. 2001. A molecular phylogenetic analysis of diversification in Amazonian *Anolis* lizards. Mol. Ecol. 10: 2661–2668.

HAACKE, W.D. 1982. *Lacerta australis* Hewitt 1926 rediscovery and report on fresh material. J. Herpetol. Assoc. Afr. 28: 19–21.

HARRIS, D.J., E.N. ARNOLD & R.H. THOMAS. 1998a. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proc. R. Soc. Lond. B 265: 1939–1948.

HARRIS, D.J., E.N. ARNOLD & R.H. THOMAS. 1998b. Rapid speciation morphological evolution and adaptation to extreme environments in South African sand lizards (*Meroles*) as revealed by mitochondria gene sequences. Mol. Phylogenet. Evol. 10: 37–48.

HEADS, M. 2005. Dating nodes on molecular phylogenies: a critique of molecular biogeography. Cladistics 21: 62–78.

HEWITT, J.R. 1926. Some new or little known lizards or batrachians from South Africa. Ann. South African Mus. 20: 473–490.

HILLIS, D.M., B.K. MABLE & C. MORITZ. 1996. Application of molecular Systematics. Pp. 515–543. *In* D.M. HILLIS, C. MORITZ, B.K. MABLE, (Eds.), Molecular Systematics. 2nd Edition. Sinauer Associates, Sunderland.

JOBB, G. 2008. TREEFINDER version of October 2008. Munich, Germany. Distributed by the author. http://www.treefinder.de.

KAPLI, P, P. LYMBERAKIS, N. POULAKAKIS, G. MANTZIOU, A. PARMAKELIS & M. MYLONAS. 2008. Molecular phylogeny of three *Mesalina* (Reptilia: Lacertidae) species (*M. guttulata*, *M. brevirostris* and *M. bahaeldini*) from North Africa and the Middle East: another case of paraphyly? Mol. Phylogenet. Evol. 49: 102–110.

LAMB, T. & A.M. BAUER. 2003. *Meroles* revisted: complementary systematic inferences from additional mitochondrial genes and complete taxon sampling of southern Africa's desert lizards. Mol. Phylogenet. Evol. 29: 360–364.

LAMB, T., A.M. MEEKER, A.M. BAUER & W.R. BRANCH. 2003. On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA sequence analysis of the African Gerrhosauridae. Biol. J. Linn. Soc. 78: 253–261.

LINDER, H.P. 2005. Evolution of diversity: the Cape flora. Trends Plant Sci. 10: 536–541.

MAKOKHA, J.S., A.M. BAUER, W. MAYER & C.A. MATTHEE. 2007. Nuclear and mtDNA-based phylogeny of southern African sand lizard *Pedioplanis* (Sauria: Lacertidae). Mol. Phylogenet. Evol. 44: 622–633.

Mayer, W. & G. Benyr. 1994. Albumin-Evolution und phylogenese in der Familie Lacertidae. Ann. Naturhist. Mus. Wien 96: 621–648.

Mayer, W. & H. Berger-Dell'mour. 1988. Protein electrophoretic investigations on the systematics of the genera *Aporosaura, Meroles, Pedioplanis, Heliobolus.* Herpetozoa 1: 23–29.

Mayer, W. & M. Pavličev. 2007. The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. Mol. Phylogenet. Evol. 44: 1155–1163.

Moritz, C., J.L. Patton, C.J. Schnieder & T.B. Smith. 2000. Diversification of rainforest faunas: an integral molecular approach. Annu. Rev. Ecol. Syst. 31: 533–563.

Mouton, P.L.F.N., B.W. Oelofsen & D.P. Mostert. 1987. New data on threatened lizard species in the south-western Cape, South Africa. S. Afr. J. Sci. 83: 48–52.

Pavličev, M. & W. Mayer. 2009. Fast radiation of the subfamily Lacertinae (Reptilia: Lacertidae): history or methodical artefact? Mol. Phylogenet. Evol. 52: 727–734.

Posada, D. 2008. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25: 1253–1256.

Poulakakis, N, P. Lymberakis, E. Valakos, E. Zouros & M. Mylonas. 2005. Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by bayesian and maximum likelihood analyses of mitochondrial DNA sequences. Mol. Phylogenet. Evol. 37: 845–857.

Rambaut, A. & A.J., Drummond. 2007. Tracer v1.4. Available from http://beast.bio.ed.ac.uk/Tracer

Richardson, J.E., F.M. Weitz, M.F. Fay, Q.C.B. Cronkk, H.P. Linder, G. Reeves & M.W. Chase. 2001. Rapid and recent origin of species richness in the Cape flora of South Africa. Nature 412: 181–183.

Ronquist, F. & J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Shi, N., R. Schneider, H.J. Beug & L.M. Dupont. 2001. Southeast trade wind variations during the last 135 kyr: evidence from pollen spectra in eastern South Atlantic sediments. Earth Planet. Sci. Lett. 187: 311–321.

Siesser, W.G. 1978. Aridification of the Namib Desert: evidence from oceanic cores. Pp. 105–113. *In* Antarctic glacial history and world palaeoenvironments, E.M. Van Zinderen Bakker (Ed.). Balkema, Rotterdam.

Siesser, W.G. 1980. Late Miocene origin of the Benguela upwelling system off Northern Namibia. Science 208: 283–285.

Strimmer, K. & A. Rambaut. 2002. Inferring confidence sets of possibly misspecified gene trees. Proc. R. Soc. Lond. B 269: 137–142.

Swofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4 (1998), beta 4.0b10 (2002). Sinauer Associates, Sunderland, Massachusetts.

Talavera, G. & J. Castresana. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56: 564–577.

Thompson, J.D., T.J. Gibson, F. Plewniak, F. Jeanmougin & D.G. Higgins. 1997. The ClustalX windows interface. Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 24: 4876–4882.

Udeze, C.U. & F.E. Oboh-Ikuenobe. 2005. Neogene palaeoceanographic and palaeoclimatic events inferred from palynological data: Cape Basin off South Africa, ODP Leg 175. Palaeogeogr. Palaeoclimateol. Palaeoecol. 219: 199–223.

Woodruff, F., S.M. Savin & R.G. Douglas. 1981. Miocene stable isotope record: a detailed deep Pacific Ocean study and its paleoclimatic implications. Science 212: 665–668.

Zachos, J., M. Pagani, L. Sloan, E. Thomas & K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693.

Received: 11 August 2010; Final acceptance: 9 December 2010