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HIGHER-LEVEL MOLECULAR PHYLOGENY OF SNAKES: CONFLICTS AND  
CONGRUENCE

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compararon los soportes de los grupos para "D" y para el "set" de datos combinados "C+D" para evaluar el aporte de los caracteres continuos al análisis. Cuando se agregan los caracteres continuos existe un aumento global de 22 en la diferencia de frecuencias, mostrando que la inclusión de los caracteres continuos otorga soporte adicional a la topología. Se concluye que los caracteres vertebrales continuos de serpientes resultan filogenéticamente informativos y se recomienda su inclusión como tales en análisis cladísticos.

## BIBLIOGRAFÍA

- Apesteguía, S. & H. Zaher. 2006. A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. *Nature* 440: 1037-104.
- Auffenberg, W. 1963. The fossil snakes of Florida. *Tulane Stud. Zool.* 10: 131-216.
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83-91.
- Goloboff, P. A., J. Farris & K. Nixon. 2003a. T.N.T. Tree Analysis Using New Technology. Program & documentation, available from the authors, and at <http://www.zmuc.dk/public/phylogeny/tnt>
- Goloboff, P. A., M. Källersjö, B. Oxelmann, M. Ramírez & C. Szumik. 2003b. Improvements to resampling measures of group support. *Cladistics* 19: 324-332.
- Goloboff, P. A., C. I. Mattoni & A. S. Quinteros. 2006. Continuous characters analyzed as such. *Cladistics* 22: 1-13.
- Johnson, R. G. 1955. The adaptive and phylogenetic significance of vertebral form in snakes. *Evolution* 9: 367-388.
- Lee, M. S. Y. & J. D. Scanlon. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. *Biol. Rev.* 77: 333-401.
- Rage, J. C. 1984. Serpentes, en: P. Wellnhofer (ed.), *Handbuch der Paläoherpetologie*, Tomo 11, xii + 80 pp. Stuttgart/New York: Gustav Fischer Verlag.
- Rieppel, O., A. G. Kluge & H. Zaher. 2002. Testing the phylogenetic relationships of the Pleistocene snake *Wonambi naracoortensis* Smith. *J. Vertebr. Paleontol.* 22: 812-829.
- Rohlf, J. F. 2004. Tps Dig 1.40. State University of New York, Stony Brook, New York. <http://life.bio.sunysb.edu/morph/>.
- Szyndlar, Z. 1984. Fossil snakes from Poland. *Acta Zool. Cracov.* 28: 1-156.

## HIGHER-LEVEL MOLECULAR PHYLOGENY OF SNAKES: CONFLICTS AND CONGRUENCE

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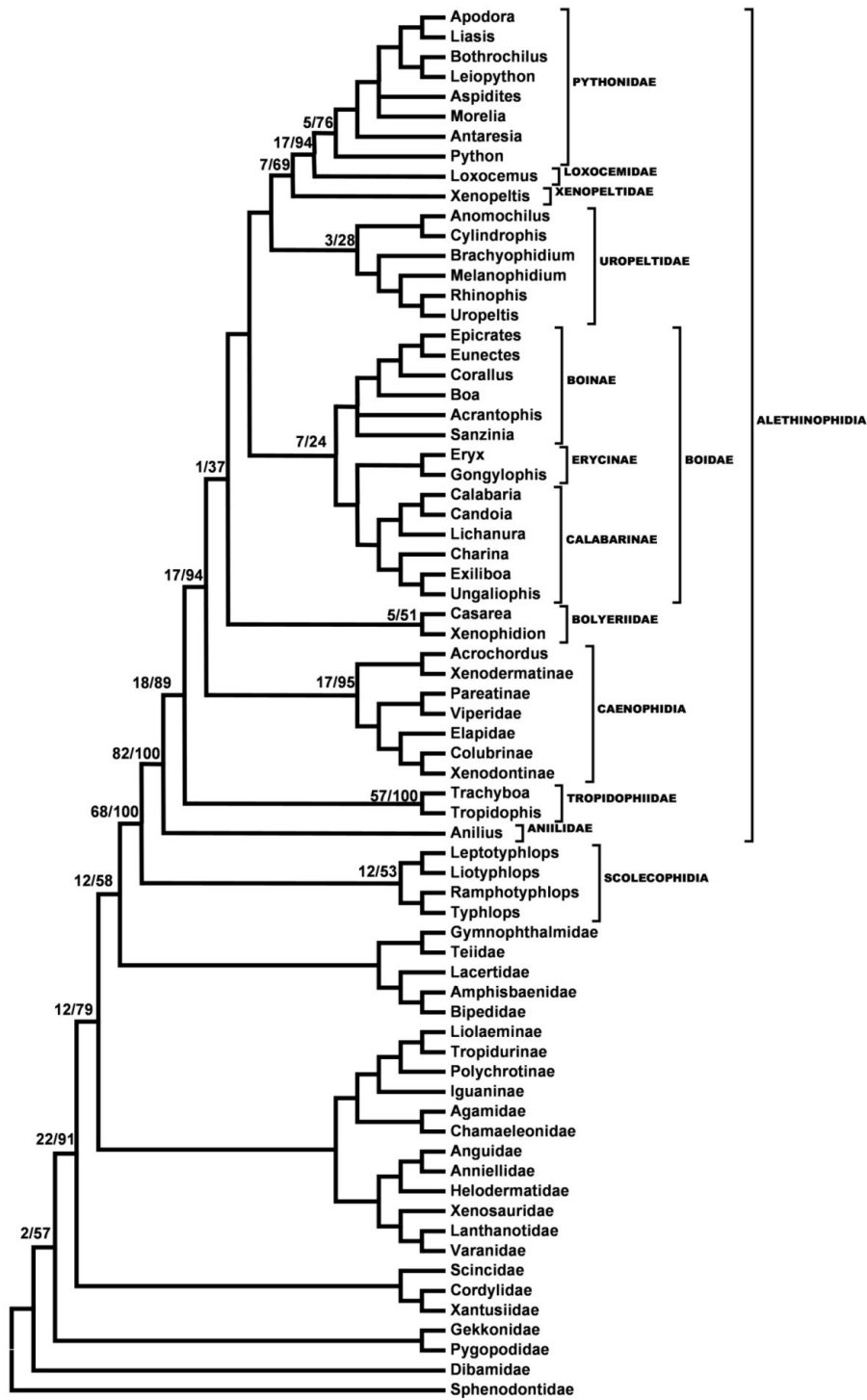
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The monophyly of snakes can be considered a well-corroborated hypothesis. However, phylogenetic relationships among the major groups of snakes remain unclear, despite the recent debate on snake origins and evolution. Important disagreements persist on several phylogenetic issues, with contrasting results emerging from both molecular and morphological analyses. The most relevant issues are: 1) the sister-group relationships of snakes within Squamates, 2) the phylogenetic position of the fossil snakes *Pachyrhachis*, *Haasiophis*, *Eupodophis*, *Dinilyisia*, and *Wonambi*, 3) the monophyly of the macrostomatans and Tropidophiidae, 4) the interrelationships of booid lineages, and 4) the sister-group relationships of caenophidians within macrostomatan snakes. In the last few

years, a significant number of studies exclusively based on DNA sequence analyses produced phylogenies that conflict in several respect with some of the clades traditionally recognized by morphologically based analyses. Although these studies have generated a considerable amount of comparative data to snake phylogeny, the complete information produced cannot be satisfactorily compared, because several taxa used by some studies were not included in others, and data sets for some key taxa are missing for nearly all approaches. We present here a molecular phylogenetic analysis of snake interrelationships based on sequences from nine genes (12S, 16S, cytb, nd4, c-mos, RAG1, 28S, NT3, BDNF) comprising a total of 10,666 bps and 4,638 parsimony informative sites for



**Fig. 1.** Phylogenetic tree based on the total evidence approach showing the relationship among the higher families of Squamata. Numbers above branches are Bremer and Bootstrap values, respectively.

seventy Squamate taxa representing all higher groups of snakes and lizards. Our results show a clear saturation sign for some genes (mitochondrial genes *cytb* and *nd4*) and an inconsistent pattern where almost all genes produce an idiosyncratic tree in a Maximum Parsimony approach. Depending on the method used to construct the matrix (DNA, Amino Acids, mitochondrial or nuclear DNA, etc), different trees were produced, although some topologies had been always recovered. Among these topologies, three of them represent singular results that are very similar to the molecular results published in the last few years and, in particular, supports the paraphyly of Macrostromatan and Anilioid snakes and the families Boidae and Erycidae, four traditionally recognized clades in morphological studies. Additionally, our molecular results also suggest that the family Tropidophiidae and the anilioid genus *Anilius* form a monophyletic assemblage, recently named formally as "Amerophidia" by Vidal et al. (2007). We suggest that some of the conflicting results obtained in molecular studies, including ours, can be interpreted as a problem of taxon sampling that produce spurious signals due to the relictual condition of the extant snake fauna (with the notable exception of Colubroids), which represents only a small and heterogeneous portion of the past diversity of the group. In order to test the molecularly supported clades, we performed a series of Kishino-Hasegawa tests implemented in PAUP\*4 using constrained topologies to reproduce the preferred morphological tree. It resulted that

the clade "Amerophidia" is not statically supported and should not be recognized (Table 1). On the other hand, the nested position within higher macrostromatans of the clade formed by *Cylindrophis*+*Anomochilus*+*Uropeltinae* (microstromata minus *Anilius*) is statistically well supported (Table 1). Finally, we performed a total evidence

**Table 1.** Results of Kishino-Hasegawa test for molecular data.

Tree	Length	Length diff	P*
MP tree	32117	(best)	
Microstromata	32209	92	<0.0001*
Paraphyletic "Amerophidia"	32124	7	0.3994

analysis (TBR search under 100 random addition trees conducted using Maximum Parsimony in PAUP\*4) where the Boinae and Erycinae are recovered as monophyletic and the "Amerophidians" are rejected as a clade (Fig. 1). A clearer picture of snake phylogeny would be possible only through a total evidence approach that includes morphology and fossil information.

## BIBLIOGRAPHY

Vidal, N.; A. S. Delmas & S. B. Hedges. 2007. The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes. R. W. Henderson and R. Powell (eds.), *Biology of the boas and pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah. Pp. 27-33.

## FILOGENIA DE CHARACIDAE (TELEOSTEI, CHARACIFORMES) Y OPTIMIZACIÓN AUTOPESADA

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En una filogenia de la familia Characidae (Mirande, en prep.) el autor realizó un análisis bajo pesos implicados (PI) ["Implied weighting"; (Goloboff, 1993)] y optimización autopesada (OA) ["Self-weighted optimization"; (Goloboff, 1997)] con una matriz de 160 especies y 360

caracteres. Las optimizaciones bajo OA son calculadas heurísticamente y son más lentas que bajo pesos iguales o implicados; aquí se describen las estrategias utilizadas para analizar esta matriz y se comparan los resultados con los obtenidos bajo PI.