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Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria

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References

- Abascal, F., Posada, D. & Zardoya, R. (2012) The evolution of the mitochondrial genetic code in arthropods revisited. *Mitochondrial DNA*, 23, 84–91.
<http://dx.doi.org/10.3109/19401736.2011.653801>
- Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19, 716–723.
<http://dx.doi.org/10.1109/tac.1974.1100705>
- Alkatib, S., Scharff, L.B., Rogalski, M., Fleischmann, T.T., Matthes, A., Seeger, S., Schöttler, M.A., Ruf, S. & Bock, R. (2012) The contributions of wobbling and superwobbling to the reading of the genetic code. *PLoS Genetics*, 8, e1003076.
<http://dx.doi.org/10.1371/journal.pgen.1003076>
- Amaro, R.C., Nunes, I., Canedo, C., Napoli, M.F. & Juncá, F.A (2013) A molecular phylogeny recovers *Strabomantis aramunha* Cassimiro, Verdade and Rodrigues, 2008 and *Haddadus binotatus* (Spix, 1824) (Anura: Terrarana) as sister taxa. *Zootaxa*, 3741, 569–582.
<http://dx.doi.org/10.11646/3897>
- Anisimova, M. & Gascuel, O. (2006) Approximate likelihood-ratio test for branches: a fast, accurate, and powerful alternative. *Systematic Biology*, 55, 539–552.
<http://dx.doi.org/10.1080/10635150600755453>
- Ardila-Robayo, M.C. (1979) Status sistemático del género *Geobatrachus* Ruthven, 1915 (Amphibia: Anura). *Caldasia*, 12, 383–495.
- Ayarzagüena, J. (1985 "1983") Una nueva especie de *Dischidiadactylus* Lynch (Amphibia, Leptodactylidae) en la cumbre del Tepui Marahuaca, Territorio Federal Amazonas—Venezuela. *Memorias de Sociedad de Ciencias Naturales La Salle, Caracas*, 43, 215–220.
- Barrio-Amorós, C.L. (2010) A new *Ceuthomantis* (Anura: Terrarana: Ceuthomantidae) from Saraisariñama Tepui, southern Venezuela. *Herpetologica*, 66, 172–181.
<http://dx.doi.org/10.1655/09-00006.1>
- Barrio-Amorós, C.L. & Molina, C.R. (2006) A new *Eleutherodactylus* (Anura: Brachycephalidae) from the Venezuelan Guayana, and redescription of *Eleutherodactylus vilarsi* (Melin). *Zootaxa*, 1302, 1–20.
- Barrio-Amorós, C.L., Heinicke, M.P. & Hedges, S.B. (2013) A new tuberculated *Pristimantis* (Anura, Terrarana, Strabomantidae) from the Venezuelan Andes, redescription of *Pristimantis pleurostriatus*, and variation within *Pristimantis vanadisae*. *Zootaxa*, 3647, 43–62.
<http://dx.doi.org/10.11646/zootaxa.3647.1.2>
- Barry, D. & Hartigan, J. (1987) Statistical analysis of hominid molecular evolution. *Statistical Science*, 2, 191–210.
<http://dx.doi.org/10.1214/ss/1177013353>
- Blackburn, D.C. & Wake, D.B. (2011) Class Amphibia Gray, 182. In: Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, 3148, 39–55.
- Blackburn, B.P. & Whelan, S. (2012) Measuring the distance between multiple sequence alignments. *Bioinformatics*, 28, 495–502.
<http://dx.doi.org/10.1093/bioinformatics/btr701>
- Blair, C. & Murphy, R.W. (2011) Recent trends in molecular phylogenetic analysis: Where to next? *Journal of Heredity*, 102, 130–138.
<http://dx.doi.org/10.1093/jhered/esq092>
- Blotto, B.L., Nuñez, J.J., Basso, N.G., Úbeda, C.A., Wheeler, W.C. & Faivovich, J. (2013) Phylogenetic relationships of a Patagonian frog radiation, the *Alsodes* + *Eupsophus* clade (Anura: Alsodidae), with comments on the supposed paraphyly of *Eupsophus*. *Cladistics*, 29, 113–131.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00417.x>
- Bock, R. (2000) Sense from nonsense: How the genetic information of chloroplasts is altered by RNA editing. *Biochimie*, 82,

- 549–557.
[http://dx.doi.org/10.1016/s0300-9084\(00\)00610-6](http://dx.doi.org/10.1016/s0300-9084(00)00610-6)
- Box, G.E. (1976) Science and statistics. *Journal of the American Statistical Association*, 71, 791–799.
<http://dx.doi.org/10.1080/01621459.1976.10480949>
- Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42, 795–803.
<http://dx.doi.org/10.2307/2408870>
- Britten, R.J., Rowen, L., Williams, J. & Cameron, R.A. (2003) Majority of divergence between closely related DNA samples is due to indels. *Proceedings of the National Academy of Sciences*, 100, 4661–4665.
<http://dx.doi.org/10.1073/pnas.0330964100>
- Brusquetti, F., Thomé, M.T.C., Canedo, C., Condez, T.H. & Haddad, C.F.B. (2013) A new species of *Ischnocnema parva* species series (Anura, Brachycephalidae) from northern state of Rio de Janeiro, Brazil. *Herpetologica*, 69, 175–185.
<http://dx.doi.org/10.1655/herpetologica-d-12-00050>
- Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33, 261–304.
<http://dx.doi.org/10.1177/0049124104268644>
- Canedo, C. & Haddad, C.F.B. (2012) Phylogenetic relationships within anuran clade Terrarana, with emphasis on the placement of Brazilian Atlantic rainforest frogs genus *Ischnocnema* (Anura: Brachycephalidae). *Molecular Phylogenetics and Evolution*, 65, 610–620.
<http://dx.doi.org/10.1016/j.ympev.2012.07.016>
- Caramaschi, U. & Canedo, C. (2006) Reassessment of the taxonomic status of the genera *Ischnocnema* Reinhardt and Lütken, 1862, and *Oreobates* Jiménez-de-la-Espada, 1872, with notes on the synonymy of *Leiuperus verrucosus* Reinhardt and Lütken, 1862 (Anura: Leptodactylidae). *Zootaxa*, 1116, 43–54.
- Cassimiro, J., Verdade, V.K. & Rodrigues, M.T. (2008) A large and enigmatic new eleutherodactyline frog (Anura, Strabomantidae) from Serra do Sincorá, Espinhaço range, northeastern Brazil. *Zootaxa*, 1761, 59–68.
- Chan, S.C., Wong, A.K.C. & Chiu, D.K.Y. (1992) A survey of multiple sequence comparison methods. *Bulletin of Mathematical Biology*, 54, 563–598.
[http://dx.doi.org/10.1016/s0092-8240\(05\)80077-1](http://dx.doi.org/10.1016/s0092-8240(05)80077-1)
- Chaparro, J.C., Motta, A.P., Gutiérrez, R.C. & Padial, J.M. (2012) A new species of *Pristimantis* (Anura: Strabomantidae) from Andean cloud forests of northern Peru. *Zootaxa*, 3192, 39–48.
- Cisneros-Heredia, D.F. (2006) *La herpetofauna de la Estación de Biodiversidad Tiputini, Ecuador*. B.Sc. Thesis. Universidad San Francisco de Quito, Quito, 129 pp.
- Clemente-Carvalho, R.B.G., Klaczko, J., Perez, I.S., Alves, A.C.R., Haddad, C.F.B. & Reis, S.F. (2011) Molecular phylogenetic relationships and phenotypic diversity in miniaturized toadlets, genus *Brachycephalus* (Amphibia: Anura: Brachycephalidae). *Molecular Phylogenetics and Evolution*, 61, 79–89.
<http://dx.doi.org/10.1016/j.ympev.2011.05.017>
- Cracraft, J. (1981) The use of functional and adaptive criteria in phylogenetic systematics. *American Zoologist*, 21, 21–36.
<http://dx.doi.org/10.1093/icb/21.1.21>
- Crawford, A.J. & Smith, E.E. (2005) Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleutherodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution*, 35, 536–555.
<http://dx.doi.org/10.1016/j.ympev.2005.03.006>
- Crawford, A.J., Lips, K.R. & Bermingham, E. (2010a) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences USA*, 107, 13777–13782.
<http://dx.doi.org/10.1073/pnas.0914115107>
- Crawford, A.J., Ryan, M.J. & Jaramillo, C.A. (2010b) A new species of *Pristimantis* (Anura: Strabomantidae) from the Pacific coast of the Darién Province, Panama, with a molecular analysis of its phylogenetic position. *Herpetologica*, 66, 192–206.
<http://dx.doi.org/10.1655/09-018r1.1>
- Crother, B.I. (2009) Are standard names lists taxonomic straightjackets? *Herpetologica*, 65, 129–135.
<http://dx.doi.org/10.1655/09-028.1>
- Darst, C.R. & Cannatella, D.C. (2004) Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 31, 462–475.
<http://dx.doi.org/10.1016/j.ympev.2003.09.003>
- De la Riva, I. (2007) Bolivian frogs of the genus *Phrynobatrachus*, with the description of twelve new species (Anura: Brachycephalidae). *Herpetological Monographs*, 21, 241–277.
<http://dx.doi.org/10.1655/07-011.1>
- De la Riva, I. & Lynch, J.D. (1997) New species of *Eleutherodactylus* from Bolivia (Amphibia: Leptodactylidae). *Copeia*, 1997, 151–157.
<http://dx.doi.org/10.2307/1447850>
- De la Riva, I., Chaparro, J.C. & Padial, J.M. (2008) The taxonomic status of *Phyllonastes Heyer* and *Phrynobatrachus peruvianus* (Noble) (Lissamphibia, Anura): resurrection of *Nobellia* Barbour. *Zootaxa*, 1685, 67–68.

- Denton, J.S. & Wheeler, W.C. (2012) Indel information eliminates trivial sequence alignment in maximum likelihood phylogenetic analysis. *Cladistics*, 28, 514–528.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00402.x>
- Dubois, A. (2005a) Amphibia Mundi 1.1. An ergotaxonomy of recent amphibians. *Alytes*, 23, 1–24.
- Dubois, A. (2005b) Proposed rules for the incorporation of nomina of higher-ranked zoological taxa in the International Code of Zoological Nomenclature. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema*, 27, 365–426.
- Dubois, A. (2006) Incorporation of nomina of higher-ranked taxa into the International Code of Zoological Nomenclature: some basic questions. *Zootaxa*, 1337, 1–37.
- Duellman, W.E. (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publications of the University of Kansas, Museum of Natural History, Lawrence*, 65, 1–352.
- Duellman, W.E. & Lynch, J.D. (1969) Descriptions of *Atelopus* tadpoles and their relevance to atelopodid classification. *Herpetologica*, 25, 231–240.
- Duellman, W.E. & Hedges, S.B. (2005) Eleutherodactyline frogs (Anura, Leptodactylidae) from the Cordillera Yanachaga in central Peru. *Copeia*, 2005, 526–538.
<http://dx.doi.org/10.1643/ch-05-019r>
- Duellman, W.E. & Köhler, J. (2005) New species of marsupial frog (Hylidae, Hemiphractinae, *Gastrotheca*) from the yungas of Bolivia. *Journal of Herpetology*, 39, 91–100.
[http://dx.doi.org/10.1670/0022-1511\(2005\)039\[0091:nsomfh\]2.0.co;2](http://dx.doi.org/10.1670/0022-1511(2005)039[0091:nsomfh]2.0.co;2)
- Duellman, W.E. & Hedges, S.B. (2007) Three new species of *Pristimantis* (Lissamphibia, Anura) from montane forests of the Cordillera Yanachaga in central Peru. *Phylomedusa*, 6, 119–135.
<http://dx.doi.org/10.11606/issn.2316-9079.v6i2p119-135>
- Duellman, W.E. & Lehr, E. (2009) *Terrestrial-breeding frogs (Strabomantidae) in Peru*. Nature und Tier Verlag, Münster, Germany, 384 pp.
- Duellman, W.E., Jungfer, K.-H. & Blackburn, D.C. (2011) The phylogenetic relationship of geographically separated "*Flectonotus*" (Anura, Hemiphractidae), as revealed by molecular, behavioral, and morphological data. *Phylomedusa*, 10, 15–29.
<http://dx.doi.org/10.11606/issn.2316-9079.v10i1p15-29>
- The ENCODE Project Consortium (2012) An integrated encyclopedia of DNA elements in the human genome. *Nature*, 489, 57–74.
<http://dx.doi.org/10.1038/nature11247>
- Edgar, R.C. (2004) MUSCLE, multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
<http://dx.doi.org/10.1093/nar/gkh340>
- Edgar, R.C. & Sjölander, K. (2003) SATChMO, sequence alignment and tree construction using hidden Markov models. *Bioinformatics*, 19, 1404–1411.
<http://dx.doi.org/10.1093/bioinformatics/btg158>
- Eernisse, D.J. & Kluge, A.G. (1993) Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. *Molecular Biology and Evolution*, 10, 1170–1195.
- Efron, B. (1979) Bootstrap methods, another look at the jackknife. *The Annals of Statistics*, 7, 1–26.
<http://dx.doi.org/10.1214/aos/1176344552>
- Efron, B., Halloran, E. & Holmes, S. (1996) Bootstrap confidence levels for phylogenetic trees. *Proceedings of the National Academy of Sciences*, 93, 13429–13429.
<http://dx.doi.org/10.1073/pnas.93.23.13429>
- Eizirik, E., Yuhki, N., Johnson, W.E., Menotti-Raymond, M., Hannah, S.S. & O'Brien, S.J. (2003) Molecular genetics and evolution of melanism in the cat family. *Current Biology*, 13, 448–453.
[http://dx.doi.org/10.1016/s0960-9822\(03\)00128-3](http://dx.doi.org/10.1016/s0960-9822(03)00128-3)
- Elmer, K.R. & Cannatella, D.C. (2008) Three new species of leaflitter frogs from the upper Amazon forests, cryptic diversity within *Pristimantis "ockendeni"* (Anura, Strabomantidae) in Ecuador. *Zootaxa*, 1784, 11–38.
- Estabrook, G.F. (1997) Ancestor–descendant relations and incompatible data, motivation for research in discrete mathematics. In: Mirkin, B. McMorris, F., Roberts, R. & Rzhetsky, A. (Eds.), *Mathematical Hierarchies and Biology*. Providence, pp. 1–28.
- Faivovich, J., Haddad, C.F.B., García, P.C.A., Frost, D.R., Campbell, J.A. & Wheeler, W.C. (2005) Systematic revision of the frog family Hylidae, with special reference to Hylinae, phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, 294, 1–240.
[http://dx.doi.org/10.1206/0003-0090\(2005\)294\[0001:sroff\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2005)294[0001:sroff]2.0.co;2)
- Farris, J.S. (1966) Estimation of conservatism of characters by constancy within biological populations. *Evolution*, 20, 587–591.
<http://dx.doi.org/10.2307/2406593>
- Farris, J.S. (1969) A successive approximations approach to character weighting. *Systematic Biology*, 18, 374–385.
<http://dx.doi.org/10.2307/2412182>

- Farris, J.S. (1970) On the relationship between variation and conservatism. *Evolution*, 24, 825–827.
<http://dx.doi.org/10.2307/2406563>
- Farris, J.S. (1973) A probability model for inferring evolutionary trees. *Systematic Biology*, 22, 250–256.
<http://dx.doi.org/10.1093/sysbio/22.3.250>
- Farris, J.S. (1983) The logical basis of phylogenetic analysis. In: Platnick, N.I. & Funk, V.A. (Eds.), *Advances in Cladistics. Proceedings of the Second Meeting of the Willi Hennig Society, Volume 2*. Columbia University Press, New York, pp. 7–36.
- Farris, J.S. (1999) Likelihood and inconsistency. *Cladistics*, 15, 199–204.
<http://dx.doi.org/10.1111/j.1096-0031.1999.tb00262.x>
- Farris, J.S. (2001) Support weighting. *Cladistics*, 17, 389–394.
<http://dx.doi.org/10.1006/clad.2001.0180>
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12, 99–124.
<http://dx.doi.org/10.1111/j.1096-0031.1996.tb00196.x>
- Farris, J.S., Kluge, A.G. & Carpenter, J.M. (2001) Popper and likelihood versus "Popper*". *Systematic Biology*, 50, 438–444.
<http://dx.doi.org/10.1080/106351501300318021>
- Felsenstein, J. (1973) Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. *Systematic Biology*, 22, 240–249.
<http://dx.doi.org/10.2307/2412304>
- Felsenstein, J. (1985) Confidence limits on phylogenies, an approach using the bootstrap. *Evolution*, 39, 783–791.
<http://dx.doi.org/10.2307/2408678>
- Felsenstein, J. (1988) Phylogenies from molecular sequences: Inference and reliability. *Annual Review of Genetics*, 22, 521–565.
<http://dx.doi.org/10.1146/annurev.genet.22.1.521>
- Felsenstein, J. (2004) *Inferring phylogenies*. Sinauer Associates, Sunderland (MA), 664 pp.
<http://dx.doi.org/10.1007/s00357-005-0009-4>
- Fleissner, R., Metzler, D. & von Haeseler, A. (2005) Simultaneous statistical multiple alignment and phylogeny reconstruction. *Systematic Biology*, 54, 548–561.
<http://dx.doi.org/10.1080/10635150590950371>
- Fontanillas, E., Welch, J.J., Thomas, J.A. & Bromham, L. (2007) The influence of body size and net diversification rate on molecular evolution during the radiation of animal phyla. *BMC Evolutionary Biology*, 7, 95.
<http://dx.doi.org/10.1186/1471-2148-7-95>
- Fouquet, A., Loebmann, D., Castroviejo-Fisher, S., Padial, J.M., Orrico, V.G.D., Lyra, M.L., Roberto, I.J., Kok, P.J.R., Haddad, C.F.B. & Rodrigues, M.T. (2012) From Amazonia to the Atlantic forest, Molecular phylogeny of Phyzelaphryininae frogs reveals unexpected diversity and a striking biogeographic pattern emphasizing conservation challenges. *Molecular Phylogenetics and Evolution*, 65, 547–561.
<http://dx.doi.org/10.1016/j.ympev.2012.07.012>
- Fouquet, P., Martinez, Q., Courtois, E. A., Dewynter, M., Pineau, K., Gaucher, P., Blanc, M., Marty, C. & Kok, P.J.R. (2013a) A new species of the genus *Pristimantis* (Amphibia, Craugastoridae) associated with the moderately elevated massifs of French Guiana. *Zootaxa*, 3750, 569–586.
<http://dx.doi.org/10.11646/zootaxa.3750.5.8>
- Fouquet, A., Blotto, B.L., Maronna, M.M., Verdade, V.K., Juncá, F.A., Sá, R.D. & Rodrigues, M.T. (2013b) Unexpected phylogenetic positions of the genera *Rupirana* and *Crossodactylodes* reveal insights into the biogeography and reproductive evolution of leptodactylid frogs. *Molecular Phylogenetics and Evolution*, 67, 445–457.
<http://dx.doi.org/10.1016/j.ympev.2013.02.009>
- Frost, D.R. (2014) *Amphibian Species of the World, an Online Reference*. Version 6.0 American Museum of Natural History, New York, USA. Available at <http://research.amnh.org/herpetology/amphibia/index.html> (accessed February 04 2014)
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
[http://dx.doi.org/10.1206/0003-0090\(2006\)297\[0001:tatol\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2006)297[0001:tatol]2.0.co;2)
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P.E., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2008) Is the Amphibian Tree of Life really fatally flawed? *Cladistics*, 24, 384–395.
<http://dx.doi.org/10.1111/j.1096-0031.2007.00181.x>
- Fusinatto, L.A., Alexandrino, J., Haddad, C.F.B., Brunes, T.O., Rocha, C.F.D. & Sequeira, F. (2013) Cryptic genetic diversity is paramount in small-bodied amphibians of the genus *Euparkerella* (Anura: Craugastoridae) endemic to the Brazilian Atlantic forest. *PLoS ONE*, 8, e79504.
<http://dx.doi.org/10.1371/journal.pone.0079504>
- Gallardo, J.M. (1965) A propósito de los Leptodactylidae (Amphibia Anura). *Papéis Avulsos do Departamento de Zoologia*,

- García-R, J.C., Crawford, A.J., Mendoza, A.M., Ospina, O., Cardenas, H. & Castro, F. (2012) comparative phylogeography of direct-developing frogs (Anura, Craugastoridae, *Pristimantis*) in the southern Andes of Colombia. *PLoS One*, 7, e46077. <http://dx.doi.org/10.1371/journal.pone.0046077>
- García-R, J.C., Mendoza A.M., Ospina, O., Cardenas, H. & Castro, F. (2014) A morphometric and molecular approach to define three closely related species of frogs of the genus *Pristimantis* (Anura: Craugastoridae) from the Cordillera Occidental in Colombia. *Journal of Herpetology*. [in press]
- Gehara, M., Canedo, C., Haddad, C.F.B. & Vences, M. (2013) From widespread to microendemic, molecular and acoustic analyses show that *Ischnocnema guentheri* (Amphibia, Brachycephalidae) is endemic to Rio de Janeiro, Brazil. *Conservation Genetics*, 14, 973–982. <http://dx.doi.org/10.1007/s10592-013-0488-5>
- Giribet, G. (2005) Generating implied alignments under direct optimization using POY. *Cladistics*, 21, 396–402. <http://dx.doi.org/10.1111/j.1096-0031.2005.00071.x>
- Goldberg, C.S., Sullivan, B.K., Malone, J.H. & Schwalbe, C.R. (2004) Divergence among barking frogs (*Eleutherodactylus augusti*) in the southwestern United States. *Herpetologica*, 60, 312–320. <http://dx.doi.org/10.1655/03-81>
- Goldman, N. (1990) Maximum-likelihood inference of phylogenetic trees, with special reference to Poisson process model of DNA substitution and to parsimony analysis. *Systematic Zoology*, 39, 345–361. <http://dx.doi.org/10.2307/2992355>
- Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–91. <http://dx.doi.org/10.1006/clad.1993.1003>
- Goloboff, P.A. (1996) Methods for faster parsimony analysis. *Cladistics*, 12, 199–220. <http://dx.doi.org/10.1006/clad.1996.0015>
- Goloboff, P.A. (1999) Analyzing large data sets in reasonable times, solutions for composite optima. *Cladistics*, 15, 415–428.
- Goloboff, P.A. (2003) Parsimony, likelihood, and simplicity. *Cladistics*, 19, 91–103. <http://dx.doi.org/10.1111/j.1096-0031.2003.tb00297.x>
- Goloboff, P.A. (2008) Calculating SPR distances between trees. *Cladistics*, 24, 591–597. <http://dx.doi.org/10.1111/j.1096-0031.2007.00189.x>
- Goloboff, P.J., Farris, S. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786. <http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x>
- Goodman, M., Weiss, M.L. & Czelusniak, J. (1982) Molecular evolution above the species level, branching patterns, rates, and mechanisms. *Systematic Zoology*, 31, 376–399. <http://dx.doi.org/10.2307/2413365>
- Grant, T. (2002) Testing methods, the evaluation of discovery operations in evolutionary biology. *Cladistics*, 18, 94–111. <http://dx.doi.org/10.1111/j.1096-0031.2002.tb00142.x>
- Grant, T. & Kluge, A.G. (2003) Data exploration in phylogenetic inference, scientific, heuristic, or neither. *Cladistics*, 19, 379–418. <http://dx.doi.org/10.1111/j.1096-0031.2003.tb00311.x>
- Grant, T. & Kluge, A.G. (2004) Transformation series as an ideographic character concept. *Cladistics*, 20, 23–31. <http://dx.doi.org/10.1111/j.1096-0031.2004.00003.x>
- Grant, T. & Kluge, A.G. (2008a) Clade support measures and their adequacy. *Cladistics*, 24, 1051–1064. <http://dx.doi.org/10.1111/j.1096-0031.2008.00231.x>
- Grant, T. & Kluge, A.G. (2008b) Credit where credit is due: The Goodman-Bremer support metric. *Molecular Phylogenetics and Evolution*, 49, 405–406. <http://dx.doi.org/10.1016/j.ympev.2008.04.023>
- Grant T. & Kluge, A.G. (2009) Parsimony, explanatory power, and dynamic homology testing. *Systematics and Biodiversity*, 7, 357–363. <http://dx.doi.org/10.1017/s147720000999017x>
- Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, B.D., Noonan, B.P., Schargel, W. & Wheeler, W.C. (2006) Phylogenetic systematics of dart-poison frogs and their relatives (Anura, Athesphatanura, Dendrobatidae). *Bulletin of the American Museum of Natural History*, 299, 1–262. [http://dx.doi.org/10.1206/0003-0090\(2006\)299\[1:psodfa\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2006)299[1:psodfa]2.0.co;2)
- Haas, A. (2001) Mandibular arch musculature of anuran tadpoles, with comments on homologies of amphibian jaw muscles. *Journal of Morphology*, 247, 1–33. [http://dx.doi.org/10.1002/1097-4687\(200101\)247:1<1::aid-jmor1000>3.0.co;2-3](http://dx.doi.org/10.1002/1097-4687(200101)247:1<1::aid-jmor1000>3.0.co;2-3)
- Hacking, I. (1965) *The Logic of Statistical Inference*. Cambridge University Press, Cambridge, 244 pp. <http://dx.doi.org/10.2307/2271929>
- Haszprunar, G. (1998) Parsimony analysis as a specific kind of homology estimation and the implications for character weighting. *Molecular Phylogenetics and Evolution*, 9, 333–339. <http://dx.doi.org/10.1006/mpev.1998.0496>
- Hecht, M.K. & Edwards, J.L. (1976) The determination of parallel or monophyletic relationships, the proteid salamanders—a

- test case. *American Naturalist*, 653–677.
<http://dx.doi.org/10.1086/283096>
- Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008a) New World direct-developing frogs (Anura, Terrarana), molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737, 1–182.
- Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008b) A replacement name for *Isodactylus* Hedges, Duellman, and Heinicke, 2008. *Zootaxa*, 1795, 67–68.
- Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by oceanic dispersal. *Proceedings of the National Academy of Sciences, USA*, 104, 10092–10097.
<http://dx.doi.org/10.1073/pnas.0611051104>
- Heinicke, M.P., Duellman, W.E., Trueb, L., Means, D.B., MacCulloch, R.D. & Hedges, S.B. (2009) A new frog family (Anura, Terrarana) from South America and an expanded direct-developing clade revealed by molecular phylogeny. *Zootaxa*, 2211, 1–35.
- Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Chicago, 280 pp.
<http://dx.doi.org/10.1002/mmnd.19820290131>
- Hertz, A., Hauenschild, F., Lotzkat, S. & Köhler, G. (2012) A new golden frog species of the genus *Diasporus* (Amphibia, Eleutherodactylidae) from the Cordillera Central, western Panama. *ZooKeys*, 196, 23–46.
<http://dx.doi.org/10.3897/zookeys.196.2774>
- Heyer, W.R. (1975) A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. *Smithsonian Contributions to Zoology*, 199, 1–55.
<http://dx.doi.org/10.5479/si.00810282.199>
- Heyer, W.R. (1977) Taxonomic notes on frogs from the Madeira and Purus rivers, Brasil. *Papeis Avulsos de Zoologia*. São Paulo, 31, 141–162.
- Hickson, R.E., Simon, C. & Perrey, S.W. (2000) The performance of several multiple-sequence alignment programs in relation to secondary-structure features for an rRNA sequence. *Molecular Biology and Evolution*, 17, 530–539.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a026333>
- Hillis, D.M. (1995) Approaches for assessing phylogenetic accuracy. *Systematic Biology*, 44, 3–16.
<http://dx.doi.org/10.1093/sysbio/44.1.3>
- Ho, S.Y. (2009) An examination of phylogenetic models of substitution rate variation among lineages. *Biology Letters*, 5, 421–424.
<http://dx.doi.org/10.1098/rsbl.2008.0729>
- Ho, S.Y., Lanfear, R., Bromham, L., Phillips, M.J., Soubrier, J., Rodrigo, A.G. & Cooper, A. (2011) Time-dependent rates of molecular evolution. *Molecular Ecology*, 20, 3087–3101.
<http://dx.doi.org/10.1111/j.1365-294x.2011.05178.x>
- Hogeweg, P. & Hesper, B. (1984) The alignment of sets of sequences and the construction of phyletic trees, an integrated method. *Journal of Molecular Evolution*, 20, 175–186.
<http://dx.doi.org/10.1007/bf02257378>
- Holmes, S. (2003) Bootstrapping phylogenetic trees, theory and methods. *Statistical Science*, 18, 241–255.
<http://dx.doi.org/10.1214/ss/1063994979>
- Holder, M.T., Lewis, P.O. & Swofford, D.L. (2010) The Akaike information criterion will not choose the no common mechanism model. *Systematic Biology*, 59, 477–485.
<http://dx.doi.org/10.1093/sysbio/syq028>
- Hoogmoed, M.S. & Lescure, J. (1984) A new genus and two new species of minute leptodactylid frogs from northern South America, with comments upon *Phyzelaphryne* (Amphibia, Anura, Leptodactylidae). *Zoologische Mededelingen*, 58, 85–113.
- Huelsenbeck, J.P. (1995) Performance of phylogenetic methods in simulation. *Systematic Biology*, 44, 17–48.
<http://dx.doi.org/10.1093/sysbio/44.1.17>
- Huelsenbeck, J.P. & Crandall, K.A. (1997) Phylogeny estimation and hypothesis testing using maximum likelihood. *Annual Review of Ecology and Systematics*, 28, 437–466.
<http://dx.doi.org/10.1146/annurev.ecolsys.28.1.437>
- Huelsenbeck, J.P. & Rannala, B. (1997) Phylogenetic methods come of age: Testing hypotheses in an evolutionary context. *Science*, 276, 227–232.
<http://dx.doi.org/10.1126/science.276.5310.227>
- Huelsenbeck, J.P., Hillis, D.M. & Nielsen, R. (1996) A likelihood-ratio test of monophyly. *Systematic Biology*, 45, 546–558.
<http://dx.doi.org/10.1093/sysbio/45.4.546>
- Huelsenbeck, J.P., Alfaro, M.E. & Suchard, M.A. (2011) Biologically inspired phylogenetic models strongly outperform the No Common Mechanism model. *Systematic Biology*, 60, 225–232.
<http://dx.doi.org/10.1093/sysbio/syq089>
- ICZN (1999) *International Code of Zoological Nomenclature*. Fourth edition. International Trust for Zoological Nomenclature, London, U.K. Available from: <http://iczn.org/iczn/index.jsp> (accessed 6 May 2014)
- Izecksohn, E. (1971) Nôvo gênero e nova espécie de Brachycephalidae do Estado do Rio do Janeiro, Brazil. (Amphibia, Anura). *Boletim do Museu Nacional, Nova Série, Zoologia*, 280, 1–12.

- Izecksohn, E. (1988) Algumas considerações sobre o gênero *Euparkerella*, com a descrição de três novas espécies (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia*, 48, 59–74.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19, 101–108. <http://dx.doi.org/10.1016/j.tree.2003.10.013>
- Kaplan, M. (2002) Histology of the anteroventral part of the breast-shoulder apparatus of *Brachycephalus ephippium* (Brachycephalidae) with comments on the validity of the genus *Psyllophryne* (Brachycephalidae). *Amphibia-Reptilia*, 23, 225–227.
- Katoh, K., Kuma, K., Toh, H. & Miyata, T. (2005) MAFFT, a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30, 3059–3066. <http://dx.doi.org/10.1093/nar/gkf436>
- Kearney, M. (2002) Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. *Systematic Biology*, 51, 369–381. <http://dx.doi.org/10.1080/10635150252899824>
- Kelchner, S.A. & Thomas, M.A. (2007) Model use in phylogenetics, nine key questions. *Trends in Ecology and Evolution*, 22, 87–94. <http://dx.doi.org/10.1016/j.tree.2006.10.004>
- Kieswetter, C.M. & Schneider, C.J. (2013) Phylogeography in the northern Andes, complex history and cryptic diversity in a cloud forest frog, *Pristimantis w-nigrum* (Craugastoridae). *Molecular Phylogenetics and Evolution*, 69, 417–429. <http://dx.doi.org/10.1016/j.ympev.2013.08.007>
- Kim, J., Kim, I., Yang, J.S., Shin, Y.E., Hwang, J., Park, S., Choi, Y.S. & Kim, S. (2012) Rewiring of PDZ domain-ligand interaction network contributed to eukaryotic evolution. *PLoS Genetics*, 8, e1002510. <http://dx.doi.org/10.1371/journal.pgen.1002510>
- Kluge, A.G. (1999) The science of phylogenetic systematics, explanation, prediction, and test. *Cladistics*, 15, 429–436. <http://dx.doi.org/10.1006/clad.1999.0123>
- Kluge, A.G. (2001) Philosophical conjectures and their refutation. *Systematic Biology*, 50, 322–330. <http://dx.doi.org/10.1080/10635150119615>
- Kluge, A.G. (2009) Explanation and falsification in phylogenetic inference, exercises in Popperian philosophy. *Acta Biotheoretica*, 57, 171–186. <http://dx.doi.org/10.1007/s10441-009-9070-4>
- Kluge, A.G. & Farris, J.S. (1969) Quantitative phyletics and the evolution of anurans. *Systematic Zoology*, 18, 1–32. <http://dx.doi.org/10.2307/2412407>
- Kluge, A.G. & Kerfoot, W.C. (1973) The predictability and regularity of character divergence. *American Naturalist*, 107, 426–442. <http://dx.doi.org/10.1086/282844>
- Kluge, A.G. & Grant, T. (2006) From conviction to anti-superfluity, old and new justifications for parsimony in phylogenetic inference. *Cladistics*, 22, 276–288. <http://dx.doi.org/10.1111/j.1096-0031.2006.00100.x>
- Köhler, J. (2000) New species of *Eleutherodactylus* (Anura, Leptodactylidae) from cloud forest of Bolivia. *Copeia*, 2000, 516–520. [http://dx.doi.org/10.1643/0045-8511\(2000\)000\[0516:nsoeal\]2.0.co;2](http://dx.doi.org/10.1643/0045-8511(2000)000[0516:nsoeal]2.0.co;2)
- Kok, P.J.R. & Barrio-Amorós, C.L. (2013) On the taxonomic validity of *Pristimantis tepuiensis* (Schlüter & Rödder, 2007) and *P. stegolepis* (Schlüter & Rödder, 2007), with remarks on the type series of *P. guaiquinimensis* (Schlüter & Rödder, 2007). *Zootaxa*, 3694, 75–80. <http://dx.doi.org/10.11646/zootaxa.3694.1.6>
- Kolaczkowski, B. & Thornton, J.W. (2004) Performance of maximum parsimony and likelihood phylogenetics when evolution is heterogenous. *Nature*, 431, 980–984. <http://dx.doi.org/10.1038/nature02917>
- Kück, P., Mayer, C., Wägele, J.W. & Misof, B. (2012) Long branch effects distort maximum likelihood phylogenies in simulations despite selection of the correct model. *PLoS One*, 7 (5), e36593. <http://dx.doi.org/10.1371/journal.pone.0036593>
- Kuhn, T.S. (1962) *The Structure of Scientific Revolutions*. University of Chicago Press. Chicago, USA, 226 pp. <http://dx.doi.org/10.1086/674521>
- La Marca, E. (2007) Sinopsis taxonómica de dos géneros nuevos de anfibios (Anura, Leptodactylidae) de los Andes de Venezuela. *Herpetotropicos*, 3, 67–87.
- Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. (2012) PartitionFinder, combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. <http://dx.doi.org/10.1093/molbev/mss020>
- Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGgettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, 23, 2947–2948. <http://dx.doi.org/10.1093/bioinformatics/btm404>

- Laurent, R.F. (1980 "1979") Esquisse d'une phylogénie des Anoures. *Bulletin de la Société Zoologique de France*, 104, 397–422.
- Laurent, R.F. (1986) Sous classe des lissamphibiens (Lissamphibia). In: Grassé, P.-P. & Delsol, M. (Eds.), *Traité de Zoologie. Anatomie, Systematique, Biologie. Vol. 14. (Batraciens). Fascicule 1B*. Masson Paris, France, pp. 594–797.
- Le Quesne, W.J. (1974) The uniquely evolved character concept and its cladistic application. *Systematic Biology*, 23, 513–517. <http://dx.doi.org/10.2307/2412469>
- Leavitt, J.R., Hiatt, K.D., Whiting, M.F. & Song, H. (2013) Searching for the optimal data partitioning strategy in mitochondrial phylogenomics, a phylogeny of Acridoidea (Insecta, Orthoptera, Caelifera) as a case study. *Molecular Phylogenetics and Evolution*, 67, 494–508. <http://dx.doi.org/10.1016/j.ympev.2013.02.019>
- Lehr, E. (2007) New eleutherodactyline frogs (Leptodactylidae, *Pristimantis*, *Phrynobius*) from Peru. *Bulletin of the Museum of Comparative Zoology*, 159, 145–178. [http://dx.doi.org/10.3099/0027-4100\(2007\)159\[145:neflpp\]2.0.co;2](http://dx.doi.org/10.3099/0027-4100(2007)159[145:neflpp]2.0.co;2)
- Lehr, E., Fritzsch, G. & Müller, A. (2005) Analysis of Andes frogs (*Phrynobius*, Leptodactylidae, Anura) phylogeny based on 12S and 16S mitochondrial rDNA sequences. *Zoologica Scripta*, 34, 593–603. <http://dx.doi.org/10.1111/j.1463-6409.2005.00212.x>
- Lehr, E., Lundberg, M., Aguilar, C. & von May, R. (2006) New species of *Eleutherodactylus* (Anura, Leptodactylidae) from the eastern Andes of central Peru with comments on central Peruvian *Eleutherodactylus*. *Herpetological Monographs*, 20, 105–128. [http://dx.doi.org/10.1655/0733-1347\(2007\)20\[105:nsoeal\]2.0.co;2](http://dx.doi.org/10.1655/0733-1347(2007)20[105:nsoeal]2.0.co;2)
- Lehr, E., Torres-Gastello, C.P. & Suárez-Segovia, J. (2007) A new species of arboreal *Eleutherodactylus* (Anura, Leptodactylidae) from the Amazonian lowlands of central Peru. *Herpetologica*, 63, 94–99. [http://dx.doi.org/10.1655/0018-0831\(2007\)63\[94:ansoae\]2.0.co;2](http://dx.doi.org/10.1655/0018-0831(2007)63[94:ansoae]2.0.co;2)
- Lehr, E., Gregory, C. & Catenazzi, A. (2013) A new species of *Pristimantis* (Amphibia: Anura: Strabomantidae) from the Rio Abiseo National Park, Peru. *Zootaxa*, 3731, 201–211. <http://dx.doi.org/10.11646/zootaxa.3731.2.1>
- Lemmon, A.R. & Moriarty, E.C. (2004) The importance of proper model assumption in Bayesian phylogenetics. *Systematic Biology*, 53, 265–277. <http://dx.doi.org/10.1080/10635150490423520>
- Lemmon, A.R., Brown, J.M., Stanger-Hall, K. & Lemmon, E.M. (2009) The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and Bayesian inference. *Systematic Biology*, 58, 130–145. <http://dx.doi.org/10.1093/sysbio/syp017>
- Liu, K., Warnow, T.J., Holder, M.T., Nelesen, S.M., Yu, J., Stamatakis, A.P. & Linder, C.R. (2012) SATé-II, very fast and accurate simultaneous estimation of multiple sequence alignments and phylogenetic trees. *Systematic Biology*, 61, 90–106. <http://dx.doi.org/10.1093/sysbio/syr095>
- Liu, K., Raghavan, S., Nelesen, S., Linder, C.R. & Warnow, T. (2009) Rapid and accurate large-scale coestimation of sequence alignments and phylogenetic trees. *Science*, 324, 1561–1564. <http://dx.doi.org/10.1126/science.1171243>
- Li, C., Lu, G. & Ortí, G. (2008) Optimal data partitioning and a test case for ray-finned fishes (Actinopterygii) based on ten nuclear loci. *Systematic Biology*, 57, 519–539. <http://dx.doi.org/10.1080/10635150802206883>
- Löytynoja, A. & Goldman, N. (2008) Phylogeny-aware gap placement prevents errors in sequence alignment and evolutionary analysis. *Science*, 320, 1632–1635. <http://dx.doi.org/10.1126/science.1158395>
- Lutz, B. (1954) Anfíbios anuros do Distrito Federal. *Memórias do Instituto Oswaldo Cruz*, 52, 155–238. <http://dx.doi.org/10.1590/s0074-02761954000100009>
- Lynch, J.D. (1971) Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *University of Kansas Museum of Natural History, Miscellaneous Publications*, 53, 1–238. <http://dx.doi.org/10.2307/1442765>
- Lynch, J.D. (1973) A new narrow-toed frog from Andean Ecuador (Leptodactylidae, *Eleutherodactylus*). *Copeia*, 1973, 222–225. <http://dx.doi.org/10.2307/1442960>
- Lynch, J.D. (1974) New species of frogs (Leptodactylidae, *Eleutherodactylus*) from the Amazonian lowlands of Ecuador. *Occasional Papers of the Museum of Natural History, University of Kansas*, 31, 1–22.
- Lynch, J.D. (1975a) A review of the broad-headed eleutherodactyline frogs of South America. *Occasional Papers of the Museum of Natural History, University of Kansas*, 38, 1–46.
- Lynch, J.D. (1975b) A review of the Andean leptodactylid frog genus *Phrynobius*. *Occasional Papers of the Museum of Natural History, University of Kansas*, 35, 1–51.
- Lynch, J.D. (1976a) The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Occasional Papers of the Museum of Natural History, University of Kansas*, 61, 1–24.
- Lynch, J.D. (1976b) Two new species of frogs of the genus *Euparkerella* (Amphibia, Leptodactylidae) from Ecuador and Perú.

- Herpetologica*, 32, 48–53.
- Lynch, J.D. (1979) A new genus for *Elosia duidensis* Rivero (Amphibia, Leptodactylidae) from southern Venezuela. *American Museum Novitates*, 2680, 1–8.
- Lynch, J.D. (1986a) The definition of the Middle American clade of *Eleutherodactylus* based on jaw musculature (Amphibia, Leptodactylidae). *Herpetologica*, 42, 248–58.
- Lynch, J.D. (1986b) New species of minute leptodactylid frogs from the Andes of Ecuador and Peru. *Journal of Herpetology*, 20, 423–431.
<http://dx.doi.org/10.2307/1564505>
- Lynch, J.D. (1993) The value of *m. depresor mandibulae* in phylogenetic hypothesis for *Eleutherodactylus* and its allies (Amphibia, Leptodactylidae). *Herpetologica*, 49, 32–41.
- Lynch, J.D. (1997) Intrageneric relationships of mainland *Eleutherodactylus* II. A review of the *Eleutherodactylus sulcatus* group. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 21, 353–372.
- Lynch, J.D. (2000) The relationships of an ensemble of Guatemalan and Mexican frogs (*Eleutherodactylus*, Leptodactylidae, Amphibia). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 24, 129–156.
- Lynch, J.D. (2001) Three new rainfrogs of the *Eleutherodactylus diastema* group from Colombia and Panama. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 25, 287–297.
- Lynch, J.D. (2005) Discovery of the richest frog fauna in the world—an exploration of the forests to the north of Leticia. *Revista de la Academia Colombiana Ciencias*, 29, 581–588.
- Lynch, J.D. & Ruiz-Carranza, P.M. (1982) A new genus and species of poison-dart frog (Amphibia, Dendrobatidae) from the Andes of Northern Colombia. *Proceedings of the Biological Society of Washington*, 95, 557–562.
- Lynch, J.D. & Myers, C.W. (1983) Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocoan South America (Leptodactylidae). *Bulletin of the American Museum of Natural History*, 175, 481–572.
- Lynch, J.D. & McDiarmid, R.W. (1987) Two new species of *Eleutherodactylus* (Amphibia, Anura, Leptodactylidae) from Bolivia. *Proceedings of the Biological Society of Washington*, 100, 337–346.
<http://dx.doi.org/10.1163/156853897x00387>
- Lynch, J.D. & Duellman, W.E. (1997) Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador, systematics, ecology, and biogeography. *University of Kansas Natural History Museum Special Publications*, 23, 1–236.
<http://dx.doi.org/10.2307/1447320>
- Maciel, N., Vaz-Silva, W., de Oliveira, R.M. & Padial, J.M. (2012) A new species of *Pristimantis* (Anura, Strabomantidae) from the Brazilian Cerrado. *Zootaxa*, 3265, 43–56.
- Masuda, I., Matsuzaki, M. & Kita, K. (2010) Extensive frameshift at all AGG and CCC codons in the mitochondrial cytochrome c oxidase subunit 1 gene of *Perkinsus marinus* (Alveolata; Dinoflagellata). *Nucleic Acids Research*, 38, 6186–6194.
<http://dx.doi.org/10.1093/nar/gkq449>
- McGuire, J.A., Witt, C.C., Altshuler, D.L. & Remsen, J.V. (2007) Phylogenetic systematics and biogeography of hummingbirds, Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Systematic Biology*, 56, 837–856.
<http://dx.doi.org/10.1080/10635150701656360>
- Means, D.B. & Savage, J.M. (2007) Three new malodorous rainfrogs of the genus *Pristimantis* (Anura, Brachycephalidae) from the Wohomung Massif in west-central Guyana, South America. *Zootaxa*, 1638, 39–56.
- Meireles, C.M., Czelusniak, J., Schneider, M.P., Muniz, J.A., Brigido, M.C., Ferreira, H.S. & Goodman, M. (1999) Molecular phylogeny of ateline new world monkeys (Platyrrhini, Atelinae) based on gamma-globin gene sequences, evidence that *Brachyteles* is the sister group of *Lagothrix*. *Molecular Phylogenetics and Evolution*, 12, 10–30.
<http://dx.doi.org/10.1006/mpev.1998.0574>
- Moravec, J., Lehr, E., Perez-Peña, P.E., Lopez, J.J., Gagliardi-Urrutia, L.A.G. & Arista-Tuanama, I. (2010) A new green, arboreal species of *Pristimantis* (Anura, Strabomantidae) from Amazonian Peru. *Vertebrate Zoology*, 60, 225–232.
- Morrison, D.A. (2007) Increasing the efficiency of searches for the maximum likelihood tree in a phylogenetic analysis of up to 150 nucleotide sequences. *Systematic Biology*, 56, 988–1010.
<http://dx.doi.org/10.1080/10635150701779808>
- Morrison, D.A. & Ellis, J.T. (1997) Effects of nucleotide sequence alignment on phylogeny estimation, a case study of 18S rDNAs of *Apicomplexa*. *Molecular Biology and Evolution*, 14, 428–441.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a025779>
- Myers, C.W. & Ford, L.S. (1986) On *Atopophrynus*, a recently described frog wrongly assigned to the Dendrobatidae. *American Museum Novitates*, 2843, 1–15.
- Myers, C.W. & Donnelly, M.A. (1997) A tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil, Report from the Phipps Tapirapecó Expedition. *American Museum Novitates*, 3213, 1–71.
- Nadeau, N.J. & Jiggins, C.D. (2010) A golden age for evolutionary genetics? Genomic studies of adaptation in natural populations. *Trends in Genetics*, 26, 484–92.
<http://dx.doi.org/10.1016/j.tig.2010.08.004>
- Neff, N.A. (1986) A rational basis for a priori character weighting. *Systematic Biology*, 35, 110–123.
<http://dx.doi.org/10.2307/2413295>

- Noble, G.K. (1926) The hatching process in *Alytes*, *Eleutherodactylus* and other amphibians. *American Museum Novitates*, 229, 1–7.
- Novák, Á., Miklós, I., Lyngsø, R. & Hein, J. (2008) StatAlign, an extendable software package for joint Bayesian estimation of alignments and evolutionary trees. *Bioinformatics*, 24, 2403–2404.
<http://dx.doi.org/10.1093/bioinformatics/btn457>
- Nixon, K.C. (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15, 407–414.
<http://dx.doi.org/10.1006/clad.1999.0121>
- Ohler, A. & Dubois A. (2012) Validation of two familial nomina nuda of Amphibia Anura. *Alytes*, 28, 162–167.
- Oreskes N., Shrader-Frechette K. & Belitz K. (1994) Verification, validation, and confirmation of numerical models in the earth sciences. *Science*, 263, 641–646.
<http://dx.doi.org/10.1126/science.263.5147.641>
- Owen, R. (1843) *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals*. Longman, Brown, Green and Longmans, London, 392 pp.
- Padial, J.M. & de la Riva, I. (2009) Integrative taxonomy reveals cryptic Amazonian species of *Pristimantis* (Anura). *Zoological Journal of the Linnean Society*, 155, 97–122.
<http://dx.doi.org/10.1111/j.1096-3642.2008.00424.x>
- Padial, J.M., McDiarmid, R.W. & de la Riva, I. (2006) Distribution and morphological variation of *Eleutherodactylus mercedesae* Lynch and McDiarmid, 1987 (Amphibia, Anura, Leptodactylidae) with first record for Peru. *Zootaxa*, 1278, 49–56.
- Padial, J.M., Castroviejo-Fisher, S., Köhler, J., Domic, E. & de la Riva, I. (2007) Systematics of the *Eleutherodactylus fraudator* species group (Anura, Brachycephalidae). *Herpetological Monographs*, 21, 214–241.
<http://dx.doi.org/10.1655/06-007.1>
- Padial, J.M., Castroviejo-Fisher, S. & de la Riva, I. (2009) The phylogenetic relationships of *Yunganastes* revisited (Anura, Terrarana). *Molecular Phylogenetics and Evolution*, 52, 911–915.
<http://dx.doi.org/10.1016/j.ympev.2009.05.006>
- Padial, J.M., Chaparro, J.C., Castroviejo-Fisher, S., Guayasamín, J.M., Lehr, E., Delgado, A.J., Vaira, M., Teixeira, M. Jr., Aguayo, R. & de la Riva, I. (2012) A revision of species diversity in the Neotropical genus *Oreobates* (Anura, Strabomantidae), with the description of three new species from the Amazonian slopes of the Andes. *American Museum Novitates*, 3752, 1–55.
<http://dx.doi.org/10.1206/3752.2>
- Pereyra, M.O., Cardozo, D.E., Baldo, J., & Baldo, D. (2014) Description and phylogenetic position of a new species of *Oreobates* (Anura: Craugastoridae) from northwestern Argentina. *Herpetologica*, 70, 211–227.
<http://dx.doi.org/10.1655/HERPETOLOGICA-D-13-00072>
- Philippe, H., Zhou, Y., Brinkmann, H., Rodrigues, N. & Delsuc, F. (2005) Heterotachy and long-branch attraction in phylogenetics. *BMC Evolutionary Biology*, 5, 50.
<http://dx.doi.org/10.1186/1471-2148-5-50>
- Philippe, H., Brinkmann, H., Lavrov, D.V., Littlewood, D.T.J., Manuel, M., Wörheide, G. & Baurain, D. (2011) Resolving difficult phylogenetic questions, why more sequences are not enough. *PLoS Biology*, 9, e1000602.
<http://dx.doi.org/10.1371/journal.pbio.1000602>
- Pinto-Sánchez N.R., Ibáñez, R., Madriñán, S., Sanjur, O.I., Bermingham, E. & Crawford, A.J. (2012) The Great American Biotic Interchange in frogs, multiple and early colonization of Central America by the South American genus *Pristimantis* (Anura, Craugastoridae). *Molecular Phylogenetics and Evolution*, 62, 954–972.
<http://dx.doi.org/10.1016/j.ympev.2011.11.022>
- Pires, Jr. O.R., Sebben, A., Schwartz, E.N.F., Morales, R.A.V., Bloch Jr, C. & Schwartz, C.A. 2005. Further report of the occurrence of tetrodotoxin and new analogues in the anuran family Brachycephalidae. *Toxicon*, 45, 73–79.
<http://dx.doi.org/10.1016/j.toxicon.2004.09.016>
- Pol, D. & Siddall, M.E. (2001) Biases in maximum likelihood and parsimony, a simulation approach to a 10-taxon case. *Cladistics*, 17, 266–281.
<http://dx.doi.org/10.1111/j.1096-0031.2001.tb00123.x>
- Pombal, J.P. Jr. (1999) Oviposition and development of pumpkin toadlet, *Brachycephalus ephippium* (Spix) (Anura, Brachycephalidae). *Revista Brasileira de Zoologia*, 16, 967–976.
<http://dx.doi.org/10.1590/s0101-81751999000400004>
- Pombal, J.P. Jr. & Gasparini, J.L. (2006) A new *Brachycephalus* (Anura, Brachycephalidae) from the Atlantic Rainforest of Espírito Santo, southeastern Brazil. *South American Journal of Herpetology* 1, 87–93.
[http://dx.doi.org/10.2994/1808-9798\(2006\)1\[87:anbabf\]2.0.co;2](http://dx.doi.org/10.2994/1808-9798(2006)1[87:anbabf]2.0.co;2)
- Pombal, J.P. Jr. & Izecksohn, E. (2011) Uma nova espécie de *Brachycephalus* (Anura, Brachycephalidae). *Papéis Avulsos de Zoologia, São Paulo*, 51, 443–451.
<http://dx.doi.org/10.1590/s0031-10492007001300001>
- Popper, K. (1959) *The Logic of Scientific Discovery*. Routledge, London, 480 pp.
<http://dx.doi.org/10.1017/s0022481200053536>
- Popper, K. (1963) *Conjectures and Refutations*. Routledge, London, 680 pp.

- http://dx.doi.org/10.1063/1.3050617
- Popper, K. (1972) *Objective Knowledge, An Evolutionary Approach*. Oxford University Press, Oxford, 390 pp.
<http://dx.doi.org/10.1007/bf02381520>
- Popper, K. (1983) *Realism and the Aim of Science*. Routledge, London, 420 pp.
<http://dx.doi.org/10.1017/s0033291700051771>
- Posada, D. (2008) jModelTest, phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256.
<http://dx.doi.org/10.1093/molbev/msn083>
- Posada, D. & Crandall, K.A. (1998) Modeltest, testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
<http://dx.doi.org/10.1093/bioinformatics/14.9.817>
- Posada, D. & Buckley, T.R. (2004) Model selection and model averaging in phylogenetics, advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, 53, 793–808.
<http://dx.doi.org/10.1080/10635150490522304>
- Pyron, R.A. & Wiens, J.J. (2011) A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, 61, 543–583.
<http://dx.doi.org/10.1016/j.ympev.2011.06.012>
- Redelings, B.D. & Suchard, M.A. (2005) Joint Bayesian estimation of alignment and phylogeny. *Systematic Biology*, 54, 401–418.
<http://dx.doi.org/10.1080/10635150590947041>
- Ripplinger, J. & Sullivan, J. (2010) Assessment of substitution model adequacy using frequentist and Bayesian methods. *Molecular Biology and Evolution*, 27, 2790–2803.
<http://dx.doi.org/10.1093/molbev/msq168>
- Rivas, E. & Eddy, S.R. (2008) Probabilistic phylogenetic inference with insertions and deletions. *PLoS Computational Biology*, 4, e1000172.
<http://dx.doi.org/10.1371/journal.pcbi.1000172>
- Rodríguez, A., Poth, D., Schultz, S. & Vences, M. (2011) Discovery of skin alkaloids in a miniaturized eleutherodactylid frog from Cuba. *Biology Letters*, 7, 414–418.
<http://dx.doi.org/10.1098/rsbl.2010.0844>
- Rodríguez, A., Alonso, R., Rodríguez, J.A. & Vences, M. (2012) Geographic distribution, color variation and molecular diversity of miniature frogs of the *Eleutherodactylus limbatus* group from Cuba. *Salamandra*, 48, 71–91.
- Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L. & Bossuyt, F. (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 887–892.
<http://dx.doi.org/10.1073/pnas.0608378104>
- Rojas-Runjaic, F.J., Delgado, A. & Guayasamin, J.M. (2014) A new rainfrog of the *Pristimantis myersi* Group (Amphibia, Craugastoridae) from Volcán Pichincha, Ecuador. *Zootaxa*, 3780, 36–50.
- Russell, R.D. & Beckenbach, A.T. (2008) Recoding of translation in turtle mitochondrial genomes, programmed frameshift mutations and evidence of a modified genetic code. *Journal of Molecular Evolution*, 67, 682–695.
<http://dx.doi.org/10.1007/s00239-008-9179-0>
- Salter, L.A. (2001) Complexity of the likelihood surface for a large DNA dataset. *Systematic Biology*, 50, 970–978.
<http://dx.doi.org/10.1080/106351501753462902>
- Sampson, L.V. (1904) A contribution to the embryology of *Hylodes martinicensis*. *American Journal of Anatomy*, 3, 473–504.
<http://dx.doi.org/10.1002/aja.1000030404>
- Sanderson, M.J. & Kim, J. (2000) Parametric phylogenetics? *Systematic Biology*, 49, 817–829.
<http://dx.doi.org/10.1080/106351500750049860>
- Sankoff, D. (1975) Minimal mutation trees of sequences. *SIAM Journal on Applied Mathematics*, 28, 35–42.
<http://dx.doi.org/10.1137/0128004>
- Sankoff, D. & Rousseau, P. (1975) Locating the vertices of a Steiner tree in an arbitrary metric space. *Mathematical Programming*, 9, 240–246.
<http://dx.doi.org/10.1007/bf01681346>
- Sankoff, D. (2000) The early introduction of dynamic programming into computational biology. *Bioinformatics*, 16, 41–47.
<http://dx.doi.org/10.1093/bioinformatics/16.1.41>
- Sankoff, D., Morel, C. & Cedergren, R.J. (1973) Evolution of 5S RNA and the non-randomness of base replacement. *Nature*, 245, 232–234.
<http://dx.doi.org/10.1038/newbio245232a0>
- Sankoff, D., Cedergren, R.J. & Lapalme, G. (1976) Frequency of insertion-deletion, transversion, and transition in the evolution of 5S ribosomal RNA. *Journal of Molecular Evolution*, 7, 133–149.
<http://dx.doi.org/10.1007/bf01732471>
- Savage, J.M. (1987) Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia, Leptodactylidae). *Fieldiana Zoology*, 33, 1–57.
<http://dx.doi.org/10.5962/bhl.title.2871>
- Savage, J.M. (1997) A new species of rainfrog of the *Eleutherodactylus diastema* group from the Alta Talamanca region of

- Costa Rica. *Amphibia-Reptilia*, 18, 241–247.
<http://dx.doi.org/10.1163/156853897x00125>
- Savage, J.M. (2002) *The Amphibians and Reptiles of Costa Rica, A Herpetofauna Between Two Continents, Between Two Seas*. University of Chicago Press, Chicago, Illinois, 954 pp.
<http://dx.doi.org/10.1093/icb/42.5.1079>
- Schwartz, A. (1981) The herpetogeography of Hispaniola, West Indies. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 189, 86–127.
- Siddall, M.E. (1998) Success of parsimony in the four-taxon case, long-branch repulsion by likelihood in the Farris Zone. *Cladistics*, 14, 209–220.
- Siddall, M.E. (2010) Unringing a bell, metazoan phylogenomics and the partition bootstrap. *Cladistics*, 26, 444–452.
<http://dx.doi.org/10.1111/j.1096-0031.2009.00295.x>
- Siddall, M. & Kluge, A.G. (1997) Probabilism and phylogenetic inference. *Cladistics* 13, 313–336.
<http://dx.doi.org/10.1111/j.1096-0031.1997.tb00322.x>
- Siddall, M. & Kluge, A.G. (1999) Letter to the Editor. *Cladistics* 15, 439–440.
<http://dx.doi.org/10.1111/j.1096-0031.1999.tb00281.x>
- Simon, C., Frati, F., Beckenbach, A.T., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651–701.
- Simmons, M.P. (2004) Independence of alignment and tree search. *Molecular Phylogenetics and Evolution*, 31, 351–362.
<http://dx.doi.org/10.1016/j.ympev.2003.10.008>
- Simmons, M.P. (2012) Misleading results of likelihood-based phylogenetic analyses in the presence of missing data. *Cladistics*, 28, 208–222.
<http://dx.doi.org/10.1111/j.1096-0031.2011.00375.x>
- Simmons, M.P. & Goloboff, P.A. (2013) An artifact caused by undersampling optimal trees in supermatrix analyses of locally sampled characters. *Molecular Phylogenetics and Evolution*, 69, 265–275.
<http://dx.doi.org/10.1016/j.ympev.2013.06.001>
- Simmons, M.P. & Norton, A.P. (2013) Quantification and relative severity of inflated branch-support values generated by alternative methods, an empirical example. *Molecular Phylogenetics and Evolution*, 67, 277–296.
<http://dx.doi.org/10.1016/j.ympev.2013.01.020>
- Slowinski, J.B. (1998) The number of multiple alignments. *Molecular Phylogenetics and Evolution*, 10, 264.
<http://dx.doi.org/10.1006/mpev.1998.0522>
- Sober, E. (2004) The contest between parsimony and likelihood. *Systematic Biology*, 53, 644–653.
<http://dx.doi.org/10.1080/10635150490468657>
- Sokal, R.R. & Sneath, P.H.A. (1963) *Principles of Numerical Taxonomy*. W.H. Freeman, 573 pp.
<http://dx.doi.org/10.2307/2411834>
- Soltis, P.S. & Soltis, D.E. (2003) Applying the bootstrap in phylogeny reconstruction. *Statistical Science*, 18, 256–267.
<http://dx.doi.org/10.1214/ss/1063994980>
- Stamatakis, A. (2006) RAxML–VI–HPC, maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stamatakis, A. (2008) *The RAxML 7.0.4 Manual*. Department of Computer Science. Ludwig Maximilians Universität München, Munich, 25 pp.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology*, 57, 758–771.
<http://dx.doi.org/10.1080/10635150802429642>
- Steel, M. (2011) Can we avoid “SIN” in the house of “No Common Mechanism”? *Systematic Biology*, 60, 96–109.
<http://dx.doi.org/10.1093/sysbio/syq069>
- Streicher J.W., Crawford, A.J. & Edwards, C.W. (2009) Multilocus molecular phylogenetic analysis of the montane *Craugastor podicipinus* species complex (Anura, Craugastoridae) in Isthmian Central America. *Molecular Phylogenetics and Evolution*, 53, 620–630.
<http://dx.doi.org/10.1016/j.ympev.2009.07.011>
- Sullivan, J. & Joyce, P. (2005) Model selection in phylogenetics. *Annual Review of Ecology, Evolution, and Systematics*, 445–466.
<http://dx.doi.org/10.1146/annurev.ecolsys.36.102003.152633>
- Swofford D.L., Olsen G.J., Waddell P.J. & Hillis D.M. (1996) Phylogenetic inference. In: Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.), *Molecular Systematics*. Sinauer, Sunderland, pp. 407–514.
- Swofford, D.L., Waddell, P.J., Huelsenbeck, J.P., Foster, P.G., Lewis, P.O. & Rogers, J.S. (2001) Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. *Systematic Biology*, 50, 525–539.
<http://dx.doi.org/10.1080/106351501750435086>
- Swofford, D.L. & Maddison, W.P. (1992) Parsimony, character-state reconstructions, and evolutionary inferences. In: Mayden, R.L. (Ed.), *Systematics, Historical Ecology, and North American Freshwater Fishes*. Stanford University Press, Stanford,

- pp. 186–223.
- Taboada, C., Grant, T., Lynch, J.D. & Faivovich, J. (2013) New morphological synapomorphies for the new world direct-developing frogs (Amphibia, Anura, Terrarana). *Herpetologica*, 69, 342–357.
<http://dx.doi.org/10.1655/herpetologica-d-13-00019>
- Taleb, N.N. (2010) *The Black Swan, The Impact of the Highly Improbable*. Random House Trade Paperbacks, New York, 480 pp.
<http://dx.doi.org/10.1007/s11138-008-0051-7>
- Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24, 1596–1599.
<http://dx.doi.org/10.1093/molbev/msm092>
- Theissen, G. (2009) Saltational evolution: hopeful monsters are here to stay. *Theory in Biosciences*, 128, 43–51.
<http://dx.doi.org/10.1007/s12064-009-0058-z>
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W, improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
<http://dx.doi.org/10.1093/nar/22.22.4673>
- Tuffley, C. & Steel, M. (1997) Links between maximum likelihood and maximum parsimony under a simple model of substitution. *Bulletin of Mathematical Biology*, 59, 581–607.
<http://dx.doi.org/10.1007/bf02459467>
- Uy, J.A., Moyle, R.G., Filardi, C.E., Cheviron, Z.A. (2009) Difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor. *American Naturalist* 2009, 174, 244–254.
<http://dx.doi.org/10.1086/600084>
- Varon, A. & Wheeler, W.C. (2012) The tree alignment problem. *BMC Bioinformatics*, 13, 293.
<http://dx.doi.org/10.1186/1471-2105-13-293>
- Varón, A. & Wheeler, W.C. (2013) Local search for the generalized tree alignment. *BMC Bioinformatics*, 14, 66.
<http://dx.doi.org/10.1186/1471-2105-14-66>
- Varón, A., Vinh, L.S. & Wheeler, W.C. (2010) POY version 4, phylogenetic analysis using dynamic homologies. *Cladistics*, 26, 72–85.
<http://dx.doi.org/10.1111/j.1096-0031.2009.00282.x>
- Vogt, L. (2002) Testing and weighting characters. *Organisms Diversity & Evolution*, 2, 319–333.
<http://dx.doi.org/10.1078/1439-6092-00051>
- Wang, I.J., Crawford, A.J. & Bermingham, E. (2008) Phylogeography of the Pygmy Rain Frog (*Pristimantis ridens*) across the lowland tropical forests of Isthmian Central America. *Molecular Phylogenetics and Evolution*, 47, 992–1004.
<http://dx.doi.org/10.1016/j.ympev.2008.02.021>
- Wenzel, J.W. & Siddall, M.E. (1999) Noise. *Cladistics*, 15, 51–64.
<http://dx.doi.org/10.1111/j.1096-0031.1999.tb00394.x>
- Wetterbom, A., Sesov, M., Cavelier, L. & Bergström, T.F. (2006) Comparative genomic analysis of human and chimpanzee indicates a key role for indels in primate evolution. *Journal of Molecular Evolution*, 63, 682–690.
<http://dx.doi.org/10.1007/s00239-006-0045-7>
- Wheeler, W.C. (1994) Sources of ambiguity in nucleic acid sequence alignment. *Exs*, 69, 323.
http://dx.doi.org/10.1007/978-3-0348-7527-1_20
- Wheeler, W.C. (1996) Optimization alignment, the end of multiple sequence alignment in phylogenetics? *Cladistics*, 12, 1–10.
- Wheeler, W.C. (2001) Homology and the optimization of DNA sequence data. *Cladistics*, 17, 3–11.
- Wheeler, W.C. (2003) Implied alignment, a synapomorphy-based multiple sequence alignment method and its use in cladogram search. *Cladistics*, 19, 261–268.
<http://dx.doi.org/10.1111/j.1096-0031.2003.tb00369.x>
- Wheeler, W.C. (2006) Dynamic homology and the likelihood criterion. *Cladistics*, 22, 157–170.
<http://dx.doi.org/10.1111/j.1096-0031.2006.00096.x>
- Wheeler, W.C. (2007) The analysis of molecular sequences in large data sets, where should we put our effort? In: Hodkinson, T.R. & Parnell, J.A.N. (Eds.), *Reconstructing the Tree of Life, Taxonomy and Systematics of Species Rich Taxa*. Systematics Association, Oxford University Press, pp. 113–128.
<http://dx.doi.org/10.1201/9781420009538.ch8>
- Wheeler, W.C. (2010) Distinctions between optimal and expected support. *Cladistics*, 26, 657–663.
<http://dx.doi.org/10.1111/j.1096-0031.2010.00308.x>
- Wheeler, W.C. (2012) *Systematics, A Course of Lectures*. Wiley-Blackwell, Hoboken, New Jersey, 446 pp.
- Wheeler, W.C. & Gladstein, D.S. (1994) MALIGN, A multiple sequence alignment program. *Journal of Heredity*, 85, 417–418.
- Wheeler, W.C. & Giribet, G. (2009) Phylogenetic hypotheses and the utility of multiple sequence alignment. In: Rosenberg, M. (Ed.), *Sequence Alignment, Methods, Models, Concepts, and Strategies*. University of California Press, Berkeley, CA, pp 95–104.
<http://dx.doi.org/10.1525/california/9780520256972.003.0006>

- Wheeler, W.C. & Pickett, K.M. (2008) Topology-Bayes versus clade-Bayes in phylogenetic analysis. *Molecular Biology and Evolution*, 25, 447–453.
<http://dx.doi.org/10.1093/molbev/msm274>
- Wheeler, W.C., Gladstein, D. & De Laet, J. (1996–2003) *POY. Phylogeny Reconstruction via Optimization of DNA Data*. Ver. 3.0. Available from: <ftp://ftp.amnh.org/pub/molecular/poy> (accessed 6 June 2014)
- Wheeler, W.C., Arango, C.P., Grant, T., Janies, D., Varón, A., Aagesen, L., Faivovich, J., D'Haese, C., Smith, W.L. & Giribet, G. (2006) *Dynamic Homology and Phylogenetic Systematics, A Unified Approach Using POY*. American Museum of Natural History, New York, 365 pp.
- Whiting A.S., Sites Jr J.W., Pellegrino K.C.M. & Rodrigues M.T. (2006) Comparing alignment methods for inferring the history of the new world lizard genus *Mabuya* (Squamata: Scincidae). *Molecular Phylogenetics and Evolution*, 38, 719–730.
<http://dx.doi.org/10.1016/j.ympev.2005.11.011>
- Wiens, J.J., Fetzner, J.W., Parkinson, C.L. & Reeder, T.W. (2005) Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology*, 54, 719–748.
- Wiley, E.O. (1975) Karl R. Popper, systematics and classification, a reply to Walter Bock and other evolutionary taxonomists. *Systematic Zoology*, 24, 233–243.
<http://dx.doi.org/10.2307/2412764>
- Wilkinson, M., Thorley, J.L. & Upchurch, P. (2000) A chain is no stronger than its weakest link, double decay analysis of phylogenetic hypotheses. *Systematic Biology*, 49, 754–776.
<http://dx.doi.org/10.1080/106351500750049815>
- Wong, K.M., Suchard, M.A. & Huelsenbeck, J.P. (2008) Alignment uncertainty and genomic analysis. *Science*, 319, 473–476.
<http://dx.doi.org/10.1126/science.1151532>
- Xia, X., Xie, Z., Salemi, M., Chen, L. & Wang, Y. (2003) An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution*, 26, 1–7.
[http://dx.doi.org/10.1016/s1055-7903\(02\)00326-3](http://dx.doi.org/10.1016/s1055-7903(02)00326-3)
- Yue, F., Shi, J. & Tang, J. (2009) Simultaneous phylogeny reconstruction and multiple sequence alignment. *BMC Bioinformatics*, 10, S11.
<http://dx.doi.org/10.1186/1471-2105-10-s1-s11>
- Zhang, P., Liang, D., Mao, R.L., Hillis, D.M., Wake, D.B. & Cannatella, D.C. (2013) Efficient sequencing of anuran mtDNAs and a mitogenomic exploration of the phylogeny and evolution of frogs. *Molecular Biology and Evolution*, 30, 1899–1915.
<http://dx.doi.org/10.1093/molbev/mst091>
- Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Ph.D. Dissertation, The University of Texas at Austin, 115 pp.