

<http://dx.doi.org/10.11646/zootaxa.3835.1.2>  
<http://zoobank.org/urn:lsid:zoobank.org:pub:9618FFD9-B836-4450-9BF5-AA2815C8756B>

## Phylogenetic relationships of Semaphore geckos (Squamata: Sphaerodactylidae: *Pristurus*) with an assessment of the taxonomy of *Pristurus rupestris*

ARNAUD BADIANE<sup>1#</sup>, JOAN GARCIA-PORTE<sup>1#</sup>, JAN ČERVENKA<sup>2</sup>, LUKÁŠ KRATOCHVÍL<sup>2</sup>, ROBERTO SINDACO<sup>3</sup>, MICHAEL D. ROBINSON<sup>4</sup>, HERNAN MORALES<sup>5</sup>, TOMÁŠ MAZUCH<sup>6</sup>, THOMAS PRICE<sup>7</sup>, FÉLIX AMAT<sup>8</sup>, MOHAMMED Y. SHOBRAK<sup>9</sup>, THOMAS WILMS<sup>10</sup>, MARC SIMÓ-RIUDALBAS<sup>1</sup>, FARAHAM AHMADZADEH<sup>11</sup>, THEODORE J. PAPENFUSS<sup>12</sup>, ALEXANDRE CLUCHIER<sup>13</sup>, JULIEN VIGLIONE<sup>13</sup> & SALVADOR CARRANZA<sup>1,14</sup>

# Both authors contributed equally to this work

<sup>1</sup>Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37-49, 08003, Barcelona, Spain

<sup>2</sup>Faculty of Science, Charles University in Prague, Department of Ecology, Viničná 7, 128 44 Praha 2, Czech Republic

<sup>3</sup>Museo Civico di Storia Naturale, via San Francesco di Sales, 88 – 10022 Carmagnola (TO), Italy

<sup>4</sup>8935 E. Michigan Ave, Sun Lakes, AZ 85248, USA.

<sup>5</sup>School of Biological Sciences, Monash University, Australia

<sup>6</sup>Dříteč 65, 53305, Czech Republic

<sup>7</sup>St. Gallen, Switzerland

<sup>8</sup>Àrea d'Herpetologia, Museu de Granollers-Ciències Naturals, Francesc Macià 51, 08400 Granollers, Catalonia, Spain

<sup>9</sup>Biology department, Faculty of Science, Taif University 888, Taif, Saudi Arabia

<sup>10</sup>Zoologischer Garten Frankfurt, Bernhard-Grzimek-Allee 1, Frankfurt am Main, Germany

<sup>11</sup>Department of Biodiversity and Ecosystem Management, Environmental Sciences Research Institute, Shahid Beheshti University, Tehran, Iran

<sup>12</sup>Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

<sup>13</sup>ECO-MED, Tour Méditerranée, 65 avenue Jules Cantini, 13298 Marseille cedex 20, France

<sup>14</sup>Corresponding author. E-mail: salvador.carranza@ibe.upf.csic.es

### Abstract

A molecular phylogeny of the sphaerodactylid geckos of the genus *Pristurus* is inferred based on an alignment of 1845 base pairs (bp) of concatenated mitochondrial (*12S*) and nuclear (*acm4*, *cmos*, *rag1* and *rag2*) genes for 80 individuals, representing 18 of the 23–26 species, and the three subspecies of *P. rupestris*. The results indicate that *P. rupestris* is polyphyletic and includes two highly divergent clades: the eastern clade, found in coastal Iran and throughout the Hajar Mountain range in northern Oman and eastern UAE; and the western clade, distributed from central coastal Oman, through Yemen, Saudi Arabia and north to southern Jordan. Inferred haplotype networks for the four nuclear genes show that the eastern and western clades of “*P. rupestris*” are highly differentiated and do not share any alleles. Moreover, although the two clades are differentiated by a morphological multivariate analysis, no one character or set of characters was found to be diagnostic. Based on the molecular analysis of specimens from the type locality of *P. rupestris rupestris*, the name *P. rupestris* is applied to the eastern clade. The name that should apply to the western clade cannot be clarified until morphological and genetic data for “*P. rupestris*” is available from the vicinity of Bosaso, Somalia, and therefore we refer to it as *Pristurus* sp. 1. The phylogenetic tree of *Pristurus* supports the hypothesis that *P. celerrimus* is sister to all the other species in the analyses and that the Socotra Archipelago was independently colonized a minimum of two times.

**Key words:** gecko, Arabia, phylogeny, taxonomy, systematics, Socotra Archipelago, mitochondrial DNA, nuclear DNA.

### Introduction

The sphaerodactylid geckos of the genus *Pristurus* Rüppell, 1835, also known as Semaphore geckos, comprise 23–26 species (Arnold 2009; Sindaco & Jeremčenko 2008; Uetz 2013), characterized by being mostly diurnal,

species of the same genus now present in Samha, Darsa and Socotra Islands (which were merged into a single island during the sea level fluctuations that occurred during the Pleistocene). This is very unusual and contrasts with what has been found in other archipelagoes. For instance, in the Canary and Cape Verde Islands, species usually colonized one of the islands of the archipelago and, from there, spread to neighboring islands (Arnold *et al.* 2008; Carranza & Arnold 2006; Carranza *et al.* 1999, 2000, 2001; Maca-Meyer *et al.* 2003; Miralles *et al.* 2011; Vasconcelos *et al.* 2010). According to Arnold (2009), *P. obsti* and *P. samhaensis* are very similar in their morphology to *P. guichardi* and *P. sokotranus*, respectively. Our molecular data indicates that the two arboreal Socotran endemics, *P. obsti* and *P. guichardi*, are genetically well differentiated. Razzetti *et al.* (2011), state that these two species segregate altitudinally within Socotra Island, with *P. obsti* being distributed at lower altitudes than *P. guichardi*. The taxonomy of *P. sokotranus* is more complicated. According to our molecular results, including three specimens from three different localities within Socotra Island, *P. samhaensis* is more closely related to one of the specimens, making *P. sokotranus* paraphyletic. Analyses with more samples from across the distribution range of *P. sokotranus* and *P. samhaensis*, including their type localities will be necessary to clarify the taxonomy of these two species (work in progress).

Relationships between members of the subgenus *Spatialura* are very similar to those recovered by Papenfuss *et al.* (2009). In both phylogenies, *P. minimus* is sister to all the other members of *Spatialura* and *P. somalicus* and *P. crucifer* are sister taxa. Moreover, like the morphological phylogeny by Arnold (2009), our results support the close relationship between *P. carteri* and *P. collaris*. The nested position of *P. adrarensis* within the clade formed by the 12 species (Fig. 2), suggests that this 4700 km range extension occurred from east to west, after the first colonization of the Socotra Archipelago. However, until more samples are included in a calibrated phylogeny of the genus, we prefer not to hypothesize about the possible causes of the presence of this isolated species in Mauritania, or the biogeography and evolution of this interesting genus of diurnal geckos.

## Acknowledgements

We wish to thank Elena Gómez-Díaz, Margarita Metallinou, Philip de Pous, Jiří Šmíd, Raquel Vasconcelos, Ali Alghafri and Sultan Khalifa for assisting in sample collection in the field and to Josep Roca for laboratory assistance. Special thanks are due to Saleh Al Saadi, Mohammed Al Shariani, Thuraya Alsariri, Ali Alkiyumi, and the other members of the Nature Conservation Department of the Ministry of Environment and Climate, Sultanate of Oman for their help and support and for issuing all the necessary permits (Refs: 08/2005; 16/2008; 38/2010; 12/2011; 13/2013; 21/2013). We thank A. K. Nasher for support and Environment Protection Agency, Sana'a, Republic of Yemen for permits (Ref. 10/2007). We are thankful to the Deanship of academic research at Taif University for funding the sample collection in Saudi Arabia (Grant no. 1-433-2108). This work was supported by the project “Field study for the conservation of reptiles in Oman” funded by the Ministry of Environment and Climate Affairs (Ref: 22412027), and grant CGL2012-36970 from the Ministerio de Economía y Competitividad, Spain (co-funded by FEDER). Authors are members of the Grup de Recerca Emergent of the Generalitat de Catalunya: 2009SGR1462. J.G.P. was supported by a JAE predoctoral grant from the CSIC, Spain and MSR is funded by a FPI grant from the Ministerio de Economía y Competitividad, Spain (BES-2013-064248).

## References

- Abràmoff, M.D., Magalhaes, P.J. & Ram, S.J. (2004) Image Processing with ImageJ. *Biophotonics International*, 11, 36–42.
- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. & Csaki, F. (Eds.), *Information theory and an extension of the maximum likelihood principle*. Akadémiai Kiadó, Budapest, pp. 267–281.
- Al-Safadi, M.M. (1989) A new species of semaphore gecko (*Pristurus*: Gekkonidae) from Yemen Arab Republic. *Proceedings of the Egyptian Academy of Sciences*, 39, 9–15.
- Arnold, E.N. (1977) The scientific results of the Oman flora and fauna survey 1975. Little-known geckos (Reptilia: Gekkonidae) from Arabia with descriptions of two new species from the Sultanate of Oman. *Journal of Oman Studies Special Report*, 1, 81–110.

- Arnold, E.N. (1980) The scientific results of the Oman flora and fauna survey 1977 (Dhofar). The reptiles and amphibians of Dhofar, southern Arabia. *Journal of Oman Studies Special Report*, 2, 273–332.
- Arnold, E.N. (1982) A new semaphore gecko (*Pristurus*: Gekkonidae) and a new dwarf snake (*Eirenis*: Colubridae) from Southwestern Arabia. *Fauna of Saudi Arabia*, 4, 468–477.
- Arnold, E.N. (1986a) New species of semaphore gecko (*Pristurus*: Gekkonidae) from Arabia and Socotra. *Fauna of Saudi Arabia*, 8, 352–377
- Arnold, E.N. (1986b) A key and annotated checklist to the lizards and amphisbaenians of Arabia. *Fauna of Saudi Arabia*, 8, 385–435.
- Arnold, E.N. (1993) Historical changes in the ecology and behavior of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. *Journal of Zoology*, 229, 353–384.  
<http://dx.doi.org/10.1111/j.1469-7998.1993.tb02642.x>
- Arnold, E.N. (2009) Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology. *Zootaxa*, 2060, 1–21.
- Arnold, E.N., Vasconcelos, R., Harris, D.J., Mateo, J.A. & Carranza, S. (2008) Systematics, biogeography and evolution of the endemic *Hemidactylus* geckos (Reptilia, Squamata, Gekkonidae) of the Cape Verde Islands: based on morphology and mitochondrial and nuclear DNA sequences. *Zoologica Scripta*, 37, 619–636.  
<http://dx.doi.org/10.1111/j.1463-6409.2008.00351.x>
- Barata, M., Carranza, S. & Harris, D.J. (2012) Extreme genetic diversity in the lizard *Atlantolacerta andreanskyi* (Werner, 1929): a montane cryptic species complex. *BMC Evolutionary Biology*, 12, 167.  
<http://dx.doi.org/10.1186/1471-2148-12-167>
- Bauer, A.M., DeSilva, A., Greenbaum, E. & Jackman, T.R. (2007) A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe*, 83 (Supplement), 22–32.
- Blanford, W.T. (1874) Description of new lizards from Persia and Baluchistān. *Annals and Magazine of Natural History*, 13, 453–455.
- Blanford, W.T. (1881) Notes on the lizards collected in Socotra by Professor I. Bayley Balfour. *Proceedings of the Zoological Society of London*, 1881, 464–469.
- Boulenger, G.A. (1895) On the reptiles and batrachians obtained by Mr. E. Lort-Philips in Somaliland. *Annals and Magazine of Natural History*, 16, 165–169.
- Carranza, S. & Arnold, E.N. (2012) A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. *Zootaxa*, 3378, 1–95.
- Carranza, S. & Arnold, E.N. (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 38, 531–545.  
<http://dx.doi.org/10.1016/j.ympev.2005.07.012>
- Carranza, S., Arnold, E.N., Mateo, J.A. & López-Jurado, L.F. (2000) Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London, Series B*, 267, 637–649.  
<http://dx.doi.org/10.1098/rspb.2000.1050>
- Carranza, S., Arnold, E.N., Mateo, J.A. & López-Jurado, L.F. (2001) Parallel gigantism and complex colonization patterns in the Cape Verde scincid lizards *Mabuya* and *Macroscincus* (Reptilia: Scincidae) revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London, Series B*, 268, 1595–1603.  
<http://dx.doi.org/10.1098/rspb.2001.1699>
- Carranza, S., Arnold, E.N., Thomas, R.H., Mateo, J.A. & López-Jurado, L.F. (1999) Status of the extinct giant lacertid lizard *Gallotia simonyi simonyi* (Reptilia: Lacertidae) assessed using mtDNA sequences from museum specimens. *Herpetological Journal*, 9, 83–86.
- Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657.  
<http://dx.doi.org/10.1046/j.1365-294x.2000.01020.x>
- Drummond, A. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214.  
<http://dx.doi.org/10.1186/1471-2148-7-214>
- Felsenstein, J. (1985) Confidence-limits on phylogenies – an approach using the bootstrap. *Evolution*, 39, 783.  
<http://dx.doi.org/10.2307/2408678>
- Flot, J.F. (2010) seqphase: a web tool for interconverting phase input/output files and fasta sequence alignments. *Molecular Ecology Resources*, 10, 162–166.  
<http://dx.doi.org/10.1111/j.1755-0998.2009.02732.x>
- Fujita, M.K. & Papenfuss, T.J. (2011) Molecular systematics of *Stenodactylus* (Gekkonidae), an Afro-Arabian gecko species complex. *Molecular Phylogenetics and Evolution*, 58, 71–75.  
<http://dx.doi.org/10.1016/j.ympev.2010.10.014>
- Gamble, T., Bauer, A.M., Greenbaum, E. & Jackman, T.R. (2008) Evidence of Gondwanan vicariance in an ancient clade of geckos. *Journal of Biogeography*, 35, 88–104

- Gamble, T., Bauer, A.M., Colli, G.R., Greenbaum, E., Jackman, T.R., Vitt, L.J. & Simons, A.M. (2011) Coming to America: multiple origins of New World geckos. *Journal of Evolutionary Biology*, 24, 231–244.  
<http://dx.doi.org/10.1111/j.1420-9101.2010.02184.x>
- Gamble, T., Greenbaum, E., Jackman, T.R., Russell, A.P. & Bauer, A.M. (2012) Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.  
<http://dx.doi.org/10.1371/journal.pone.0039429>
- Geniez, P. & Arnold, E.N. (2006) A new species of semaphore gecko *Pristurus* (Squamata: Gekkonidae) from Mauretania, represents a 4700km range extension for genus. *Zootaxa*, 1317, 57–68.
- Gómez-Díaz, E., Sindaco, R., Pupin, F., Fasola, M. & Carranza, S. (2012) Origin and in situ diversification in *Hemidactylus* geckos of the Socotra Archipelago. *Molecular Ecology*, 21, 4074–4092.  
<http://dx.doi.org/10.1111/j.1365-294x.2012.05672.x>
- Gholamifard, A., Esmaeili, H.R. & Kami, H.G. (2009) First report of Blanford's semaphore gecko, *Pristurus rupestris* (Blanford 1874) (Sauria: Gekkonidae) in Fars Province, Iran. *Iranian Journal of Animal Biosystematics*, 5, 91–93.
- Gray, J.E. (1863) Description of new lizard obtained by Mr. Henry Carter on the south-east coast of Arabia. *Proceedings of the Zoological Society of London*, 1863, 236–237.
- Gvoždík, V., Moravec, J. & Kratochvíl, L. (2008) Geographic morphological variation in parapatric Western Palearctic tree frogs, *Hyla arborea* and *Hyla savignyi*: are related species similarly affected by climatic conditions? *Biological Journal of the Linnean Society*, 95, 539–556.  
<http://dx.doi.org/10.1111/j.1095-8312.2008.01056.x>
- Haas, G. (1943) On a collection of reptiles from Palestine, Transjordan and Sinai. *Copeia*, 1943, 10–15.  
<http://dx.doi.org/10.2307/1437872>
- Harrigan, R.J., Mazza, M.E. & Sorenson, M.D. (2008) Computation vs. cloning: evaluation of two methods for haplotype determination. *Molecular Ecology Resources*, 8, 1239–1248.  
<http://dx.doi.org/10.1111/j.1755-0998.2008.02241.x>
- Huelsenbeck, J.P. & Rannala, B. (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology*, 53, 904–913.  
<http://dx.doi.org/10.1080/10635150490522629>
- Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9, 286–298.  
<http://dx.doi.org/10.1093/bib/bbn013>
- Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X. & Wilson, A.C. (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA*, 86, 6196–6200.  
<http://dx.doi.org/10.1073/pnas.86.16.6196>
- Lanza, B. & Sassi, A.R. (1968) On a new genus and species of gekkonid lizard from Somalia. *Monitore Zoologico Italiano*, 2 (suplemento), 17–26.
- Leviton, A.E., Anderson, S.C., Adler, K. & Minton, S.A. (1992) *Handbook to Middle East amphibians and reptiles*. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, 252 pp.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. 10th Edition*. Laurentii Salvii, Holmiæ. 824 pp.
- Loveridge, A. (1947) Revision of the African lizards of the family Gekkonidae. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 98, 3–469.
- Maca-Meyer, N., Carranza, S., Rando, J.C., Arnold, E.N. & Cabrera, V.M. (2003) Status and relationships of the extinct giant Canary Island *Gallotia goliath* (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. *Biological Journal of the Linnean Society*, 80, 659–670.  
<http://dx.doi.org/10.1111/j.1095-8312.2003.00265.x>
- Mertens, R. (1970) Neues über einige Taxa der Geckonengattung *Phelsuma*. *Senckenbergiana biologica*, 51, 1–13.
- Metallinou, M., Arnold, E.N., Crochet, P.-A., Geniez, P., Brito, J.C., Lymberakis, P., Baha El Din, S., Sindaco, R., Robinson, M. & Carranza, S. (2012) Conquering the Sahara and Arabian deserts: Systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). *BMC Evolutionary Biology*, 12, 258.  
<http://dx.doi.org/10.1186/1471-2148-12-258>
- Metallinou, M. & Carranza, S. (2013) New species of *Stenodactylus* (Squamata: Gekkonidae) from the Sharqiyah Sands in northeastern Oman. *Zootaxa*, 3745 (4), 449–468.  
<http://dx.doi.org/10.11646/zootaxa.3745.4.3>
- Metallinou, M. & Crochet, P.-A. (2013) Nomenclature of African species of the genus *Stenodactylus* (Squamata: Gekkonidae). *Zootaxa*, 3691 (3), 365–376.  
<http://dx.doi.org/10.11646/zootaxa.3691.3.5>
- Miralles, A., Vasconcelos, R., Perera, A., Harris, D.J. & Carranza, S. (2011) An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). *Zoologica Scripta*, 40, 16–44.

- Oksanen, J., Blanchet, F.G, Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G. L., Solymos P., Stevens M.H.H. & Wagner H. (2013) Vegan: Community Ecology Package. R package version 2.0-7. Available from: <http://CRAN.R-project.org/package=vegan> (accessed 4 June 2014)
- Papenfuss, T.J., Jackman, T., Bauer, A., Stuart, B.L., Robinson, M.D., Parham, J.F. (2009) Phylogenetic relationships among species in the sphaerodactylid lizard genus *Pristurus*. *Proceedings of the California Academy of Sciences*, 60, 675–681.
- Parker, H.W. (1932) Two collection of amphibians and reptiles from British Somaliland. *Proceedings of the Zoological Society of London*, 1932, 335–367.
- Parker, H.W. (1938) A new gecko from Socotra. *Annals and Magazine of Natural History*, 1, 305–307.
- Peters, W. (1871) Über neue Reptilien aus Ostafrika und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genua. *Monatsberichte der Königlich Akademie der Wissenschaften zu Berlin*, 1871, 566–581.
- Posada, D. (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256.  
<http://dx.doi.org/10.1093/molbev/msn083>
- R Core Team (2013) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available from: <http://www.R-project.org/> (accessed 4 June 2014)
- Rambaut, A. & Drummond, A.J. (2007) Tracer v1. 4. Available from: <http://beast.bio.ed.ac.uk/> (accessed 1 July 2014)
- Razzetti, E., Sindaco, R., Grieco, C., Pella, F., Ziliani, U., Pupin, F., Riservato, E., Pellitteri-Rosa, D., Suleiman, A.S., Al-Aseily, B.A., Carugati, C., Boncompagni, E. & Fasola, M. (2011) Annotated checklist and distribution of the Socotran Archipelago Herpetofauna (Reptilia). *Zootaxa*, 2826, 1–44.
- Rösler, H., Köhler, J., Böhme, W. (2008) A new species of the diurnal gekkonid genus *Pristurus*, Rüppell, 1835 from the Red Sea island Hanish al-Kabir, Yemen. *Amphibia-Reptilia*, 29, 217–227.  
<http://dx.doi.org/10.1163/156853808784124983>
- Rösler, H. & Wranik, W. (1999) Beiträge zur Herpetologie der Republik Jemen. 5. Drei neue Gecko-Arten vom Sokotra-Archipel (Reptilia: Sauria: Gekkonidae). *Zoologische Abhandlungen Staatliches Museum für Tierkunde, Dresden*, 50, 249–265.
- Ross, W. (1990) Notes on the behaviour of *Pristurus rupestris* (Reptilia: Gekkonidae) with special reference to tail signaling. *Fauna of Saudi Arabia*, 11, 300–305.
- Rüppell, E. (1835) *Neue Wirbeltiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben. Amphibien*. S. Schmerber, Frankfurt A. M., 148 pp.
- Schärtti, B., & Gasperetti, J. (1994) A contribution to the herpetofauna of Southwest Arabia. *Fauna of Saudi Arabia*, 14, 348–423.
- Schmidt, K.P. (1852) Diagnoses of new amphibians and reptiles from Iran. *Natural History Miscellanea*, 93, 1–2.
- Sindaco, R. & Jeremčenko, V.K. (2008) *The reptiles of the Western Palearctic. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia*. Monografie della Societas Herpetologica Italica – I, 579 pp.
- Sindaco, R., Metallinou, M., Pupin, F., Fasola, M. & Carranza, S. (2012) Forgotten in the ocean: systematics, biogeography and evolution of the *Trachylepis* skinks of the Socotra Archipelago. *Zoologica Scripta*, 41, 346–362.  
<http://dx.doi.org/10.1111/j.1463-6409.2012.00540.x>
- Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Karim Naser, A. & Moravec, J. (2013a) Out of Arabia: A complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). *PLoS ONE*, 8, e64018.  
<http://dx.doi.org/10.1371/journal.pone.0064018>
- Šmíd, J., Moravec, J., Kratochvíl, L., Gvoždík, V., Karim Naser, A., Busais, S.M., Wilms, T., Shobrak, M.Y. & Carranza, S. (2013b) Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys*, 355, 79–107.  
<http://dx.doi.org/10.3897/zookeys.355.6190>
- Smith, S.A. & Dunn, C.W. (2007) Phyutility: a phyloinformatics tool for trees, alignments and molecular data. *Bioinformatics*, 24, 715–716.  
<http://dx.doi.org/10.1093/bioinformatics/btm619>
- 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>
- Steindachner, F. (1867) *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair (Zoologie)*. Vol. 1. Part 3. Reptilien. K. Gerold's Sohn/Kaiserlich-Königl. Hof- und Staatsdruckerei, Wien, pp.1–98. [1869 on title page]
- Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, 68, 978–989.  
<http://dx.doi.org/10.1086/319501>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using Maximum Likelihood, evolutionary distance, and Maximum Parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.  
<http://dx.doi.org/10.1093/molbev/msr121>

- Uetz, P. (2013) The Reptile Database. Available from: <http://www.reptile-database.org> (accessed 4 December 2013)
- Valenciennes, A. (1861) Notes sur les animaux d'Abysinie rapportés par M. Courbon. *Compte Rendu des Séances de l'Académie des Sciences*, 52, 433–434. [Paris]
- Vasconcelos, R., Carranza, S. & Harris, D.J. (2010) Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago. *Journal of Biogeography*, 37, 1047–1060.  
<http://dx.doi.org/10.1111/j.1365-2699.2009.02254.x>
- Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25, 361–371.  
[http://dx.doi.org/10.1016/s1055-7903\(02\)00244-0](http://dx.doi.org/10.1016/s1055-7903(02)00244-0)