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Deliberate tail loss in *Dolichophis caspius* and *Natrix tessellata* (Serpentes: Colubridae) with a brief review of pseudoautotomy in contemporary snake families

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Abstract. Deliberate tail loss was recorded for the first time in three large whip snakes (*Dolichophis caspius*) and one dice snake (*Natrix tessellata*). Observations were made in different years and in different locations. In all cases the tail breakage happened while snakes were being handled by researchers. Pseudoautotomy was confirmed in one large whip snake by an X-Ray photo of a broken piece of the tail, where intervertebral breakage was observed. This evidence and literature data suggest that many colubrid species share the ability for deliberate tail loss. However, without direct observation or experiment it is not possible to prove a species' ability for pseudoautotomy, as a broken tail could also be evidence of an unsuccessful predator attack, resulting in a forcefully broken distal part of the tail.

Key words: deliberate tail loss, pseudoautotomy, Colubridae, *Dolichophis caspius*, *Natrix tessellate*.

Deliberate loss of the distal portion of the tail is a widespread defense mechanism in representatives of the reptile orders Rhynchocephalia and Squamata (after Benton 2014), with general reviews on this topic including Arnold 1984, Bellairs & Bryant 1985, Brito et al. 2001, Seligmann et al. 2008, Bateman & Fleming 2009 and Pafilis et al. 2009. There are two main types of deliberate tail loss, with and without regeneration of the broken part. The difference in terminology is summarized in Costa et al. (2014), explaining the main differences in "urotomy", which represents any type of tail breakage (both inter- and intra-vertebral), "autotomy" (intravertebral tail breakage followed by the regeneration of the lost part) and "pseudoautotomy" (intervertebral non-spontaneous breakage of the tail, without regeneration). Within Squamata (see Reeder et al. 2015), numerous taxa display various types of tail-breakage ranging from autotomy and pseudoautotomy to intervertebral urotomy with regeneration; however, in monophyletic group of Serpentes only pseudoautotomy occurs. Costa et al. (2014) listed three families and a number of subfamilies of snakes where species expressed deliberate tail loss. He created an overview of references, going back to Kaufman & Gibbons (1975). The term "autotomy" also has a general meaning as it refers to a specific predator-escape mechanism, recorded in a wide variety of animal taxa, including both invertebrates and vertebrates (see Jagnandan et al. 2014).

According to literature data, pseudoautotomy was described in the snake families Colubridae, Elapidae and Lamprophiidae, occurring in species known for their relatively long tails (see Costa et al. 2014). Here we report the first observation of deliberate tail loss in two Palearctic colubrid species in Europe, namely the large whip snake (*Dolichophis caspius*) and the dice snake (*Natrix tessellata*) (Table 1).

Table 1. List of recorded deliberate tail-loss events in two colubrid species in Serbia and Hungary. Su – sex unknown; L-total length; Lb – length of broken part of the tail; n_{SC} – number of subcaudal scales on broken piece of tail.

Age/Sex	L/Lb (mm)	n_{SC}	Latitude (degrees)	Longitude (degrees)	Altitude (m.a.s.l.)	Date (dd/mm/yyyy)	Country
Dolichophis caspius							
Adult/Su no. 1	>1000/-	-	43.033	21.867	367	22/05/2009	Serbia
Adult/female no. 2	1630/32	16	44.450	22.144	250	20/06/2014	Serbia
Adult/female no. 3	1580/225	52	47.560	18.980	311	14/06/2014	Hungary
Natrix tessellata							
Adult/Su	700 /35	16	43.323	19.675	530	06/07/2011	Serbia

In all four cases, deliberate tail loss happened in the field while a researcher was measuring the snake, handling it by the distal portion of the tail. In both species, deliberate tail loss was preceded by a particular type of behavior, which consisted of fast circular body movements along the longitudinal axis, already described in Sharma (1980), Cooper & Alfieri (1993), Marco (2002) etc. and elaborated also in Costa et al. (2014) on the basis of extensive literature and personal experience. These fast spinning movements led to cracking of the distal part of the tail while the snake was being handled by the researcher, and this was followed by the successful escape of the snake. Both species are sexually dimorphic, males having larger tails than females. Unfortunately, incomplete data (see Table 1) made comparison of the relation between the relative length of the broken piece of the tail and total relative tail length in different sexes impossible. In *D. caspius* specimens no. 1 and 2 and in the *N. tessellata,* only measurements of the total length were done, as researchers did not expect their snakes to escape. In *D. caspius* no. 3, all available measurements were taken from photos made on site and done by SnakeMeasurer 1.0 software. The number of caudal vertebrae in the broken piece of tail was countable only in *D. caspius* no. 3 (N=54), thanks to the opportunity of taking an X-ray photo (Fig. 1). Additionally, the free movements of the broken piece of the tail in the same individual were recorded by Panasonic Lumix DMC- FT2 camera by the third author (B.H.).

Examined *D. caspius* individuals no. 2 and no. 3 were adult females of almost the same size but the lengths of their broken tails differed apparently (1:7). Weight of the broken piece of tail in snake no. 3 was 4.5 g. Occurrence of intervertebral tail breakage was confirmed by the X-ray photo (Fig. 1). Moreover, before the incident the tail length in no. 3 was estimated as 415 mm, which indicates that more than 50% of the tail was deliberately lost in a single pseudoautotomy event. In all cases, less than 8 minutes passed from the start of handling to the moment of the tail breaking and the consequent escape of the snake. Only in large whip snake no. 3 did B. H. have the opportunity to observe the broken part of the tail moving freely on the surface for about 2 min, changing direction from left to right and *vice versa*. In the other three reported cases the authors did not check the ability of the broken tail to twitch autonomously after breakage.

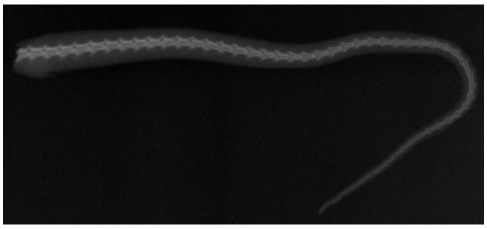

Figure 1. X-Ray photo of broken piece of tail of *Dolichophis caspius* from Hungary.

Looking at the list of published occasions of snake tail breakage collected from Google Scholar (Table 2), the majority of reports referred to the Colubridae family (46 reported species from 34 genera), followed by Lamprophiidae (4 reported species from 2 genera), Viperidae (2 reported species from 2 genera) and Elapidae (1 reported species). Pseudoautotomy was witnessed in 41% and 25% of listed colubrid and lamprophiid snake species, respectively. In colubrids, it was recorded in large, fast, mainly arboreal species (Sheehy 2006), and/or in those having active foraging behaviour (Pleguezuelos et al. 2010). The phenomenon of pseudoautotomy was also detected in the semiaquatic Natricinae subfamily (see Table 2 for species' list and references) and our report on *N. tessellata* implies that pseudoautotomy could also occur in two other members of the genus *Natrix*. Records of tail injuries and tail breakage were already documented in both *N. natrix* (Nagy 2001, Borczyk 2004, Bakiev 2005, Gregory & Isaac 2005) and *N. maura* (Santos et al. 2011). Apart from Natricinae, the other European colubrid species from the list mainly occur in open (including altered) habitats, while South American colubrids are associated with forests.

While collecting evidence of pseudoautotomy in snake species, we separated direct observations of deliberate tail loss (bolded species' names in Table 2, for elaboration see Clause & Capaldi 2006 or Bateman & Fleming 2009) from simple evidence that part of tail is missing. The latter could be the result of either pseudoautotomy or injury (in terms of forced severance of the distal part of the tail) by a predator. The reports on broken tails available to us were acquired either from analyses of museum specimens (specimens with broken tails that were noticed during measurements for various taxonomic or natural history purposes) or from intentional inspections of frequency of broken tails in particular populations (elaborated also in Costa et al. 2014). Twitching of the detached tail, confirmed here in one of four witnessed cases, was recorded also in other snake species (see for example Savage & Slowinski 1996, Marco 2002, Todd & Wassersug 2010), but c.f. Hoogmoed & Avilla-Pires (2011).

Moreover, our data showed a difference in length of the broken tail between two individuals of the same species, sex, and approximate size, which is concordant with the statements of Clause & Capaldi (2006) on "inner control" of the process. It could be the result of different amounts of

Table 2. Evidence of tail loss in various snake families, following phylogeny by Pyron et al. (2011). Latin names of species where deliberate tail loss was directly observed, are denoted by bolded font.

Species	Family	Reference
Europe		
Hierophis viridiflavus	Colubridae	Capula et al. (2010)
Dolichophis caspius	Colubridae	This study
Hemorrhois hyppocrepis	Colubridae	Marco (2002)
Natrix maura	Colubridae	Santos et al. (2011)
Natrix natrix	Colubridae	Nagy (2001); Borczyk (2004); Bakiev (2005); Gregory & Isaac (2005)
Natrix tessellata	Colubridae	This study
North America		
Agkistrodon piscivorus	Viperidae	Kauffman & Gibbons (1975);
Coluber constrictor	Colubridae	Kauffman & Gibbons (1975);
Crotalus horridus	Viperidae	Kauffman & Gibbons (1975);
Drymobius sp.	Colubridae	Mendelson (1991)
Elaphe obsoleta	Colubridae	Kauffman & Gibbons (1975);
Heterodon plathyrinos	Colubridae	Kauffman & Gibbons (1975);
Lampropeltis getula	Colubridae	Kauffman & Gibbons (1975);
Masticophis flagellum	Colubridae	Kauffman & Gibbons (1975);
Nerodia erythrogaster	Colubridae	Hampton (2007)
Nerodia sipedon	Colubridae	Kauffman & Gibbons (1975); Fitch (1999); Bowen (2004); Lockhart & Amiel (2011)
Nerodia taxispilota	Colubridae	Kauffman & Gibbons (1975); White et al. (1982)
Opheodrys aestivus	Colubridae	Gritis (1992)
Rhadinaea sp.	Colubridae	Jayne & Bennett (1989)
Tamnophis butleri	Colubridae	Willis et al. (1982)
Tamnophis sauritus	Colubridae	Willis et al. (1982); Todd & Wassersug (2010)
Tamnophis sirtalis	Colubridae	Willis et al. (1982); Cooper & Alfieri (1993); Fitch (2003); Placyk & Burghardt (2005)
South America		
Alsophis sp.	Colubridae	Seidel & Franz (1994)
Coniophanes fissidens	Colubridae	Zug et al. (1979); Mendelson (1991)
Dendrophidium brunneum	Colubridae	Cadle (2010)
Dendrophidium dendrophis	Colubridae	Martins (1996); Prudente et al. (2007); Hoogmoed & Avila-Pires (2011); Dourado et al. (2013); Santos-Costa et al. (2015)
Dipsas catesbyi	Colubridae	Zug et al. (1979)
Drymobius sp.	Colubridae	Mendelson (1991)
Drymoluber brasilii	Colubridae	Costa et al.(2014)
Drymoluber dichrous	Colubridae	Costa et al.(2014)
Echinanthera undulata	Colubridae	Gomes & Marques (2012)
Enulius sp.	Colubridae	Savage & Slowinski (1996)
Imantodes cenchoa	Colubridae	Zug et al. (1979)
Mastigodryass bifossatus	Colubridae	Leite et al. (2009); Dourado et al. (2013)
Mastigodryass boddaerti	Colubridae	Roberto (2011); Siqueira et al. (2013)
Mastigodryas heathii	Colubridae	Cadle (2012)
Pliocercus elapoides	Colubridae	Liner (1960)
Rhadinaea sp.	Colubridae	Jayne & Bennett (1989)
Scaphiodontophis sp.	Colubridae	Taylor (1954); Savage & Crother (1989); Slowinski & Savage (1995); Savage & Slowinski (1996)
Urotheca sp	Colubridae	Savage & Crother (1989)
Africa		
Natriciteres variegata	Colubridae	Broadley (1987)
Gastrophyxis sp/Hapsidophrys sp.	Colubridae	Spawls et al. (2002)
Grayia sp.	Colubridae	Spawls et al. (2002)
Mehelya sp.	Lamprophidae	Spawls et al. (2002)
Rhinechis scalaris	Colubridae	Pleguezuelos et al. (2010)
Psammophis notostictus	Lamprophiidae	Broadley (1987)
Psammophis'phillipsii'	Lamprophiidae	Broadley (1987); Akani et al. (2002)
Psammophis similans	Lamprophiidae	Broadley (1987)

Table 2. (continued)

Species	Family	Reference
Asia		
Amphiesma stolata	Colubridae	Sharma (1980)
Boiga sp.	Colubridae	Whitaker & Captain (2004)
Sibynophis sp.	Colubridae	Taylor & Elbel (1958)
Xenochrophis piscator	Colubridae	Ananjeva & Orlov (1994)
Australia		
Boiga sp.	Colubridae	Whitaker & Captain (2004)
Notechis ater occidentalis	Elapidae	Aubret et al. (2005)

strength used by researchers to secure large whip snakes no. 2 and no. 3 by the tail during handling (also, no. 2 was held by the end of its tail while no. 3 was held by the mid-section of its tail).

To our knowledge, no case of pseudoautotomy was recorded in vipers, although cases of broken tail were documented in some species (for two of them see the reference above). We often hold vipers by the tail (where it is not possible to catch them safely by the head and when we are without proper handling equipment) but deliberate tail loss has never happened. The tail also has a defensive role in those relatively short-tailed and slow-moving snakes, through tail displaying behaviour (Greene 1973) although this is not exclusive to vipers (see Martins 1996 and Parellada & Santos 2002 for review). We observed tail display of *Vipera ammodytes* in laboratory conditions in the presence of prey, and this type of behavior, called "caudal luring", has been extensively reported elsewhere (Parellada and Santos 2002). Perhaps the same behavior is applied to attract a predator's attention to the peripheral part of the snake's body (as described in Sheehy 2006) in order to be more effective in biting or escaping. In some snake species there is also "passive misdirection" of the predator by simply positioning the tail towards it without a particular display (Gritis 1992). All these defensive tactics result in evidence of broken tails in snake species, but do not necessarily confirm pseudautotomy. The fact that vipers have relatively short tails implies that deliberate tail loss could be more costly for them and thus ineffective.

In conclusion, our observations contribute to the growing evidence of snake species being capable of pseudoautotomy. In this respect, we would consider as perhaps premature the statement that pseudoautotomy evolved independently several times within various snake taxa (see Costa et al. 2014) as the field researcher's opportunity to record this type of behavior depends largely on chance, if not applied intentionally (which could be considered unethical). It further suggests that the list of the snake species capable of pseudo-autotomy is still open (as commented also in Sheehy 2006) and implies that we could expect the establishment of more coherent insights into the evolution of this defense behavior in the future.

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References

Akani, G.C., Luiselli, L., Warikobo, S.M., Ude, L., Angelici, F.M. (2002): Frequency of tail autotomy in the African Olive Grass snake, *Psammophis'phillipsii'* from three habitats in southern Nigeria. African Journal of Herpetology 51: 143-146.

Ananjeva, N.B., Orlov, N.I. (1994): Caudal autotomy in colubrid snake *Xenochrophis piscator* from Vietnam. Russian Journal of Herpetology 1: 169-171.

Aubret, F., Bonnet, X., Maumelat, S. (2005): Tail loss, body condition and swimming performances in Tiger Snakes, *Notechis ater occidentalis*. Journal of Experimental Zoology 303: 894-903.

Bakiev, A.G. (2005): Helminths and trophic relations of colubrid snakes (Colubridae) in the Volga-Kama region. Russian Journal of Herpetology12 (Supplement): 252-253.

Bateman, P.W., Fleming, P.A. (2009): To cut a long tail short: a review of lizard caudal autotomy studies carried over the last 20 years. Journal of Zoology 277: 1-14.

Bellairs, d'A., Bryant, S.V. (1985): Autotomy and regeneration in reptiles. pp. 301-410. In : Gans, C., Billet, F. (eds.) Biology of the Reptilia. Development B, Vol. 15. Wiley, Inc., New York.

Benton, M.J. (2014): Vertebrate Palaeontology (4th ed.). Oxford: Blackwell Science Ltd.

Borczyk, B. (2004): Causes of mortality and bodily injury in grass snakes (*Natrix natrix*) from the Stawy Milickie nature reserve (SW Poland). Herpetological Bulletin 90: 22-26.

Bowen, K.D. (2004): A report on tail breakage of the Northern Watersnake, *Nerodia sipedon sipedon*. The Canadian Field-Naturalist 118: 435-437.

Brito, S. P., Andrade, D.V., Abe, A.S. (2001): *Amphisbaena mertensi* (NCN): Defensive behaviour. Herpetological Review 32: 43-44.

Broadley, D.G. (1987): Caudal autotomy in African snakes of the genera *Natriciteres* Loveridge and *Psammophis* Boie. Journal of the Herpetological Association of Africa 33: 18-19.

Cadle, J.E. (2010): Systematics, natural history, and hemipenial morphology of D*endrophidion brunneum* (Günther) (Serpentes: Colubridae), a poorly known snake from the Andes of Ecuador and Peru. Zootaxa 2433: 1-24.

Cadle, J.E. (2012): Rediscovery of the holotype of *Mastigodryas heathii* (Cope) (Serpentes: Colubridae) and additional notes on the species. South American Journal of Herpetology 7: 16-24.

Capula, M., Filippi, E., Luiselli, L., Aguilar, J.R., Rugiero, L. (2000): Body size and some demographic characteristics in two populations of *Coluber viridiflavus* in the countryside of Rome. pp. 435-438. In: Atti del I Congresso Nazionale della Societas Herpetologica Italica. Museo Regionale di Scienze Naturali, Torino.

Clause, A.R., Capaldi, E.A. (2006): Caudal autotomy and regeneration in lizards. Journal of Experimental Zoology 305: 965-973.

Cooper, W.E., Alfieri, K.J. (1993): Caudal autotomy in the eastern garter snake, *Thamnophis s. sirtalis*. Amphibia-Reptilia 14: 86-89.

Costa, H.C., Moura, M.R., Feio, R.N. (2014): A tale of lost tails: Pseudoautotomy in the Neotropical snake genus *Drymoluber* (Serpentes: Colubridae). Canadian Journal of Zoology 92: 811-816.

Dourado, A.C.M., Oliveira, L., Prudente, A.L.C. (2013): Pseudoautotomy in *Dendrophidion dendrophis* and *Mastigodryas bifossatus* (Serpentes: Colubridae): tail morphology and breakage frequency. Copeia 2013: 132-141.

Fitch, H. S. (1999): A Kansas snake community: Composition and changes over 50 years. Krieger Publishing Company, Malabar, Florida.

Fitch, H. S. (2003): Tail loss in Garter Snakes. Herpetological Review 34: 212-213.

Gomes, C.A., Marques, O.A.V. (2012): Food habits, reproductive biology, and seasonal activity of the dipsadid snake, *Echinanthera undulata* (Wied, 1824), from the Atlantic Forest in southeastern Brazil. South American Journal of Herpetology 7: 233-240.

Greene, H.W. (1973): Defensive tail display by snakes and amphisbaenians. Journal of Herpetology 7: 143-161.

Gregory, P.T., Isaac, L.A. (2005): Close encounters of the worst kind: Patterns of injury in a population of grass snakes (*Natrix natrix*). Herpetological Journal 15: 213-219.

Gritis, P. (1992): Osteology and miology of the tail in the Green Snake *Opheodrys aestivus* (Serpentes: Colubridae): Patterns of morphological change. M.Sc. Thesis, Lehigh University, Pennsylvania.

Hampton, P.M. (2007): *Nerodia erythrogaster flavigaster* (yellow-bellied watersnake): anti-predatory behavior. Herpetological Review 38: 91.

Hoogmoed, M.S., Avila-Pires, T.C.S. (2011): A case of voluntary tail autotomy in the snake *Dendrophidion dendrophis* (Schlegel, 1837) (Reptilia: Squamata: Colubridae). Boletim do Museu Paraense Emílio Goeldi Ciencias Naturais Belém 6: 113-117.

Jagnandan, K., Russell, A.P., Higham,T.E. (2014): Tail autotomy and subsequent regeneration alter the mechanics of locomotion in lizards. The Journal of Experimental Biology 217: 3891-3897.

Jayne, B. C., Bennett, A. F. (1989): The effect of tail morphology on locomotor performance of snakes: A comparison of experimental and correlative methods. The Journal of Experimental Biology 252:126-133.

Kaufman, G.A., Gibbons, J.W. (1975): Weight–length relationships in thirteen species of snakes in the southeastern United States. Herpetologica 31: 31-37.

Leite, P.T., Nunes, S.F., Kaefer, I.L., Cechin, S.Z. (2009): Reproductive biology of the swamp racer *Mastigodryas bifossatus* (Serpentes: Colubridae) in subtropical Brazil. Zoologia 26: 12-18.

Liner, E.A. (1960): A new subspecies of False Coral Snake (*Pliocercus elapoides*) from San Luis Potosi, Mexico. Southwestern Naturalist 5: 217-220.

Lockhart, J., Amiel, J. (2011): *Nerodia sipedon* (northern water snake): Defensive behavior. Herpetological Review 42: 296-297.

Marco, A. (2002): *Coluber hippocrepis* (horseshoe whip snake): Caudal autotomy. Herpetological Review 33: 210.

Martins, M. (1996): Defensive tactics in lizards and snakes: The potential contribution of the Neotropical fauna. Anais de Etologia 14: 185-199.

Mendelson, J.R., III. (1991): Tail breakage in *Coniophanes fissidens* and other tropical colubrid snakes. M. S. Thesis, University of Texas at Arlington, Arlington, TX.

Nagy, Z.T. (2001): Verletzungen und Antipradator-Reaktionen in eier ungarischen Ringelnatter-Population (*Natrix natrix* (L.)). Salamandra 37: 117-121.

Parellada, X., Santos, X. (2002): Caudal luring in free-ranging adult *Vipera latasti*. Amphibia-Reptilia 23: 343-347.

Placyk, J.S., Burghardt, G.M. (2005): Geographic variation in the frequency of scarring and tail stubs in eastern gartersnakes (*Thamnophis s. sirtalis*) from Michigan, USA. Amphibia-Reptilia 26: 353-358.

Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P., Valakos, E.D. (2009): Tail shedding in island lizards (Lacertidae, Reptilia): Decline of antipredator defenses in relaxed predation environments. Evolution 63: 1262-1278.

Piron, A.R., Burbrink, F.T., Colli, G.R., Nieto Montes de Oca, A., Vitt, L.J. (2011): The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. Molecular Phylogeny and Systematics 58: 329-342.

Pleguezuelos, J.M., Feriche, M., Reguero, S., Santos, X. (2010): Patterns of tail breakage in the ladder snake (*Rhinechis scalaris*) reflect differential predation pressure according to body size. Zoology 113: 269-274.

Prudente, A.L.C., Maschio, G.F., Yamashina, C.E., and Santos-Costa, M.C. (2007): Morphology, reproductive biology and diet of *Dendrophidion dendrophis* (Schlegel, 1837) (Serpentes, Colubridae) in Brazilian Amazon. South American Journal of Herpetology 2: 53-58.

Reeder, T.W, Townsend, T.M., Mulcahy, D.G., Noonan, B.P.; Wood, P.L., Sites, J.W., Wiens, J.J. (2015): Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. Plos One 10: e0118199.

Roberto, I.J. (2011): *Mastigodryas boddaerti* (Boddaert's tropical racer): Defensive behavior. Herpetological Review 42: 440.

Santos, X., Feriche, M., Leon, R., Filippakopoulou, A., Vidal-Garcia, M., Llorente, G.A., Pleguezuelos, J.M. (2011): Tail breakage frequency as an indicator of predation risk for the aquatic snake *Natrix maura*. Amphibia-Reptilia 32: 375-383.

Santos-Costa, M.C., Maschio, G.F., da Costa Prudente, A.L.C. (2015): Natural history of snakes from Floresta Nacional de Caxiuaña, eastern Amazonia, Brazil. Herpetology Notes 8: 69-98.

Savage, J.M., Crother, B.I. (1989): The status of *Pliocercus* and *Urotheca* (Serpentes: Colubridae), with a review of included species of coral snake mimics. Zoological Journal of The Linnean Society 95: 335-362.

Savage, J.M., and Slowinski, J.B. (1996): Evolution of coloration, urotomy and coral snake mimicry in the snake genus *Scaphiodontophis* (Serpentes: Colubridae). Biological Journal of the Linnean Society 57: 129-194.

Seidel, M. E., Franz, R. (1994): Amphibians and reptiles (exclusive of marine turtles) of the Cayman Islands. pp. 407-433. In: (Brunt, M.A., Davies, J. E. eds), The Cayman Islands: natural history and biogeography. Kluwer Academic Publishing, Netherlands.

Seligmann, H., Moravec, J., Werner, Y.L. (2008): Morphological, functional and evolutionary aspects of tail autotomy and regeneration in the "living fossil" *Sphenodon* (Reptilia: Rhynchocephalia). Biological Journal of the Linnean Society 93: 721-743.

Sharma, B.D. (1980): A rare case of autotomy seen in *Amphiesma stolata* (Linn., Serpentes, Colubridae). Snake 12: 60.

Sheehy, C.M. III. (2006): On the structure and function of tails in snakes: Relative length and arboreality. M.Sc.Thesis, University of Florida, USA.

Siqueira, D.M., Nascimento, L.P., Montingelli, G.G., Santos-Costa, M.C. (2013): Geographical variation in the reproduction and sexual dimorphism of the Boddaert's tropical racer, *Mastigodryas boddaerti* (Serpentes: Colubridae). Zoologia 30: 475-481.

Slowinski, J.B., Savage, J.M. (1995): Urotomy in *Scaphiodontophis*: evidence for the multiple tail break hypothesis in snakes. Herpetologica 51: 338-341.

Spawls, S., Howell, K., Drewes, R., Ashe, J. (2002): A field guide to the reptiles of East Africa. Academic Press, San Diego, CA.

Taylor, E.H. (1954): Further studies on the serpents of Costa Rica. University of Kansas Science Bulletin 36: 673-801.

Taylor, E.H., Elbel, R.E. (1958): Contribution to the herpetology of Thailand. University of Kansas Science Bulletin 38: 1033-1189.

Todd, J., Wassersug, R. (2010): Caudal pseudoautotomy in the eastern ribbon snake *Tamnophis sauritus*. Amphibia-Reptilia 31: 213-215.

Whitaker, R., Captain, A. (2004): Snakes of India: The field guide. Draco Books, Chennai, India.

White, D.R., Mitchell, J.C., Woolcott, W.S. (1982): Reproductive cycle and embryonic development of *Nerodia taxispilota* (Serpentes: Colubridae) at the northeastern edge of its range. Copeia 1982: 646-652.

Willis, L., S. Threlkeld, T., Carpenter, C.C. (1982): Tail loss patterns in *Thamnophis* (Reptilia: Colubridae) and the probable fate of injured individuals. Copeia 1982: 98-101.

Zug, G.R., Hedges, S.B., Sunkel, S. (1979): Variation in reproductive parameters of three neotropical snakes,*Coniophanes fissidens*, *Dipsas catesbyi*, and *Imantodes cenchoa.* Smithsonian Contributions to Zoology 300: 1-18.