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A taxonomic mystery for more than 150 years: Identity, systematic position and Malagasy origin of the snake *Elapotinus picteti* Jan, 1862, and synonymy of *Exallodontophis* Cadle, 1999 (Serpentes: Lamprophiidae)

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Abstract

Elapotinus picteti Jan, 1862 is an enigmatic snake taxon that has been described without locality data. Genus and species, both based on the unique holotype, were considered to belong to the venomous African Aparallactinae for more than a century, but although this taxon was never rediscovered it was accepted as a valid species until present. To clarify the taxonomic status of *E. picteti* its characters were compared with literature and determination keys for the whole world. This literature survey and the subsequent study of type specimens revealed that the monotypic *Elapotinus* is a subjective senior synonym of the monotypic Malagasy pseudoxyrhophiine snake genus *Exallodontophis* Cadle, 1999 which is characterized by its unique aglyphous dentition. We therefore transfer *Elapotinus* from the lamprophiid subfamily Aparallactinae to the subfamily Pseudoxyrhophiinae. Furthermore, *Elapotinus picteti* strongly resembles the Malagasy species *Exallodontophis albignaci* (Domergue, 1984) in external morphology, coloration and dentition. As a consequence we consider *Elapotinus picteti* a subjective senior synonym of *Exallodontophis albignaci*.

Key words: *Elapotinus picteti*, *Exallodontophis* **syn. nov.**, *Pararhadinaea albignaci* **syn. nov.**, Lamprophiidae, Aparallactinae, Pseudoxyrhophiinae, Madagascar, Africa, morphology, dentition, coloration, micro-computed tomography

Introduction

In 1862 Jan described the monotypic snake genus *Elapotinus* with the species *picteti* based on a single specimen without locality data (Jan 1862a, and reprint in the same year 1862b), which is still housed in the collection of the Muséum d'Histoire naturelle de Genève (MHNG). The description itself lacks an explanation for the species name “Picteti”, but it has been named almost certainly in honour of François Jules Pictet de la Rive (27 September 1809 –15 March 1872), professor of zoology, palaeontology, and comparative anatomy at the University of Genève, from whom Giorgio Jan received specimens for examination (Beolens *et al.* 2011, Weber pers. com. 2011). For his time the description was unusually comprehensive and Jan classified the species within his very diverse “Calamaridae” group. Later in 1863 Jan listed his new taxon again in the “Elenco”, the annotated checklist to the Iconografia Generale, a book with illustrations of snakes, where the holotype is pictured (Jan & Sordelli 1865: 13 Livr., pl. III, fig. 1). In the “Elenco” *Elapotinus* is listed as “Aglyphodonta” in the subfamily Elapomorphae as part of the family Calamaridae, whereas the remaining genera of the today Aparallactinae are mentioned under the group “Glyphodonta” of the Elapomorphae. In 1873 the new genus was listed in the Nomenclator Zoologicus (Marschall 1873). In his contribution to the Neotropical genus *Elapomorphus*, Strauch (1884) mentioned *Elapotinus picteti* in a footnote concerning the comparison of *Elapomorphus scalaris* [= *Xenopholis scalaris*] with *Elapotinus picteti*. Strauch emphasized that both have 17 dorsal scale rows but *Elapotinus* shows ungrooved

Elapotinus Picteti Jan, 1862a: 31–Jan 1862b: 31 (reprint of Jan 1862a); Jan 1863: 36; Troschel 1863: 634; Jan & Sordelli 1865: 13 Livr., pl. III, fig. 1; Strauch 1884: 548; Strauch 1888: 151; Anonymous 1889: 11; Hoffmann 1890: 1658.

Elapotinus picteti—Boulenger 1896: 245; Werner 1925: 153; Witte & Laurent 1947: 15; Mahnert 1976: 490; Welch 1982: 141; Ananjeva *et al.* 1988: 299; Williams & Wallach 1989: 54; Meirte 1992: 8, 53, 106, 122; Welch 1994: 59; Frank & Ramus 1995: 219; Schätti & Perret 1997: 368; Wallach 1998: 195; Mattison 1999: 160; Schätti *et al.* 2002: web site; Hutchins *et al.* 2003: 556; Wrobel 2004: 184; Brogard 2005: 123; Valli 2007: 89; Valenta 2010: 254; Beolens *et al.* 2011: 207; Uetz & Hallermann 2013: web site; Wallach *et al.* 2014: 261.

Pararhadinaea albignaci Domergue, 1984: 153—Glaw & Vences 1994: 335; Raxworthy & Nussbaum 1994a: 68, 1994b: 31; Wallach 1998: 195; Cadle 1999: 411; Mattison 1999: 168; Raselimanana *et al.* 2000: 162; Rakotomalala & Raselimanana 2003: 158, 167, 174, 187, 189, 193.

Exallodontophis Cadle, 1999: 414 (type species *Pararhadinaea albignaci* Domergue, 1984).—Zug, Vitt & Caldwell 2001: 526; Cadle 2003: 998, 1002; Glaw 2004: 21; Brogard 2005: 182; Lawson *et al.* 2005: 597; Glaw & Vences 2007: 430; Vidal *et al.* 2008: 52; D'Cruze *et al.* 2008: 50; Cadle 2009: 492; Zaher *et al.* 2009: 137; Nagy *et al.* 2012: 6, 8; Pyron *et al.* 2013a: 48; Pyron *et al.* 2013b: 972; Uetz & Hallermann 2013: web site; Wallach *et al.* 2014: 288.

Exallodontophis albignaci—Cadle 1999: 414; Cadle 2003: 1003; Hutchins *et al.* 2003: 560; Rakotomalala & Raselimanana 2003: 175; Raxworthy 2003: 944; Brogard 2005: 182; Glaw, Vences & Nussbaum 2005: 278; Rakotondravony 2006: 112, 118, 124, 125, 133, 139, 140; Glaw & Vences 2007: 430; Cundall & Irish 2008: 572, 639; D'Cruze *et al.* 2008: 50; Franzen *et al.* 2009: 178; Durkin *et al.* 2011: 216; Nagy *et al.* 2012: fig. S2, S3, S4, Tab. S1; Uetz & Hallermann 2013: website; Wallach *et al.* 2014: 289.

Pictures are published in: *Elapotinus picteti* —Jan 1862b: pl. e; Jan & Sordelli 1865: 13 Livr., pl. III, fig. 1; Witte & Laurent 1947: 15; *Pararhadinaea albignaci*—Domergue 1984: 154, 155; Raxworthy & Nussbaum 1994b: 32; *Exallodontophis albignaci*—Cadle 1999: 412, 413, 429; Glaw & Vences 2007: 431.

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References

- Ananjeva, N.B., Borkin, L.Y., Darevsky, I.S. & Orlov, N.L. (1988) *Dictionary of animal names in five languages. Amphibians and reptiles. Latin, Russian, English, German, French.* Russky Yazyk Publishers, Moscow, 556 pp.
- Anonymous (1889) *Jahresbericht des Naturhistorischen Museums in Lübeck für das Jahr 1888.* Rathgens, Lübeck, 14 pp.
- Beolens, B., Watkins, M. & Grayson, M. (2011) *The eponym dictionary of reptiles.* The John Hopkins University Press, Baltimore, xvi + 296 pp.

- Boettger, O. (1898) *Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main. II. Teil (Schlangen)*. Gebrüder Knauer, Frankfurt a. Main, 160 pp.
- Bogert, C.M. (1940) Herpetological results of the Vernay Angola Expedition. Part I. Snakes including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History*, 77, 1–107, 1 pl.
- Boulenger, G.A. (1893) *Catalogue of the snakes in the British Museum (Natural History). Vol. I, containing the families Typhlopidae, Glauconidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae, and Colubridae Aglyphae, part*. Trustees of the British Museum (Natural History), London, xiii + 448, pls. 1–28.
- Boulenger, G.A. (1894) *Catalogue of the snakes in the British Museum (Natural History). Vol. II. Containing the conclusion of the Colubridae Aglyphae*. Trustees of the British Museum (Natural History), London, xi + 382 pp., pls. 1–20.
- Boulenger, G.A. (1896) *Catalogue of the snakes in the British Museum (Natural History). Vol. III. Containing the Colubridae (Opisthoglyphae and Protoglyphae), Amblycephalidae, and Viperidae*. Trustees of the British Museum (Natural History), London, xiv + 727 pp., pls. 1–25.
- Boulenger, G.A. (1903) Reptilia and Batrachia. *The Zoological Record* 1902, 39, 1–32.
- Bourgeois, M. (1968) Contribution à la morphologie comparée du crâne des ophidiens de l'Afrique Centrale. *Publications de l'Université Officielle du Congo à Lubumbashi*, 18, 1–293, 2 tab.
- Branch, B. (2003) African burrowing snakes (Atractaspididae). In: Hutchins, M., Murphy, J.B. & Schlager, N. (Eds.), *Grzimek's animal life encyclopedia. 2nd Edition. Vol. 7. Reptiles*. Gale, Farmington Hill, pp. 461–464.
- Broadley, D.G. (1971) Revision of the African snake genera *Amblyodipsas* and *Xenocalamus* (Colubridae). *Occasional Papers of the National Museum Rhodesia*, B4 (33), 629–697.
- Brogard, J. (2005) *Inventaire zoogéographique des reptiles – Zoogeographical checklist of reptiles. Vol. 1. Région afrotrropicale et région paléarctique – Afrotrropical and paleartic realms*. Jacques Brogard, France, 301 pp.
- Cadle, J.E. (1999) The dentition, systematics, and phylogeny of *Pseudoxyrhopus* and related genera from Madagascar (Serpentes: Colubridae), with description of a new species and a new genus. *Bulletin of the Museum of Comparative Zoology*, 155 (8), 381–443.
- Cadle, J.E. (2003) Colubridae, snakes. In: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago and London, pp. 997–1004.
- Cadle, J.E. (2009) Sexual dimorphism and reproductive biology in the Malagasy snake genus *Liopholidophis* (Lamprophiidae: Pseudoxyrhophiinae). *Proceedings of the California Academy of Sciences*, Series 4, 60, 461–502.
- Cadle, J.E. & Ineich, I. (2008) Nomenclatural status of the Malagasy snake genus *Bibilava* Glaw, Nagy, Franzen & Vences (2007) Resurrection of *Thamnosophis* Jan and designation of a lectotype for *Leptophis lateralis* Duméril, Bibron, and Duméril (Serpentes: Colubridae). *Herpetological Review*, 39 (3), 285–288.
- Carus, J.V. (1868–1875) *Handbuch der Zoologie. Erster Band. Wirbelthiere, Mollusken und Molluscoiden*. Wilhelm Engelmann, Leipzig, x + 894 pp.
- Cogger, H.G. (2000) *Reptiles & Amphibians of Australia*. Ralph Curtis Books, Sanibel Island, FL., 808 pp.
- Cope, E.D. (1863) On Part II. of Prof. G. Jan's Prodrómo della Iconografia Generale degli ofidi. *The American Journal of Science and Arts*, Series 2, 35 (105), 455–458.
- Cundall, D. & Irish, F. (2008) The snake skull. In: Gans, C., Gaunt, A.S. & Adler, K. (Eds.), *Biology of the Reptilia. Vol. 20. Morphology H. The skull of Lepidosauria*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA, pp. 349–692.
- David, P. & Ineich, I. (1999) Les serpents venimeux du monde: systématique et répartition. *Dumerilia*, 3, 3–499.
- D'Cruze, N., Köhler, J., Franzen, M. & Glaw, F. (2008) A conservation assessment of the amphibians and reptiles of the Forêt d'Ambre Special Reserve, North Madagascar. *Madagascar Conservation & Development*, 3 (1), 44–54.
<http://dx.doi.org/10.4314/mcd.v3i1.44136>
- de Rooij, N. (1917) *The reptiles of the Indo-Australian Archipelago. II. Ophidia*. E. J. Brill Ltd., Leiden, xiv + 331 pp.
- Ditmars, R.L. (1926) *Reptiles of the World: Tortoises and turtles, crocodilians, lizards and snakes of the eastern and western hemisphere*. The Macmillan Company, New York, Xi + [9 unpaginated] + 373, 89 pls.
- Domergue, C.A. (1984) Notes sur les serpents de la région malgache IV. Le genre *Pararhadinaea* Boettger, 1898. Descriptions d'une espèce et d'une sous- espèce nouvelles. *Bulletin du Muséum national d'Histoire naturelle*, Series 4, 6, 149–157.
- Dowling, H.G. (1951a) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1 (5), 97–99.
- Dowling, H.G. (1951b) A proposed method of expressing scale reductions in snakes. *Copeia*, 1951 (2), 131–134.
- Dowling, H.G. & Savage, J.M. (1960) A guide to the snakes hemipenis: a survey of basic structure and systematic characteristics. *Zoologica*, 45 (2), 17–28, pls 1–3.
- Durkin, L., Steer, M.D. & Belle, E.M.S. (2011) Herpetological surveys of forest fragments between Montagne d'Ambre National Park and Ankarana Special Reserve, northern Madagascar. *Herpetological Conservation and Biology*, 6 (1), 114–126.
- Ernst, C.J. & Ernst, E.M. (2003) *Snakes of the United States and Canada*. Smithsonian Institution Press, Washington, 680 pp.
- Frank, N. & Ramus, E. (1995) *A complete guide to scientific and common names of reptiles and amphibians of the world*. N G Publishing, Pottsville, 377 pp.
- Franzen, M., Jones, J., Raselimanana, A.P., Nagy, Z.T., D'Cruze, N., Glaw, F. & Vences, M. (2009) A new black-bellied snake (Pseudoxyrhophiinae: *Liophidium*) from western Madagascar, with notes on the genus *Pararhadinaea*. *Amphibia-Reptilia*,

30, 173–183.

<http://dx.doi.org/10.1163/156853809788201171>

- Glaw, F. (2004) Die Herpetofauna Madagaskars: Vielfalt, Lebensweise und Gefährdung. *Draco*, 5 (19), 4–21.
- Glaw, F., Nagy, Z.T., Franzen, M. & Vences, M. (2007) Molecular phylogeny and systematics of the pseudoxyrhophiine snake genus *Liopholidophis* (Reptilia, Colubridae): evolution of its exceptional sexual dimorphism and descriptions of new taxa. *Zoologica Scripta*, 36, 291–300.
<http://dx.doi.org/10.1111/j.1463-6409.2007.00278.x>
- Glaw, F. & Vences, M. (1994) *A fieldguide to the amphibians and reptiles of Madagascar. 2nd Edition*. Vences & Glaw Verlag, Cologne, 480 pp., 48 pls.
- Glaw, F. & Vences, M. (2007) *A field guide to the amphibians and reptiles of Madagascar. 3rd Edition*. Vences & Glaw Verlag, Cologne, 496 pp.
- Glaw, F., Vences, M. & Nussbaum, R.A. (2005) A new species of *Heteroliodon* (Reptilia: Squamata: Colubridae) from Montagne des Français, far northern Madagascar. *Herpetologica*, 61 (3), 275–280.
<http://dx.doi.org/10.1655/01-101.1>
- Golvan, Y.-J. (1965) *Répertoire des noms de genres de Vertébrés*. Masson et C^{ie}, Paris, [4 unpag.] + 3 “Errata” + [4 unpag.] + 383 pp.
- Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchie, G., Benavides, M.A., Zhang, Y.-P. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 28, 437–459.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00393.x>
- Hoffmann, C.K. (1890) *Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild; Sechster Band, III. Abtheilung, Reptilien, III. Schlangen und Entwicklungsgeschichte der Reptilien*. C. F. Winter'sche Verlagshandlung, Leipzig, 689 pp. [1401–2089], 63 pl. [CVIII–CLXX].
- Hutchins, M., Murphy, J.B. & Schlager, N. (2003) Reptiles species list. In: Hutchins, M., Murphy, J.B. & Schlager, N. (Eds.), *Grzimek's animal life encyclopedia. 2nd 2nd Edition. Vol. 7. Reptiles*. Gale, Farmington Hill, pp. 520–570.
- Jäger, G. (1883) *Handwörterbuch der Zoologie, Anthropologie und Ethnologie. 2. Band. Caayguas – Elomys*. Eduard Trewendt, Breslau, 544 pp.
- Jan, G. (1862a) Enumerazione sistematica delle specie d'ofidi del gruppo Calamaridae. *Archivio per la zoologia l'anatomia e la fisiologia*, 2 (1), 1–76, + 2 pl.
- Jan, G. (1862b) *Prodromo dell' Iconografia generale degli ofidi. II. parte. V. Gruppo: Calamaridae*. R. I. de' Sordo-Muti, Genova, xii + 76 + 7 pl. [reprint of Jan (1862a)]
- Jan, G. (1863) *Elenco sistematico degli ofidi decritti e disegnati per l'Iconografia generale*. A. Lombardi, Milano, viii + 9–143 pp.
- Jan, G. & Sordelli, F. (1860–1881) *Iconographie générale des ophiidiens. Vol. 1. –3. Livr. 1 – 50*. Jan & Sordelli, Milan, 300 pls.
- Kelly, C.M.R., Barker, N.P., Villet, M.H. & Broadley, D.G. (2009) Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics*, 25, 38–63.
<http://dx.doi.org/10.1111/j.1096-0031.2008.00237.x>
- Knauer, F. (1887) *Handwörterbuch der Zoologie*. Verlag Ferdinand Enke, Stuttgart, xiv + 828 pp., 9 pls.
- Lawson, R., Slowinski, J.B., Crother, B.J. & Burbrink, F.T. (2005) Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, 37, 581–601.
<http://dx.doi.org/10.1016/j.ympev.2005.07.016>
- 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, Athens, OH, vii + 252 pp., pl. 1–33.
- Mahnert, V. (1976) Catalogue des types de poissons, amphibiens et reptiles du Muséum d'Histoire naturelle de Genève. *Revue Suisse de Zoologie*, 83 (2), 471–496.
- Manthey, U. & Grossmann, W. (1997) *Amphibien & Reptilien Südasiens*. NTV, Münster, 512 pp.
- Marschall, de A. (Ed.) (1873) *Nomenclator Zoologicus: continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum disposita*. Typis Caroli Ueberreuter (M. Salzer), Vindobonae, vi + 482 pp.
- Master, F.J. (2008) *Snakes to Simillimum. Demystifying Venoms*. Archibel S.A., Isnes, Belgium, xx + 812 pp.
- Mattison, C. (1999) *Die Schlangen Enzyklopädie: Alle Arten der Welt*. BLV Verlagsgesellschaft, München, Wien, Zürich, 192 pp.
- Meirte, D. (1992) Clés de détermination des serpents d'Afrique. *Annales du Musée royal de l'Afrique centrale, sciences Zoologiques*, 267, 1–152.
- Mosmann, M.N. (2001) *Guia das Principais Serpentes do Mundo. Vol. 2*. Editora da Ulbra, Canoas, 367 pp.
- Nagy, Z.T., Sonet, G., Glaw, F. & Vences, M. (2012) First large-scale DNA barcoding assessment of reptiles in the biodiversity hotspot of Madagascar, based on newly designed COI primers. *PLoS ONE*, 7, e34506.
<http://dx.doi.org/10.1371/journal.pone.0034506>
- Noguchi, H. (1909) *Snake venoms. An investigation of venomous snakes with special reference to the phenomena of their venoms*. Carnegie Institution of Washington, Washington, xvii + [2 unpaginated] + 315 pp.
- Nopcsa, F. (1928) The genera of reptiles. *Palaeobiologica*, 1, 163–188.
- O'Shea, M. (1996) *A guide to the snakes of Papua New Guinea*. Independent Publ., Independent Group Pty Ltd., Port Moresby,

xii + 239 pp.

- Peters, J.A. & Orejas-Miranda, B. (1986) *Catalogue of Neotropical Squamata. Part I. Snakes. With new material by P. E. Vanzolini*. Smithsonian Institution Press, Washington, viii + 347 pp.
- Phelps, T. (1981) *Poisonous snakes*. Blandford Press, Poole, Dorset, viii + 237 pp.
- Phisalix, M. (1922) *Animaux venimeux et venins. Tome second*. Masson & C^{ie}, Paris, 864 pp.
- Pyron, R.A., Burbrink, F.T., Colli, G.R., Montes de Oca, A.N., Vitt, L.J., Kuczynski, C.A. & Wiens, J.J. (2011) The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution*, 58, 329–342.
<http://dx.doi.org/10.1016/j.ympev.2010.11.006>
- Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013a) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13 (93), 1–53.
<http://dx.doi.org/10.1186/1471-2148-13-93>
- Pyron, R.A., Kandambi, H.K.D., Hendry, C.R., Pushpamal, V., Burbrink, F.T. & Somaweera, R. (2013b) Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Molecular Phylogenetics and Evolution*, 66, 969–978.
<http://dx.doi.org/10.1016/j.ympev.2012.12.004>
- Rakotomalala, D. & Raselimanana, A. (2003) Les amphibiens et les reptiles des massifs de Marojejy, d'Anjanaharibe-Sud et du couloir forestier de Betaolana. In: Goodman, S.M. & Wilmé, L. (Eds.), *Nouveaux résultats d'inventaires biologiques faisant référence à l'altitude dans la région des massifs montagneux de Marojejy et d'Anjanaharibe-Sud.. Recherches pour le Développement, Série Sciences Biologiques*, 19, 147–202.
- Rakotondravy, H.A. (2006) Patterns de la diversité des reptiles et amphibiens de la région de Loky-Manambato. In: Goodman, S.M. & Wilmé, L. (Eds.), *Inventaires de la faune et de la flore du nord de Madagascar dans la région Loky-Manambato, Analamerana et Andavakoera. Recherches pour le Développement, Série Sciences Biologiques*, 23, 101–148.
- Raselimanana, A.P., Raxworthy, C.J. & Nussbaum, R.A. (2000) Herpetofaunal species diversity and elevational distribution within the Parc National de Marojejy. *Fieldiana Zoology, New Series*, 97, 157–174.
- Raxworthy, C.J. (2003) Introduction to the reptiles. In: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago and London, pp. 934–949.
- Raxworthy, C.J. & Nussbaum, R.A. (1994a) A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation*, 69, 65–73.
- Raxworthy, C.J. & Nussbaum, R.A. (1994b) A review of the Madagascan snake genera *Pseudoxyrhopus*, *Pararhadinaea*, and *Heteroliodon* (Squamata: Colubridae). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 182, v + 1–37.
- Romer, A.S. (1956) *Osteology of the reptiles*. The University of Chicago Press, Chicago, Illinois, xxi + 772 pp.
- Romer, A.S. (1997) *Osteology of the reptiles. Reprint edition*. Krieger Publishing Company, Malabar, Florida, xxviii + 772 pp.
- Ruthensteiner, B. & Heß, M. (2008) Embedding 3D models of biological specimens in PDF publications. *Microscopy Research and Technique*, 71, 778–786.
<http://dx.doi.org/10.1002/jemt.20618>
- Schätti, B. & Perret, J.L. (1997) Catalogue révisé des types d'amphibiens et de reptiles du Muséum d'Histoire naturelle de Genève. *Revue Suisse de Zoologie*, 104 (2), 357–370.
- Schätti, B., Perret, J.-L. & Mariaux, J. (2002) Catalogue commenté des types d'amphibiens et de reptiles du Muséum d'histoire naturelle Genève. Available from: <http://www.ville-ge.ch/mhng/erpi/cat1.html> (accessed 11 June 2014)
- Schulze, F.E., Kükenthal, W. & Heider, K. (1928) *Nomenclator animalium generum et subgenerum. 2. Band, 9. Lieferung (Derot.-Electre.)*. Verlag der Preußischen Akademie der Wissenschaften, Berlin, 160 pp. [957–1116]
- Scudder, S.H. (1882) *Nomenclator Zoologicus. An alphabetical list. II. Universal Index*. Smithsonian Institution, Washington, 340 pp.
- Sedgwick, A. (1932) *A student's textbook of Zoology. Vol. II. Chordata to mammalian. 2nd Edition*. George Allen & Unwin Ltd., London, xvi + 705 pp.
- Senna, A. (1886) Sulla distribuzione geografica generale degli ofidi. *Atti della Società Italiana di Scienze Naturali*, 29 (4), 477–516.
- Smith, H.M. & Taylor, E.H. (1945) An annotated checklist and key to the snakes of Mexico. *Bulletin of the United States National Museum*, 187, 1–239.
<http://dx.doi.org/10.5479/si.03629236.187.1>
- Smith, M.A. (1943) *The fauna of British India, Ceylon and, Burma, including the whole of the Indo-Chinese subregion. Reptilia and Amphibia. Vol. III. Serpentes*. Francis & Taylor, London, xii + 583 pp.
- Strauch, A. (1884) Bemerkungen über die Schlangengattung *Elapomorphus* aus der Familie der Calamariden. *Bulletin de l'Académie impériale des sciences de St.-Petersbourg*, 29, 541–590.
- Strauch, A. (1888) Bemerkungen über die Schlangengattung *Elapomorphus* aus der Familie der Calamariden. *Mélanges biologiques tirés du Bulletin de l'Académie impériale des sciences de St.-Petersbourg*, 12, 141–211.
- Szczerbak, N. (2003) *Guide to the reptiles of the Eastern Palearctic*. Krieger Publishing Company Melbourne, FL., 260 pp. [+ 72 unpaginated pages with plates]
- Szyndlar, Z. (1981) Nieznane węże jadowite [Unknown venomous snakes]. *Kosmos, Seria A Biologia*, 30 (3), 259–269. [in

Polish]

- Taylor, E.H. (1922) *Snakes of the Philippine Islands*. Department of Agriculture and Natural resources, Bureau of Science, Publ. no. 16, Manila, 312 pp.
- Taylor, E.H. (1965) The serpents of Thailand and adjacent waters. *University of Kansas Science Bulletin*, 45 (9), 609–1096.
- Troschel, H. (1863) Bericht über die Leistungen in der Herpetologie während des Jahres 1862. *Archiv für Naturgeschichte*, 29 (2), 620–641.
- Uetz, P. & Hallermann, J. (2013) The Reptile Database. Available from: www.reptile-database.org (accessed 4 October 2013)
- Underwood, G. (1979) Classification and distribution of venomous snakes in the world. In: Lee, C.-Y. (Ed.), *Snake Venoms*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 15–40.
- Underwood, G. & Kochva, E. (1993) On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zoological Journal of the Linnean Society*, 107, 3–64.
<http://dx.doi.org/10.1111/j.1096-3642.1993.tb01252.x>
- Valenta, J. (2010) *Venomous snakes—Envenoming, Therapy*. Nova Science Publishers, New York, xvi + 340 pp.
- Valli, V. (2007) *Actualisation des connaissances sur la systématique et la phylogénie des serpents*. Thèse Diplôme d'Etat, Université Paul-Sabatier de Toulouse, 257 pp. Available from http://oatao.univ-toulouse.fr/1770/1/celdran_1770.pdf (accessed 3 March 2010)
- Vidal, N., Branch, W.R., Pauwels, O.S.G., Hedges, S.B., Broadley, D.G., Wink, M., Cruaud, C., Joger, U. & Nagy, Z.T. (2008) Dissecting the major African snake radiation: a molecular phylogeny of the Lamprophiidae Fitzinger (Serpentes, Caenophidia). *Zootaxa*, 1945, 51–66.
- Wallach, V. (1998) The lungs of snakes. In: Gans, C. & Gaunt, A.S. (Eds.), *Biology of the Reptilia. Vol. 19. Morphology G: Visceral organs*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA, pp. 93–295.
- Wallach, V. & Jones, G.S. (1992) *Cryptophidion annamense*, a new genus and species of cryptozoic snake from Vietnam (Reptilia: Serpentes). *Cryptozoology*, 11, 1–37.
- Wallach, V., Williams, K.L., Boundy, J. (2014) *Snakes of the world. A catalogue of living and extinct species*. CRC Press, Boca Raton, Florida, xxviii + 1209 pp.
- Welch, K.R.G. (1982) *Herpetology of Africa: a checklist and bibliography of the orders Amphisbaenia, Sauria and Serpentes*. Krieger Publishing Company, Malabar, Florida, x + 293 pp.
- Welch, K.R.G. (1994) *Snakes of the world: a checklist. 1. Venomous snakes*. The Longdunn Press Ltd., Bristol, 135 pp.
- Werner, F. (1925, „1924“) Übersicht der Gattungen und Arten der Schlangen der Familie Colubridae. II. Teil (Dipsadomorphinae und Hydrophiinae). *Archiv für Naturgeschichte*, 90A (12), 108–166.
- Williams, K.L. & Wallach, V. (1989) *Snakes of the world. Vol. I. Synopsis of snake generic names*. Krieger Publishing Company, Malabar, Florida, viii + 234 pp.
- Witte, G.-F. de & Laurent, R. (1947) Révision d'un groupe de Colubridae Africains. Genres *Calamelaps*, *Miodon*, *Aparallactus* et formes affines. *Mémoires du Musée royal d'Histoire naturelle de Belgique (Bruxelles)*, Series 2, 29, 1–134.
- Wrobel, M. (2004) *Elsevier's dictionary of reptiles: in Latin, English, German, French and Italian*. Elsevier, Amsterdam, 747 pp.
- Zaher, H. (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1–168.
- Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., Moura-Leite, de J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia*, 49 (11), 115–153.
<http://dx.doi.org/10.1590/s0031-10492009001100001>
- Zhao, E.M. (2006) *Zhongguo Shelei – The Snakes of China*. Anhui Science and Technology Publishing House, Hefei, China, Bd. I [10 unpag.] + 4 + 6 + 12 + 372 pp., Band II [4 unpag.] + 280 pp.
- Ziegler, T. & Böhme, W. (1997) Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. *Mertensiella*, 8, 1–207.
- Zug, G.R., Vitt, L.J. & Caldwell, J.P. (2001) *Herpetology. An introductory biology of amphibians and reptiles. 2nd Edition*. Academic Press, San Diego, xiv + 630 pp.