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The last amphisbaenian (Squamata) from continental Eastern Europe

Le dernier amphisbaenien (Squamata) d'Europe de l'Est continentale

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A B S T R A C T

The fossil record of amphisbaenians in Europe has recently been augmented through the description of new finds across the continent. It has been suggested that the post-Miocene range of amphisbaenians followed a progressive southward constriction that ultimately lead to their extant disjunct distribution. We herein describe amphisbaenian vertebral material from the Pliocene of northern Greece, which demonstrates that these reptiles were still present in the late Neogene of the southern Balkans. The new find represents the youngest occurrence of amphisbaenians in continental Eastern Europe and further highlights the role of the Greek area as a biogeographic "refugium" for certain reptile groups during the late Neogene and Quaternary.

Mots clés :
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R É S U M É

Les archives fossiles des amphisbaeniens en Europe ont récemment été augmentées grâce à la description de nouvelles découvertes à travers le continent. Il a été suggéré à plusieurs reprises que l'extension des amphisbaeniens post-Miocène a subi une réduction progressive vers le sud qui a finalement conduit à leur distribution disjointe actuelle. Nous décrivons ici une vertèbre d'amphisbaenien du Pliocène du nord de la Grèce, ce qui démontre que ces reptiles étaient présents dans le Néogène tardif du sud des Balkans. La nouvelle découverte représente la plus récente occurrence d'amphisbaeniens en l'Europe de l'Est continentale et met davantage en évidence le rôle de la région grecque en tant que « refuge » biogéographique pour certains groupes de reptiles pendant le Néogène tardif et le Quaternaire.

1. Introduction

Amphisbaenians (or worm lizards) are squamates characterized by a peculiar external morphology and skeletal anatomy, and are currently distributed in various parts of Europe, Africa, Western Asia, and North, Central, and South America (Estes, 1983; Kearney, 2003). In the extant European herpetofauna, amphisbaenians are currently represented solely by the genus *Blanus* Wagler, 1830 (Sindaco and Jeremčenko, 2008; Sillero et al., 2014; Speybroeck et al., 2016). Within *Blanus*, two different species complexes are currently recognized that are also reflecting their highly disjunct geographic distribution: the *Blanus cinereus* complex in the Iberian Peninsula and northwestern Africa (Albert and Fernández, 2009; Ceríaco and Bauer, 2018) and the *Blanus strauchi* complex in Anatolia and parts of the Middle East, but also present in certain islands in the southern Aegean Sea (Sindaco et al., 2014). Nevertheless, the fossil record already attests a much more diverse amphisbaenian European fauna with a much broader geographic distribution since at least the early Paleogene, with Late Cretaceous records also existing (Rage, 1999; Augé, 2005, 2012; Blain et al., 2010; Folie et al., 2013). The post-Miocene distribution of European amphisbaenians

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shows a gradual southward constriction of their range to Mediterranean Europe (Delfino, 1997, 2003; Delfino and Bailon, 2000; Blain et al., 2007). However, all Pliocene and Quaternary amphisbaenian records were so far solely confined to the Western and Central parts of Mediterranean Europe (Delfino, 1997, 2003; Delfino and Bailon, 2000; Blain et al., 2007). Coeval records from the Balkans were totally absent, whereas a sporadic occurrence from Anatolia also exists (Rage and Sen, 1976). We here describe an amphisbaenian vertebra from the early Pliocene (MN 15) of Spilia-4 locality in northern Greece, which demonstrates that amphisbaenians were present in the southern Balkan Peninsula as well, and further represents their youngest occurrence in continental Eastern Europe. We further describe and figure, for the first time, vertebral laminae on amphisbaenian vertebrae, following the terminology that has recently been suggested for lacertid lizards (Tschopp, 2016).

Institutional abbreviations: MDHC, Massimo Delfino Herpetological Collection, University of Torino, Torino, Italy; UU, University of Utrecht, Utrecht, The Netherlands.

2. Material and methods

The single amphisbaenian trunk vertebra, which forms the basis of this study, was found in the locality of Spilia-4 in northern Greece. The material is permanently curated in the collections of the Department of Earth Sciences of UU and is accessioned under the collection number UU SP4 501. Comparative material consisted of extant skeletons of amphisbaenians housed in MDHC. Anatomical terminology of vertebral structures follows Estes (1983) and Augé (2005) and terminology of vertebral laminae follows Tschopp (2016). Regarding the terminology of vertebral laminae, it is worth noting that Tschopp (2016, his figure 1) depicted the centropostzygapophyseal and the spinopostzygapophyseal laminae in an erroneous inverted way, whereas they are correctly defined and their terminology is rather clear in his main text (the names of the laminae are also self-explanatory even from an etymological point of view).

3. Locality

The locality of Spilia-4 is situated near the city of Serres, in the administrative region of Central Macedonia in northern Greece (Fig. 1). Spilia-4 belongs to the Spilia Formation of the Strymon (or Serres) Basin, along with the adjacent localities of Spilia-0, Spilia-1, and Spilia-3 (Van Der Meulen and Van Kolfschoten, 1986; de Bruijn, 1989; Koufos, 2006). At its lower part, the Spilia Formation consists of sands, marls and occasional lignites, whereas at its top there is an increasing amount of conglomerates with crystalline material (de Bruijn, 1989). All different localities within Spilia are of early Pliocene age, with Spilia-0 and Spilia-1 being the oldest (MN 14), whereas Spilia-3 and Spilia-4 are younger (MN 15), mostly dated on the basis of micromammal finds (de Bruijn, 1989; Koufos, 2006). The micromammal fauna of Spilia-4 comprises only rodents, pertaining to murids, glirids, and arvicolids, whereas no large mammals have been recovered so far (Koufos, 2006). No squamates or other reptiles had been described so far from Spilia-4 or the adjacent Spilia localities. To the contrary, within the Strymon Basin, in the nearby Lefkon formation, the older localities of Ano Metochi (MN 13) and Maramena (MN 13/14) have also produced abundant

Fig. 1. Map of Greece with the black circle indicating the locality of Spilia-4. The black filling in certain Aegean Islands and parts of Anatolia indicate the extant distribution of *Blanus strauchi* in the area.
Carte de la Grèce avec le cercle noir indiquant la localité de Spilia-4. Le remplissage noir de certaines Îles de la mer Égée et de certaines parties de l'Anatolie indique la répartition actuelle de Blanus strauchi *dans la région.*

Fig. 2. Trunk vertebra (UU SP4 501) of Amphisbaenia indet. from Spilia-4, in dorsal (A), left lateral (B), anterior (C), ventral (D), right lateral (E), and posterior (F) views. Scale bar is 1 mm.
Vertèbre dorsale (UU SP4 501) d'Amphisbaenia indet. de Spilia-4, en vues dorsale (A), latérale gauche (B), antérieure (C), ventrale (D), latérale droite (E) et postérieure (F). L'échelle représente 1 mm.

squamate remains (Richter, 1995; Szyndlar, 1995; Georgalis et al., 2017a).

4. Systematic Palaeontology

Reptilia Laurenti, 1768
Squamata Oppel, 1811
Amphisbaenia Gray, 1844
Amphisbaenia indet.

Material: UU SP4 501, a trunk vertebra (Figs. 2 and 3).

Locality: Early Pliocene (MN 15) of Spilia-4 locality, Central Macedonia, Greece.

Description: UU SP4 501 is a small trunk vertebra, with a centrum length equal to 2.4 mm (Fig. 2). The vertebral centrum is procoelous and dorsoventrally compressed. It has a flat ventral surface and subparallel lateral margins. Two rather large subcentral foramina are present near the sides of the ventral surface, at one third of the centrum length. The cotyle is elliptical. The condyle is eroded, but the original elliptical shape is still recognizable. In anterior view, the neural canal is subtriangular and smaller than the anterior cotyle. The lateral walls of the neural arch are moderately robust. Because of this robustness and of the flat anterior surfaces, the lateral walls of the neural arch do not form true centroprezygapophyseal laminae anteriorly. On the other hand, they grow thinner posteriorly, forming moderately robust centropostzygapophyseal laminae (Fig. 3B). Laterally, there are no posterior centrosynapophyseal laminae. The synapophyses are eroded. Nevertheless, it is still possible to recognize their massive and rounded shape. The dorsal surface of the neural arch is weakly convex, lacking a neural spine. In lateral view, the neural arch rises distinctly with a gentle curve towards the posterior end. In dorsal view, the arch is constricted in the middle. The anterior margin of the arch is straight, whereas the posterior one is slightly concave. In anterior view, the anterior margin of the arch has a rounded edge, therefore not forming a real interprezygapophyseal lamina. The posterior margin is slightly more sharpened in posterior view, even though real spinopostzygapophyseal laminae are not present (also because of the absence of the neural spine). There is no zygosphene and no zygantrum. The zygapophyses are robust and moderately large in comparison to the overall size of the vertebra, and they are rather slightly tilted in dorsal direction. In lateral view, each prezygapophysis is connected to the related postzygapophysis by a rather low postzygoprezygapophyseal lamina (Fig. 3A). The prezygapophyseal facets are subcircular, whereas the postzygapophyseal ones are suboval and slightly anteroposteriorly elongated. The lateral margins of the prezygapophyses are damaged and so it is not clear whether small prezygapophyseal processes were present or not.

Remarks: The vertebra from Spilia-4 can be assigned to Amphisbaenia on the basis of the following combination of characters: dorsoventrally compressed centrum with a flat ventral surface and roughly parallel lateral margins, massive and rounded synapophyses, absence of zygosphene, and a dorsally weakly convex neural arch lacking a neural spine (Estes, 1983). Currently, no clear diagnostic feature allowing identification at family level is known for isolated trunk vertebrae of this group of squamates (Estes, 1983; Augé, 2005, 2012; Georgalis et al., 2016c, 2018a).

5. Discussion

Fossil amphisbaenians from the Northeastern Mediterranean region (Balkans and Anatolia) were so far restricted to indeterminate vertebral material from the late Miocene (MN 9) of Plakias, Crete (Georgalis et al., 2016c) and the Pliocene (MN 15) of Çalta, Anatolia (Rage and Sen, 1976), whereas cranial material from the middle Miocene (MN 7/8) of Gebeceler, Anatolia (Georgalis et al., 2018a) and the middle Miocene (MN 7/8) of Tauţ, Romania (Venczel and Ştiucă, 2008) demonstrate the presence of the extant genus

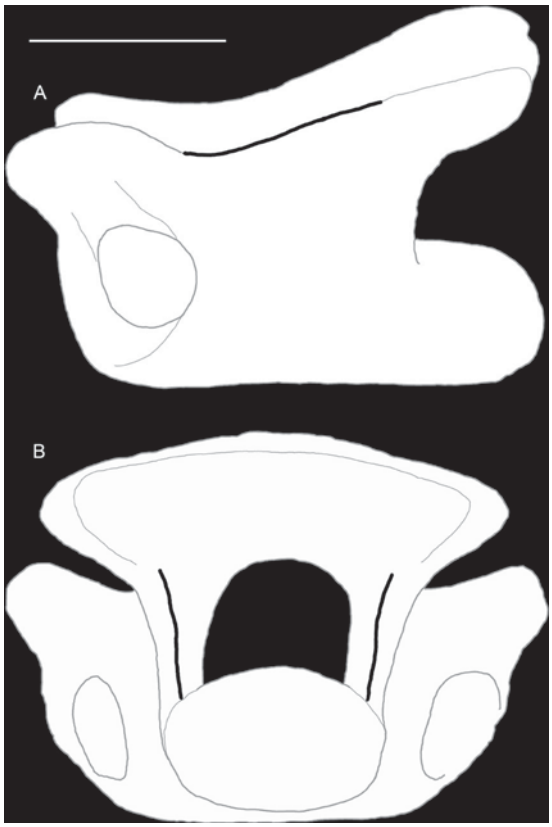

Fig. 3. Trunk vertebra (UU SP4 501) of Amphisbaenia indet. from Spilia-4, in left lateral (A) and posterior (B) views, indicating the left postzygoprezygapophyseal lamina (A) and the centropostzygapophyseal laminae (B). The laminae are represented by a thick black line. Scale bar is 1 mm.
Vertèbre dorsale (UU SP4 501) d'Amphisbaenia indet. Spilia-4, en vues latérale gauche (A) et postérieure (B), montrant la lame postzygoprézygapophysaire gauche (A) et les lames centropostzygapophysaires (B). Les lames sont représentées par une ligne noire épaisse. L'échelle représente 1 mm.

Blanus in the area as early as the middle Miocene. Despite the fact that *Blanus strauchi* (Bedriaga, 1884) occurs today in certain Greek Islands of the Aegean Sea (Sindaco et al., 2014) and that amphisbaenians were, as noted above, present in the Miocene of the Island of Crete (Georgalis et al., 2016c), no amphisbaenians (extinct or extant) had ever been recorded from the mainland of Greece. The new amphisbaenian from Spilia-4 demonstrates that these squamates achieved a much wider geographic distribution during the Neogene, which encompassed also northern Greece. Nevertheless, the presence of amphisbaenians in the Pliocene of northern Greece is consistent with a southward withdrawal of the European range of worm lizards during the late Neogene, as has already been previously suggested (Alexander, 1966; Delfino, 1997, 2003; Bolet et al., 2014; Georgalis et al., 2018a), but this range is herein demonstrated for the first time to confidently include also the southern Balkans. In any case, such biogeographic pattern of amphisbaenians is fully concordant with similar southward range withdrawals observed for other reptile clades during the Plio-Pleistocene, such as pan-trionychids, geoemydids, large-sized testudinids, agamids, the large-sized anguid *Pseudopus*, varanids, scolecophidians, erycine booids, elapids, and "Oriental Vipers" (Szyndlar and Rage, 1990; Szyndlar, 1991; Bailon and Blain, 2007; Chesi et al., 2007; Delfino et al., 2008; Georgalis and Kear, 2013; Georgalis et al., 2016a, 2017b, 2018a; Georgalis and Joyce, 2017). Especially as it concerns Greece and the southern Balkans, this area has repeatedly served as a biogeographic "refugium" for many reptiles: indeed, several of the above mentioned clades currently have their sole extant European ranges only in that area (e.g., agamids, *Pseudopus*, scolecophidians, "Oriental Vipers", and erycine booids) (Szyndlar, 1991; Delfino et al., 2008; Georgalis et al., 2016a), whereas others, which are now locally extinct, have their youngest fossil occurrences from the continent also from that area (e.g., varanids) (Georgalis et al., 2017b). Note that a recently described population of *Eryx jaculus* (Linnaeus, 1758) from Sicily could most probably be the product of human transportation during Antiquity, however, this hypothesis has still to be evaluated (Insacco et al., 2015).

Amphisbaenian vertebrae can offer no further insight about a more precise taxonomic determination (Estes, 1983; Delfino, 1997, 2003; Georgalis et al., 2016c). On the basis of a biogeographic rationale and taking also into consideration the previously described cranial elements from the middle Miocene of Romania and Turkey (Venczel and Ştiucă, 2008; Georgalis et al., 2018a), it seems probable that the material could belong to the genus *Blanus*. However, the absence of skull material from Spilia-4 precludes any such generic assignment with confidence.

6. Conclusions

We herein describe an amphisbaenian vertebra from the Pliocene of the Spilia-4 locality in northern Greece. Amphisbaenians are today living in certain Greek islands of the Aegean Sea and, furthermore, the clade has an indeterminate fossil record from the Miocene of Crete Island (Georgalis et al., 2016c). Nevertheless, the new find from Spilia-4 represents the first occurrence of an amphisbaenian from the Greek mainland, it further expands the late Neogene distribution range of that squamate clade and, most importantly, it marks its youngest record from continental Eastern Europe. In addition, the new amphisbaenian from Spilia-4 adds further evidence to the recently growing record of fossil squamates from Greece (Georgalis et al., 2016a, 2016b, 2016c, 2017a, 2017b, 2018a, 2018b, 2018c).

Disclosure of interest

The authors declare that they have no competing interest.

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References

Albert, E.M., Fernández, A., 2009. Evidence of cryptic speciation in a fossorial reptile: description of a new species of *Blanus* (Squamata: Amphisbaenia: Blanidae) from the Iberian Peninsula. Zootaxa 2234, 56–68.
Alexander, A.A., 1966. Taxonomy and variation of *Blanus strauchi* (Amphisbaenia, Reptilia). Copeia 1966, 205–224.
Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Mémoires du Muséum national d'Histoire naturelle, Paris 192, 1–369.
Augé, M., 2012. Amphisbaenians from the European Eocene: a biogeographical review. Palaeobiodiversity and Palaeoenvironments 92, 425–443.
Bailon, S., Blain, H.-A., 2007. Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. Quaternaire 18, 55–63.
Bedriaga, J., 1884. Nachträgliche Bemerkung über *Amphisbaena strauchi* v. Bedr. Zoologischer Anzeiger 7, 346.

Blain, H.-A., Bailon, S., Agusti, J., 2007. Anurans and squamate reptiles from the latest early Pleistocene of Almenara-Casablanca-3 (Castellón, East of Spain). Systematic, climatic and environmental considerations. Geodiversitas 29, 269–295.
Blain, H.A., Canudo, J.I., Cuenca-Bescós, G., López-Martínez, N., 2010. Amphibians and squamate reptiles from the latest Maastrichtian (Upper Cretaceous) of Blasi 2 (Huesca, Spain). Cretaceous Research 31, 433–446.
Bolet, A., Delfino, M., Fortuny, J., Almécija, S., Robles, J.M., Alba, D.M., 2014. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards. PLoS One 9, e98082.
de Bruijn, H., 1989. Smaller mammals from the Upper Miocene and lower Pliocene of the Strimon basin, Greece. Part 1. Rodentia and Lagomorpha. Bollettino della Società Paleontologica Italiana 28, 189–195.
Ceríaco, L.M.P., Bauer, A.M., 2018. An integrative approach to the nomenclature and taxonomic status of the genus *Blanus* Wagler, 1830 (Squamata: Blanidae) from the Iberian Peninsula. Journal of Natural History, http://dx.doi.org/10.1080/00222933.2017.1422283.
Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the Central Mediterranean. Rivista Italiana di Paleontologia e Stratigrafia 113, 287–297.
Delfino, M., 1997. *Blanus* from the Early Pleistocene of Southern Italy: another small tessera from a big mosaic. In: Böhme, W.I., Bischoff, W., Ziegler, T. (Eds.), Herpetologica Bonnensis. SEH, Bonn, pp. 89–97.
Delfino, M., 2003. A Pleistocene amphisbaenian from Sicily. Amphibia-Reptilia 24, 407–414.
Delfino, M., Bailon, S., 2000. Early Pleistocene herpetofauna from Cava Dell' Erba and Cava Pirro (Apulia, Southern Italy). Herpetological Journal 10, 95–110.
Delfino, M., Kotsakis, T., Arca, M., Tuveri, C., Pitruzzella, G., Rook, L., 2008. Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. Geodiversitas 30, 641–656.
Estes, R., 1983. Sauria Terrestria, Amphisbaenia. Part 10A. In: Wellnhofer, P. (Ed.), Encyclopedia of Paleoherpetology. Gustav Fisher Verlag, Stuttgart/New York (249 pp.).
Folie, A., Smith, R., Smith, T., 2013. New amphisbaenian lizards from the Early Paleogene of Europe and their implications for the early evolution of modern amphisbaenians. Geologica Belgica 16, 227–235.
Georgalis, G.L., Halaçlar, K., Mayda, S., Kaya, T., Ayaz, D., 2018a. First fossil find of the *Blanus strauchi* complex (Amphisbaenia, Blanidae) from the Miocene of Anatolia. Journal of Vertebrate Paleontology, http://dx.doi.org/10.1080/02724634.2018.1437044.
Georgalis, G.L., Joyce, W.G., 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58, 115–208.
Georgalis, G.L., Kear, B.P., 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios 46, 299–311.
Georgalis, G.L., Rage, J.-C., de Bonis, L., Koufos, G., 2018b. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences, http://dx.doi.org/10.1007/s00015-017-0291-2.
Georgalis, G.L., Szyndlar, Z., Kear, B.P., Delfino, M., 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences 109, 103–116.
Georgalis, G.L., Villa, A., Delfino, M., 2016b. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature 103, 12.
Georgalis, G.L., Villa, A., Delfino, M., 2017a. Fossil lizards and snakes from Ano Metochi–a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology 29, 730–742.
Georgalis, G.L., Villa, A., Delfino, M., 2017b. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. Journal of Vertebrate Paleontology 37, e1301946.
Georgalis, G.L., Villa, A., Ivanov, M., Roussiakis, S., Skandalos, P., Delfino, M., 2018c. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia–bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology, http://dx.doi.org/10.1080/08912963.2017.1417404.
Georgalis, G.L., Villa, A., Vlachos, E., Delfino, M., 2016c. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios 49, 433–444.
Gray, J.E., 1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians in the Collection of the British Museum. British Museum of Natural History, London (80 pp.).
Insacco, G., Spadola, F., Russotto, S., Scaravelli, D., 2015. *Eryx jaculus* (Linnaeus, 1758): a new species for the Italian herpetofauna (Squamata: Erycidae). Acta Herpetologica 10, 149–153.
Kearney, M., 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. Herpetological Monographs 17, 1–74.
Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology, and biostratigraphy. Annales Géologiques des Pays Helléniques 4, 183–214.
Laurenti, J.N., 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod authoritate et consensu. Joan. Thomae, Vienna (217 pp.).
Linnaeus, C., 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Stockholm (824 pp.).
Oppel, M., 1811. Die Ordnungren, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, Munchen (108 pp.).
Rage, J.C., 1999. Squamates (Reptilia) from the Upper Cretaceous of Laño (Basque Country, Spain). Estudios del Museo de Ciencias Naturales de Alava 14, 121–133.
Rage, J.-C., Sen, S., 1976. Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie). Géologie méditerranéenne 3, 127–134.
Richter, A., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowissenchaften Abhandlungen 28, 35–38.
Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.-A., Crnobrnja Isailović, J., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., Vences, M., 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. Amphibia-Reptilia 35, 1–31.
Sindaco, R., Jeremčenko, V.K., 2008. The reptiles of the Western Palearctic. 1. 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. Edizioni Belvedere, Latina (Italy) (580 pp.).
Sindaco, R., Kornilios, P., Sacchi, R., Lymberakis, P., 2014. Taxonomic reassessment of *Blanus strauchi* (Bedriaga, 1884) (Squamata: Amphisbaenia: Blanidae), with the description of a new species from south-east Anatolia (Turkey). Zootaxa 3795, 311–326.
Speybroeck, J., Beukema, W., Bok, B., Van der Voort, J., 2016. Field guide to the amphibians and reptiles of Britain and Europe. Bloomsbury Publishing, London (432 pp.).
Szyndlar, Z., 1991. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47, 103–126.
Szyndlar, Z., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowissenschaftliche Abhandlungen (Reihe A) 28, 35–39.
Szyndlar, Z., Rage, J.-C., 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. Amphibia-Reptilia 11, 385–400.
Tschopp, E., 2016. Nomenclature of vertebral laminae in lizards, with comments on ontogenetic and serial variation in Lacertini (Squamata, Lacertidae). PLoS ONE 11, e0149445.
Van Der Meulen, A., Van Kolfschoten, T., 1986. Review of the Late Turolian to Early Biharian mammal faunas from Greece and Turkey. Memorie della Società Geologica Italiana 31, 201–211.
Venczel, M., Ştiucă, E., 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania. Geodiversitas 30, 731–763.
Wagler, J.G., 1830. Natürliches System der Amphibien, mit vorangehender Classification der Saügthiere und Vögel. J. G. Cotta, Munich (354 pp.).