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First fossil remains of the extant colubrid *Zamenis situla* (Linnaeus, 1758) (Serpentes) from the island of Crete, Greece

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Massimo DELFINO & Georgios L. GEORGALIS

SNAKES FROM THE CENOZOIC OF EUROPE
– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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First fossil remains of the extant colubrid *Zamenis situla* (Linnaeus, 1758) (Serpentes) from the island of Crete, Greece

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ABSTRACT

We here provide the first description of fossil remains of the colubrid snake cf. *Zamenis situla* from Crete, Greece, originating from the Late Pleistocene of the Rethymnon fissure. Although *Zamenis situla* (Linnaeus, 1758) is a widespread snake species in Greece, including Crete, its fossil record in the area has thus far been restricted to Middle Pleistocene material from Tourkobounia 2, near Athens, which also represents the sole confirmed fossil occurrence of the species. We provide a comparison of the fossil specimens to other extant Cretan snakes, and highlight key morphological features that distinguish it from other colubrids. This fossil material provides further support to recent molecular studies suggesting long-term presence of *Z. situla* on the island. However, due to the scarcity of the fossil record, it remains unclear whether *Z. situla* inhabited Crete continuously since the Late Pleistocene or was instead reintroduced to it later on. Finally, we investigate skeletal material of *Z. situla*, providing anatomical descriptions of key cranial and vertebral structures, which could facilitate in future fossil identifications and comparisons among colubrid snakes.

KEY WORDS
Serpentes,
Colubridae,
Crete,
Pleistocene,
skeletal anatomy.

RÉSUMÉ

Premiers restes fossiles du colubridé actuel Zamenis situla *(Linnaeus, 1758) (Serpentes) provenant de l'île de Crète, en Grèce.*

Nous fournissons ici la première description de restes fossiles du serpent colubridé cf. *Zamenis situla* en provenance de Crète, en Grèce, datant du Pléistocène tardif et issus de la fissure de Réthymnon. Bien que *Zamenis situla* (Linnaeus, 1758) soit une espèce de serpent largement répandue en Grèce, y compris en Crète, son registre fossile dans la région était jusqu'à présent limité au Pléistocène moyen de Tourkobounia 2, près d'Athènes, qui constitue également la seule occurrence fossile confirmée de l'espèce. Nous comparons les spécimens fossiles à d'autres serpents crétois actuels et mettons en évidence les caractéristiques morphologiques clés qui le distinguent des autres colubridés. Ce matériel fossile apporte un soutien supplémentaire aux études moléculaires récentes suggérant une présence à long terme de *Z. situla* sur l'île. Cependant, en raison de la rareté du registre fossile, il reste incertain si *Z. situla* a habité la Crète de manière continue depuis le Pléistocène tardif ou s'il y a été réintroduit ultérieurement. Enfin, nous examinons le matériel squelettique de *Z. situla*, en fournissant des descriptions anatomiques des structures clés du crâne et des vertèbres, ce qui pourrait faciliter les futures identifications fossiles et les comparaisons entre les colubridés.

MOTS CLÉS
Serpentes,
Colubridae,
Crète,
Pléistocène,
anatomie du squelette.

INTRODUCTION

Islands represent natural laboratories of evolution, characterized by pristine environments and habitats for various animal groups, as well as evolutionary pressures that differ significantly from those on the mainland (Whittaker & Fernández-Palacios 2007; Van der Geer *et al.* 2010). This is also observed in the Mediterranean Islands, where extant faunas and fossil record together document a diversity of endemic and peculiar taxa. One of the largest Mediterranean islands, Crete, represents no exception to this rule, as several endemic forms have been identified (e.g., Lymberakis *et al.* 2008; Triantis *et al.* 2018), while the fossil record documents a variety of bizarre, now extinct, taxa (Van der Geer *et al.* 2010). Cretan Late Pleistocene fauna is mostly known from representatives of mammals that underwent insular dwarfism such as the deer *Candiacervus* Kuss, 1975, the hippopotamid *Hippopotamus creutzburgi* Boekschoten & Sondaar, 1966, and the proboscideans *Mammuthus creticus* (Bate, 1907) and *Palaeoloxodon creutzburgi* Kuss, 1965, but also large-sized rodents (see Van der Geer *et al.* 2010).

Contrary to mammals, however, our current knowledge about the fossil Cretan herpetofauna is much more limited, practically restricted to material from the Late Miocene (MN 9) of Plakias described by Georgalis *et al.* (2016), plus Quaternary remains from a few cave localities (Bachmayer *et al.* 1975; Kotsakis 1977; Szyndlar 1991a, b; Georgalis & Kear 2013; Vlachos 2022; Delfino & Georgalis 2022; Georgalis & Delfino 2022). Nevertheless, this scarce and limited fossil record still documents the presence in Crete of "exotic" (or at least now locally extirpated) taxa in the Miocene, such as crocodylians, trionychid turtles, and amphisbaenians (Georgalis *et al.* 2016), but also in the Pleistocene, such as testudinid turtles (Bachmayer *et al.* 1975; Georgalis & Kear 2013; Vlachos 2022), as well as representatives of certain extant taxa (Kotsakis 1977; Szyndlar 1991b; Vlachos 2022). Accordingly, even this limited fossil record provides some valuable information on the presence of taxa that are now absent from Crete, but also on the emergence of the extant herpetofaunas of the island.

Zamenis situla (Linnaeus, 1758) is a principal component of the extant herpetofauna of Crete. This colubrid species, which is widespread across Greece, represents one of the four species of snakes that occur today in the island, along with the other colubrids *Hierophis gemonensis* (Laurenti, 1768) and *Telescopus fallax* (Fleischmann, 1831), plus one representative of natricids, *Natrix tessellata* (Laurenti, 1768). *Zamenis situla* was long placed into the wastebasket genus *Elaphe* Fitzinger *in* Wagler, 1833, until the phylogenetic analysis of Utiger *et al.* (2002) showed that it belonged to the genus *Zamenis* Wagler, 1830. The known fossil record of *Z. situla* in Greece is scarce and its so far described occurrences exclusively consist of material from the Middle Pleistocene of Tourkobounia 2 locality, near Athens. In addition, Szyndlar (1991a) mentioned the occurrence of this species also from the Late Pleistocene of Rethymnon in the island of Crete. However, this mention was not accompanied by any description or figure. Here, we provide the first description of this material from Crete, documenting the first occurrence of this species in the fossil record of the island. Additionally, based on extant skeletal material, cranial and vertebral features of *Z. situla* are presented, which would eventually aid future identifications of the fossil remains.

MATERIAL AND METHODS

All fossil specimens were found in the Late Pleistocene fissure locality of Rethymnon, near the homonymous city in Crete, and are permanently curated at the collections of UU. The age of the locality is considered as Late Pleistocene (e.g., Szyndlar 1991a), though it has also been recently regarded as indeterminate Pleistocene (e.g., Vlachos 2022). Among reptiles, besides the herein documented snake material, the site has yielded also the geoemydid turtle *Mauremys* cf. *rivulata*. Comparative material of skeletons of extant *Zamenis situla* was studied at the collections of ISEA and MGPT-MDHC.

Anatomical terminology follows Rage (1984), Szyndlar (1984), and Szyndlar & Georgalis (2023); measurements of snake vertebrae follow Georgalis *et al.* (2021).

INSTITUTIONAL ABBREVIATIONS

ISEA	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków;
MGPT-MDHC	Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino, Torino;
UU	Department of Earth Sciences, University of Utrecht, Utrecht.

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
CAENOPHIDIA Hoffstetter, 1939
COLUBROIDES Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009
COLUBRIFORMES Schlegel, 1837
(*sensu* Zaher *et al.*, 2009)
COLUBROIDEA Oppel, 1811 (*sensu* Zaher *et al.*, 2009)
COLUBRIDAE Oppel, 1811 (*sensu* Zaher *et al.*, 2009)
Zamenis Wagler, 1830
Zamenis situla (Linnaeus, 1758)

cf. ***Zamenis situla***
(Figs 1; 2)

MATERIAL EXAMINED. — **Greece** • Two anterior trunk vertebrae (UU RE 408 and UU RE 409); 40 trunk vertebrae (UU RE 406, UU RE 407, UU RE 410, UU RE 411, UU RE 412, UU RE 414, UU RE 417, UU RE 418, UU RE 419, and UU RE 416 [31 vertebrae]); and one caudal vertebra (UU RE 415).

DESCRIPTION

Several trunk and a single caudal vertebrae are available in our sample. Trunk vertebrae are longer than wide, with a centrum length to neural arch width ratio over 1.0.

There are two anterior trunk vertebrae, which are mainly characterized by the presence of hypapophysis instead of haemal keel. Their centrum lengths are equal to 3.4 mm. In the anterior trunk vertebrae UU RE 408 and UU RE 409 (Fig. 1), in anterior view (Fig. 1A, F), the zygosphene is thin, the prezygapophyseal articular facets are almost horizontal. The cotyle is orbicular in shape. The neural canal is higher than wide. In posterior view (Fig. 1B, G), the neural arch is vaulted, with a vaulting ratio (*sensu* Georgalis *et al.* 2021) equal to 0.45. The condyle is orbicular. In lateral view (Fig. 1C, H), the neural spine of anterior trunk vertebrae is prominent and of medium height, overhanging both anteriorly and posteriorly. The centrum is wider than it is tall. The interzygapophyseal ridges are very weakly defined. The paradiapophyses are clearly divided into distinct diapophyses and parapophyses. Subcentral ridges extend longitudinally from the parapophyses to the beginning of the condyle. A hypapophysis is present, elongated, somewhat linear in shape, and pointy at the posterior end. It is only slightly flattened ventrally and almost completely straight dorsally. Lateral foramina are present, below the level of the interzygapophyseal ridges. In dorsal view (Fig. 1D, I), the zygosphene possesses two lateral lobes, although its mid-part is damaged. The prezygapophyseal articular facets are slightly elongated laterally. The neural spine commences posteriorly to the level of the zygosphene, crossing around 3/5 of the entire midline's length. The interzygapophyseal constriction is deep. In ventral view (Fig. 1E, J), the hypapophysis is thin anteriorly and thickens posteriorly. The postzygapophyseal articular facets are damaged but seem to be more circular than oval in shape and do not extend beyond the level of the condyle. The prezygapophyseal accessory processes are short and point laterally. The subcentral grooves are shallow. It is worth noting that UU RE 408 (Fig. 1A-E) is a pathological specimen, because of the deformity of the left paradiapophysis.

Mid-trunk to posterior trunk vertebrae (e.g., UU RE 406, UU RE 407, UU RE 410, UU RE 414, UU RE 412, UU RE 411, UU RE 417; Figs 1K-T; 2A-O) are principally characterized by the presence of haemal keel instead of hypapophysis. Their centrum lengths are between 3.5 mm to 3.9 mm. In anterior view (Figs 1K, P; 2A, K) the zygosphene is thin, and the prezygapophyses are almost horizontal, only slightly elevated. Paracotylar foramina are present, situated one on each side of the cotyle; they can be occasionally large. The cotyle is orbicular. The neural canal is more square-like in shape ventrally but circular dorsally. In posterior view (Figs 1L, Q; 2B, L), the neural arch is relatively depressed, with a vaulting ratio (*sensu* Georgalis *et al.* 2021) equal to around 0.25. The neural arch is more depressed in UU RE 417 (Fig. 2L), but can be occasionally slightly more vaulted as in UU RE 407 (Fig. 1Q) or UU RE 410 (Fig. 2B). The condyle is orbicular. In lateral view (Figs 1M, R; 2C, H, I, M), the neural spine is shorter and more elongated than in anterior trunk vertebrae, although it still overhangs anteriorly and posteriorly. The interzygapophyseal ridges are prominent. The subcentral ridges are thick and raised. The haemal keel is well-defined ventrally, with a "step" of varying degree that can be observed in the material: it is absent in UU RE 407 (Fig. 1R), visible in UU RE 406 and UU RE 411 (Figs 1M; 2I), and very deep in UU RE 410, UU RE 412, and UU RE 417 (Fig. 2C, H, M). Lateral foramina are visible. The paradiapophyses form distinct parapophyseal and diapophyseal portions. The diapophyses are oriented slightly posteriorly, whereas the parapophyses are oriented more ventrally rather than anteriorly or posteriorly, and are either almost the same size as the diapophyses like in UU RE 407 (Fig. 1Q) or only slightly larger like in UU RE 406 (Fig. 1R). In dorsal view (Figs 1N, S; 2G, N), the prezygapophyseal articular facets are oval in shape and elongated laterally. The neural spine covers around two-thirds of the entire midline length of

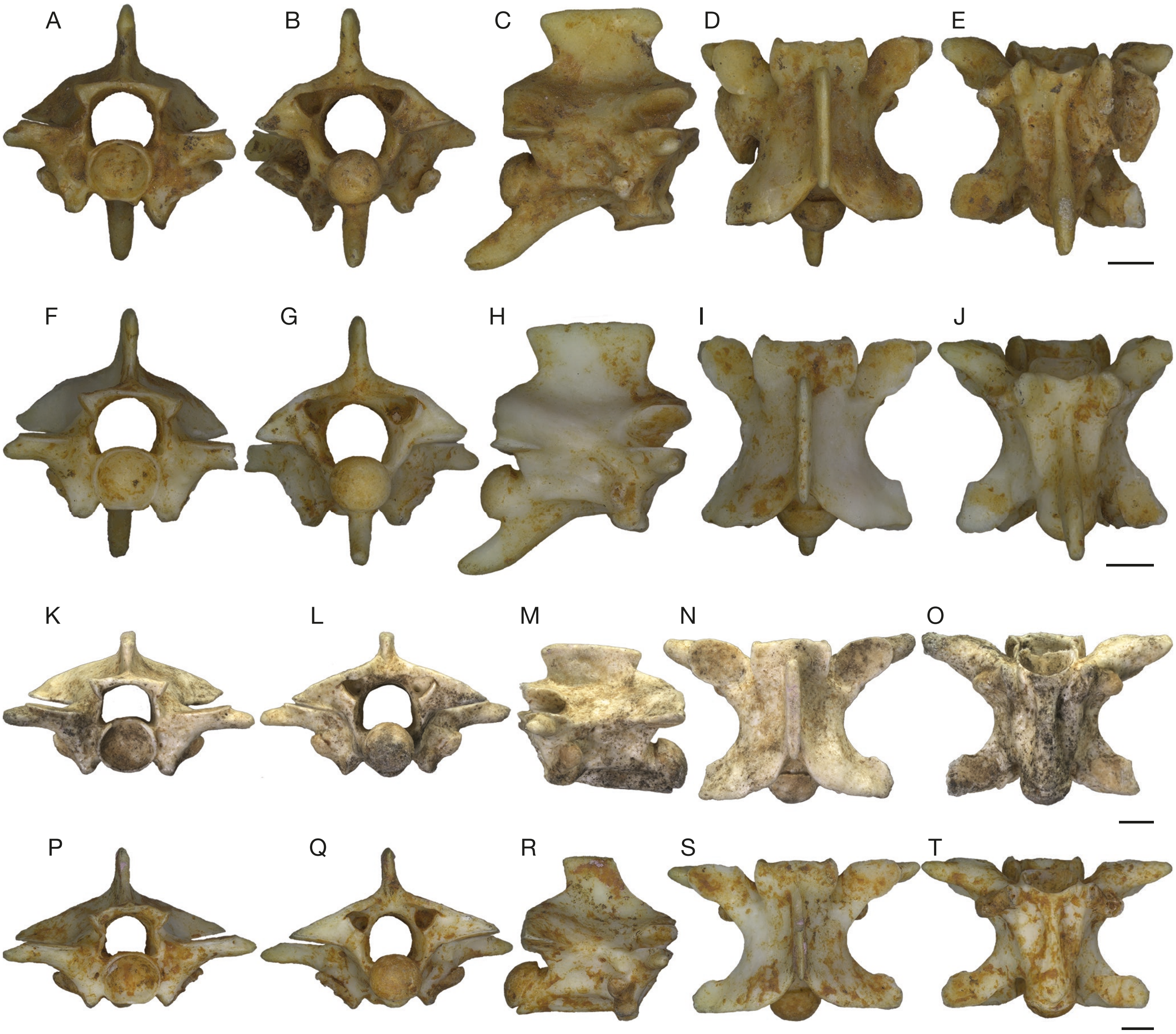

Fig. 1. — **A**-**E**, Anterior trunk vertebra UU RE 408 in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views; **F**-**J**, anterior trunk vertebra UU RE 409 in anterior (**F**), posterior (**G**), right lateral (**H**), dorsal (**I**), and ventral (**J**) views; **K**-**O**, mid-/posterior trunk vertebra UU RE 406 in anterior (**K**), posterior (**L**), left lateral (**M**), dorsal (**N**), and ventral (**O**) views; **P**-**T**, mid-/posterior trunk vertebra UU RE 407 in anterior (**P**), posterior (**Q**), right lateral (**R**), dorsal (**S**), and ventral (**T**) views. Scale bars: 1 mm.

the neural arch, similarly to the preceding anterior trunk vertebrae, though it is somehow anteroposteriorly longer. The zygosphene is triangular and possesses two lateral lobes and a median one. The prezygapophyseal accessory processes are more pronounced and longer than in the anterior trunk vertebrae, but not longer than half the greatest length of the prezygapophyseal articular facets. Their tips can be more obtuse like in UU RE 406 (Fig. 1N), or acute like in UU RE 407 (Fig. 1S). The interzygapophyseal constriction is deeper than in the anterior trunk vertebrae. The posterior median notch of the neural arch is deep. In ventral view (Figs 1O, T; 2D, E, F, J, O), the centrum is wider than long. The haemal keel is relatively thick. It is thicker in its posterior portion but narrows slightly in its anterior section; its maximum width is observed near both its anteriormost and posteriormost margins. This narrowing of the haemal keel is more prominent in UU RE 407, UU RE 414, and UU RE 411 (Figs 1T; 2E, J) than in UU RE 406, UU RE 410, and UU RE 417 (Figs 1O; 2D, O). The postzygapophyseal articular facets are oval in shape, elongated laterally, and do not extend beyond the level of the condyle. The subcentral grooves are deep.

Posterior trunk vertebrae are very similar to mid-trunk vertebrae, but can be differentiated from the preceding mid-trunk vertebrae by a relatively more depressed neural arch, the prominent and very wide haemal keel, and relatively deeper subcentral grooves (Fig. 2K-O).

A single caudal vertebra, UU RE 415 (Fig. 2P-T), is available in our fossil sample. Its centrum length is equal to 1.7 mm. In anterior view (Fig. 2P), the zygosphene is thinly built. Paracotylar foramina are present. The neural

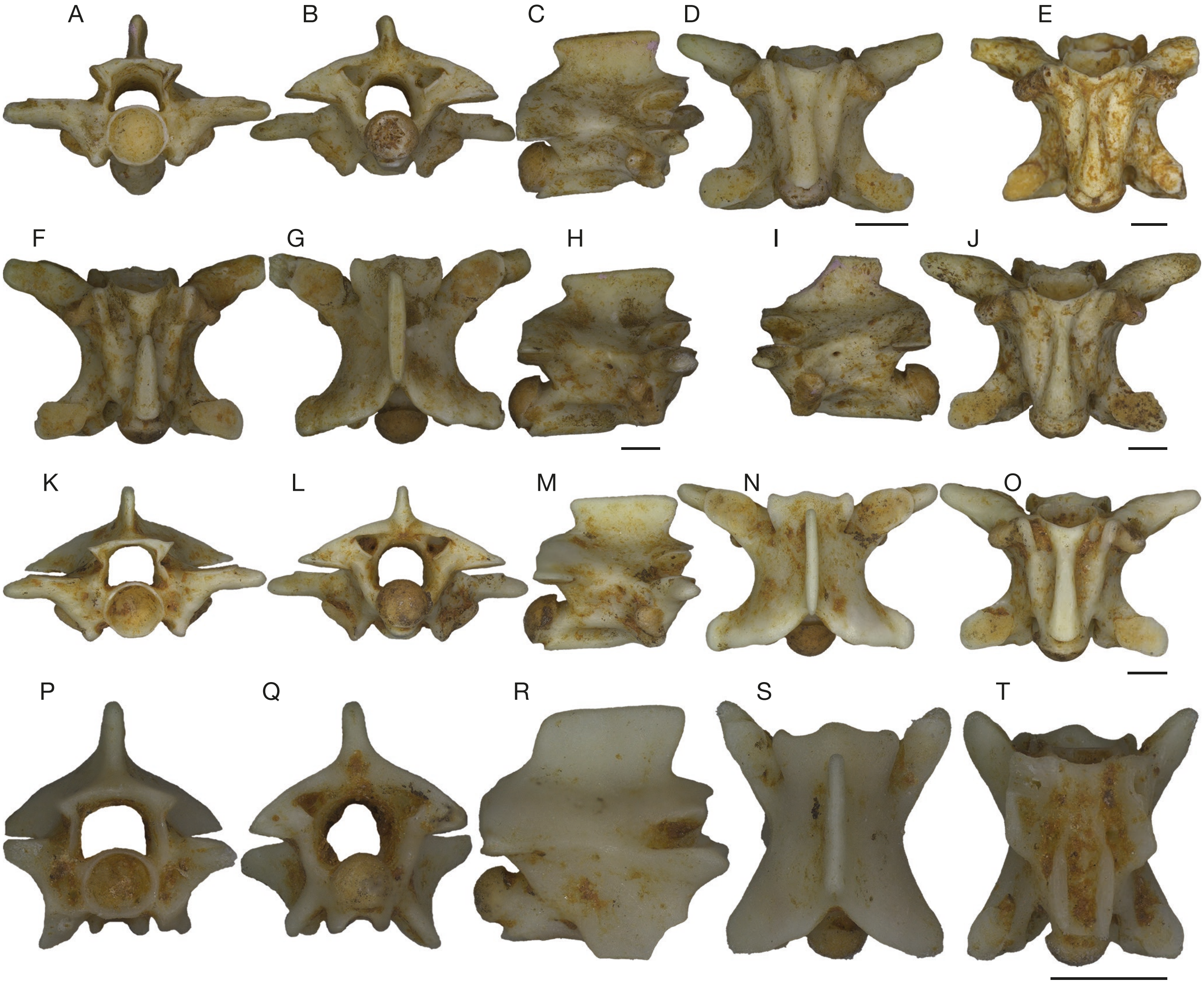

FIG. 2. — **A**-**D**, Posterior trunk vertebra UU RE 410 in anterior (**A**), posterior (**B**), right lateral (**C**), and ventral (**D**) views; **E**, posterior trunk vertebra UU RE 414 in ventral view; **F**-**H**, posterior trunk vertebra UU RE 412 in ventral (**F**), dorsal (**G**), and right lateral (**H**) views; **I**, **J**, posterior trunk vertebra UU RE 411 in left lateral (**I**) and ventral (**J**) views; **K**-**O**, posterior trunk vertebra UU RE 417 in anterior (**K**), posterior (**L**), right lateral (**M**), dorsal (**N**), and ventral (**O**) views; **P**-**T**, caudal vertebra UU RE 415 in anterior (**P**), posterior (**Q**), right lateral (**R**), dorsal (**S**), and ventral (**T**) views. Scale bars: 1 mm.

canal is still flattened laterally and circular dorsally. The cotyle is orbicular. The pleurapophyses and haemapophyses are mostly broken off, though it still can be seen that the pleurapophyses are ventrally oriented with wide gap between them and the prezygapophyses. In posterior view (Fig. 2Q), the neural arch is relatively vaulted and almost semicircular in shape, with a vaulting ratio (*sensu* Georgalis *et al.* 2021) equal to 0.38. The condyle is orbicular. In lateral view (Fig. 2R), the neural spine is higher than in the mid-trunk vertebrae and overhangs only anteriorly. The interzygapophyseal ridges are still visible; the subcentral ridges are not easily distinguishable. Lateral foramina are present. In dorsal view (Fig. 2S), the prezygapophyseal articular facets are oval in shape and elongated anteriorly. The neural spine covers, again, around 3/5 of the entire midline length of the neural arch. The interzygapophyseal constriction is deep. The zygosphene is triangular with three prominent lobes. The prezygapophyseal accessory processes are short and point anteriorly. In ventral view (Fig. 2T), the prezygapophyseal accessory processes are still recognisable but much less pronounced. The prezygapophyses are very short laterally, and the prezygapophyseal accessory processes only slightly go beyond the length of the prezygapophyseal articular facets. The pleurapophyses have a wide base, covering around half of the ventral surface of the centrum. The postzygapophyseal articular facets are oval in shape and elongated posteriorly.

SKELETAL ANATOMY OF *ZAMENIS SITULA*

Even though *Zamenis situla* is a ubiquitous element of Greek and many other European herpetofaunas, its skeletal morphology has not been so far comprehensively investigated, for example only a few works have so far dealt with some

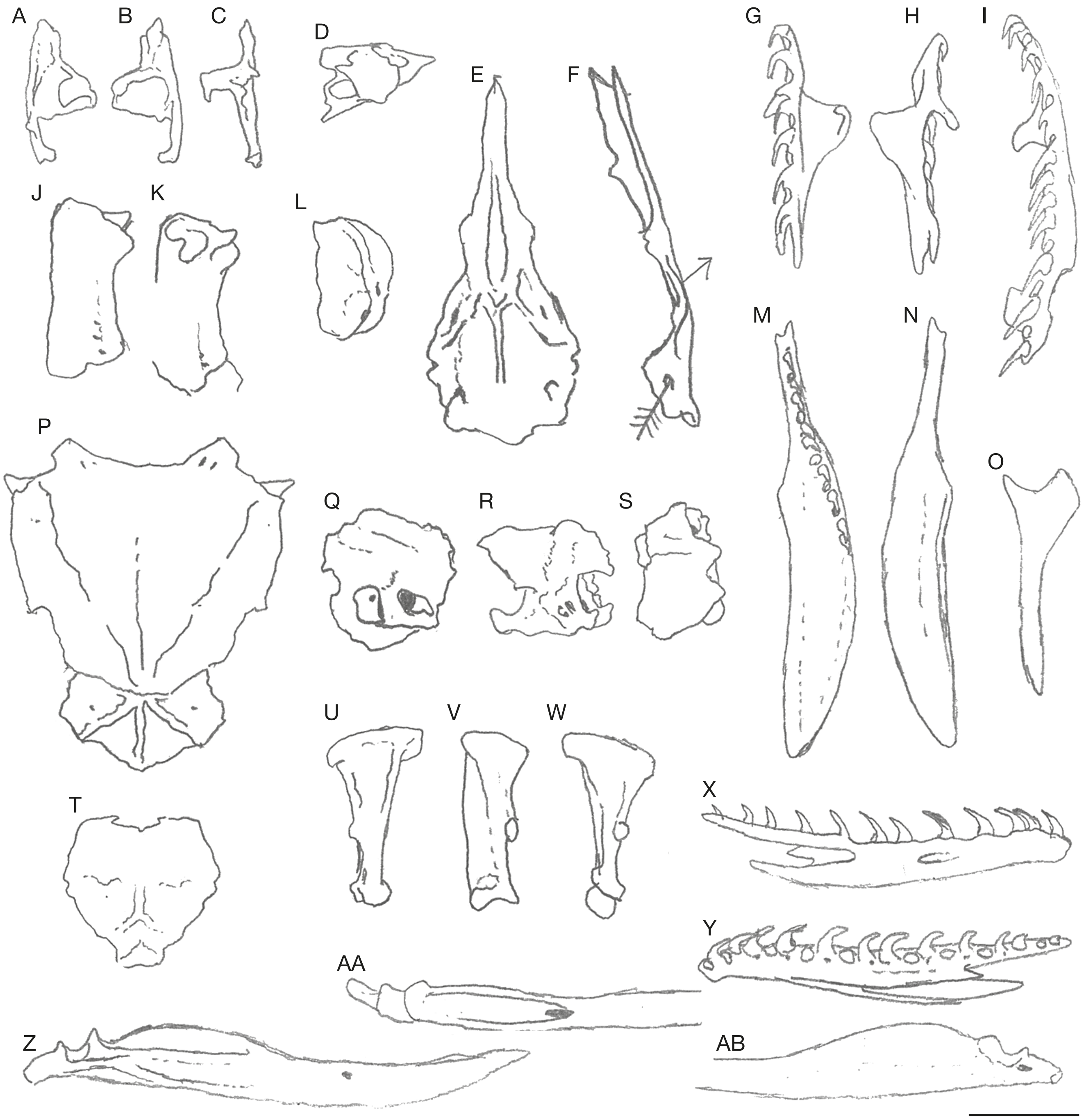

FIG. 3. — The skull of *Zamenis situla* (Linnaeus, 1758) (ISEA R/349): **A**-**C**, intranasal in dorsolateral (**A**), ventral (**B**), and medial (**C**) views; **D**, right vomer in lateral view; **E**, **F**, basiparasphenoid in ventral (**E**) and lateral (**F**) views; **G**, **H**, right palatine in ventral (**G**) and dorsal (**H**) views; **I**, left maxilla in ventrolabial view; **J**, **K**, frontal in dorsal (**J**) and ventral (**K**) views; **L**, right prefrontal in posterolateral view; **M**, **N**, right pterygoid in ventral (**M**) and dorsal (**N**) views; **O**, right ectopterygoid in dorsal view; **P**, parietal and supraoccipital in dorsal view; **Q**, right prootic in lateral view; **R**, **S**, right exoccipital in lateral (**R**) and dorsal (**S**) views; **T**, basioccipital in dorsal view; **U**-**W**, right quadrate in lateral (**U**), anterior (**V**), and medial (**W**) views; **X**, **Y**, right dentary in lateral (**X**) and medial (**Y**) views; **Z**-**AB**, right compound bone in labial (**Z**), dorsal (**AA**), and medial (**AB**) views. Scale bar: 2 mm.

parts of its skull (e.g., Szunyoghy 1932; Bogert 1947). We therefore take this opportunity to provide some observations on the skull and vertebral column morphology of this species, though a complete bone by bone cranial documentation is beyond the scope of this paper. The intranasal (Fig. 3A, B, C) is slightly curved, widens laterally and ventrally at around mid-length. This expansion bears the ascendens nasal process that is directed dorsolaterally. The intranasal is convex dorsally and concave ventrally, and at its posterior end a frontal process is located, that points laterally. The vomer (Fig. 3D) possesses well-pronounced premaxillary and posterior-inferior processes, but the postero-superior process is less developed; the lamina spheroidea palatina is shifted posteriorly. The vomerine foramen is relatively large and oval in shape. The basiparasphenoid (Fig. 3E, F) has a central area, that is distinct from the lateral area. The basisphenoid crest is well-developed, with suborbital flanges being distinct. The parasphenoid process possesses a deep groove on the ventral side, that culminates in width just before the suborbital flanges. The basipterygoid processes are very subtle. The pterygoid crests project ventrally and are inclined along half of their length, making the central area bridge-like in appearance. Above the midpoint of each pterygoid crest, and approximately in the centre of the lateral area, the anterior orifices of the Vidian canals are located. The openings of the anterior orifices of the Vidian canals are oriented anteriorly. The basisphenoid crest is well pronounced only in its anterior part, diminishing posteriorly and ending well before the posterior edge of the bone. The postpterygoid area shows a visible constriction on its surface due to the presence of the posterior orifices of the Vidian canals, whose openings are oriented posterolaterally. The frontal crest, located on the dorsal surface of the bone, has a pointed base that ends beyond the anterior edge of the parasphenoid process, which also has a pointed end. The frontal crest is located just below half of the length of the parasphenoid process. The palatine (Fig. 3G, H) possesses 12 teeth, distributed almost throughout its entire length. The maxillary process points posterolaterally; the choanal process runs anteromedially but is relatively curved at the end, pointing laterally. The maxilla (Fig. 3I) possesses 19 tooth positions along its length. The prefrontal process is present at approximately the level of the 8th-9th tooth position and points posteromedially. The ectopterygoid process is present at the level of the 17th tooth position and points anteromedially. The frontal (Fig. 3J, K) is almost straight, widening at its distal part. The prefrontal (Fig. 3L) has a lacrimal foramen, with another foramen also visible on its lateral surface. On its mediodorsal side, where it is connected with the frontal, there is a process that points posterodistally. The pterygoid (Fig. 3M, N) has a spatula-like shape. It is broad in its posterior portion but narrow in the anterior one. The anterior portion has 14 teeth and is terminated into two branched processes, of which the medial one is longer. The ectopterygoid (Fig. 3O) is Y-shaped and elongated posteriorly. Anteriorly it bears two branches: the medial one is pointed, while the lateral one is broad. The parietal (Fig. 3P) has an anterior border forming a broad U-shape. The parietal crests converge just before the posterior border, which is almost semicircular. This part of the parietal connects to the supraoccipital, which features a well-developed sagittal crest and occipital crests. Supraoccipital foramina are present. The prootic (Fig. 3Q) has anterior and posterior trigeminal foramina that have irregular shapes; a small facial nerve foramen can be seen. The exoccipital (Fig. 3R, S) has not a well-developed occipital crest. The parotic process and protuberantia postoccipitalis are clearly visible but not well developed. The vagus-hypoglossal nerve foramen is clearly visible. The exoccipital condyle is triangular in shape in lateral view. The basioccipital (Fig. 3T) is somewhat pentagonal in shape with a flattening at its anterior border. The crests on the basioccipital are clearly visible. The quadrate (Fig. 3U, V, W) possesses a dorsal crest and is not highly tilted, remaining almost horizontal with a slight curvature, giving it an almost T-shape. The quadrate crest is visible, and the stapedial process is well-pronounced. The dentary (Fig. 3X, Y) possesses 21 tooth positions. An elongated mental foramen is present at the level of 9th-10th tooth, and the compound notch closes at approximately the level of 13th tooth. The dorsal and ventral processes at the posterior end of the dentary are prominent. The compound bone (Fig. 3Z, ZA, ZB) features an angular retroarticular process that points ventrally. Its posterior articular facet is not very deep. The prearticular crest is clearly separated from the base of the bone. The mandibular fossa is deep, with a foramen visible in dorsal view. The supraangular foramen (*sensu* Szyndlar 1984) is present in lateral view, and another foramen is visible on the retroarticular process in medial view.

The axis of *Zamenis situla* has a typical colubrid morphology (Fig. 4A). In anterior view, the transverse processes are short. The neural canal is considerably wider than in other parts of the column. In dorsal view, the zygosphene is rather wide and concave. The neural spine is high. In lateral view, the neural spine overhangs both anteriorly and posteriorly, with the anterior overhanging being shorter than the posterior. The hypapophysis is projecting anteroventrally in similar fashion to the anterior trunk vertebrae.

As in all colubrids, anterior trunk vertebrae are characterized by the presence of a hypapophysis (Fig. 4B). These vertebrae have also an anteroposteriorly shorter centrum, smaller prezygapophyseal articular facets, and a more vaulted neural arch (Fig. 4B). In succeeding trunk vertebrae, the hypapophysis is substituted by a haemal keel (Fig. 4C). This haemal keel becomes progressively wider in ventral view, towards the posterior mid- and posterior portion of the trunk column. The neural spine in these vertebrae is shorter and the neural arch becomes gradually more depressed. These vertebrae are more elongated when compared with anterior trunk vertebrae. The prezygapophyseal accessory processes are more pronounced.

As typical for snakes, cloacal vertebrae are characterised primarily by the presence of lymphapophyses (Fig. 4D). The lymphapophyses possess a relatively wide gap, with clear separation of dorsal and ventral branches, that are running ventrolaterally. Progressing in posterior direction, the vertebrae become shortened and relatively wider. In this part of the vertebral column, the neural spine overhangs primarily posteriorly, with this trend persisting across succeeding caudal vertebrae. The prezygapophyseal accessory processes are shorter in this part of the column. A prominent (but not so thick) haemal keel is present on the ventral surface of the centrum of the cloacal vertebrae.

Caudal vertebrae (Fig. 4E, F) are characterized primarily by the presence of pleurapophyses and haemapophyses. In anterior view, pleurapophyses are elongated and ventrolaterally oriented (Fig. 4E) but they shorten and gradually become more ventrally oriented in succeeding caudal vertebrae (Fig. 4F). The gap between prezygapophyses and pleurapophyses successively

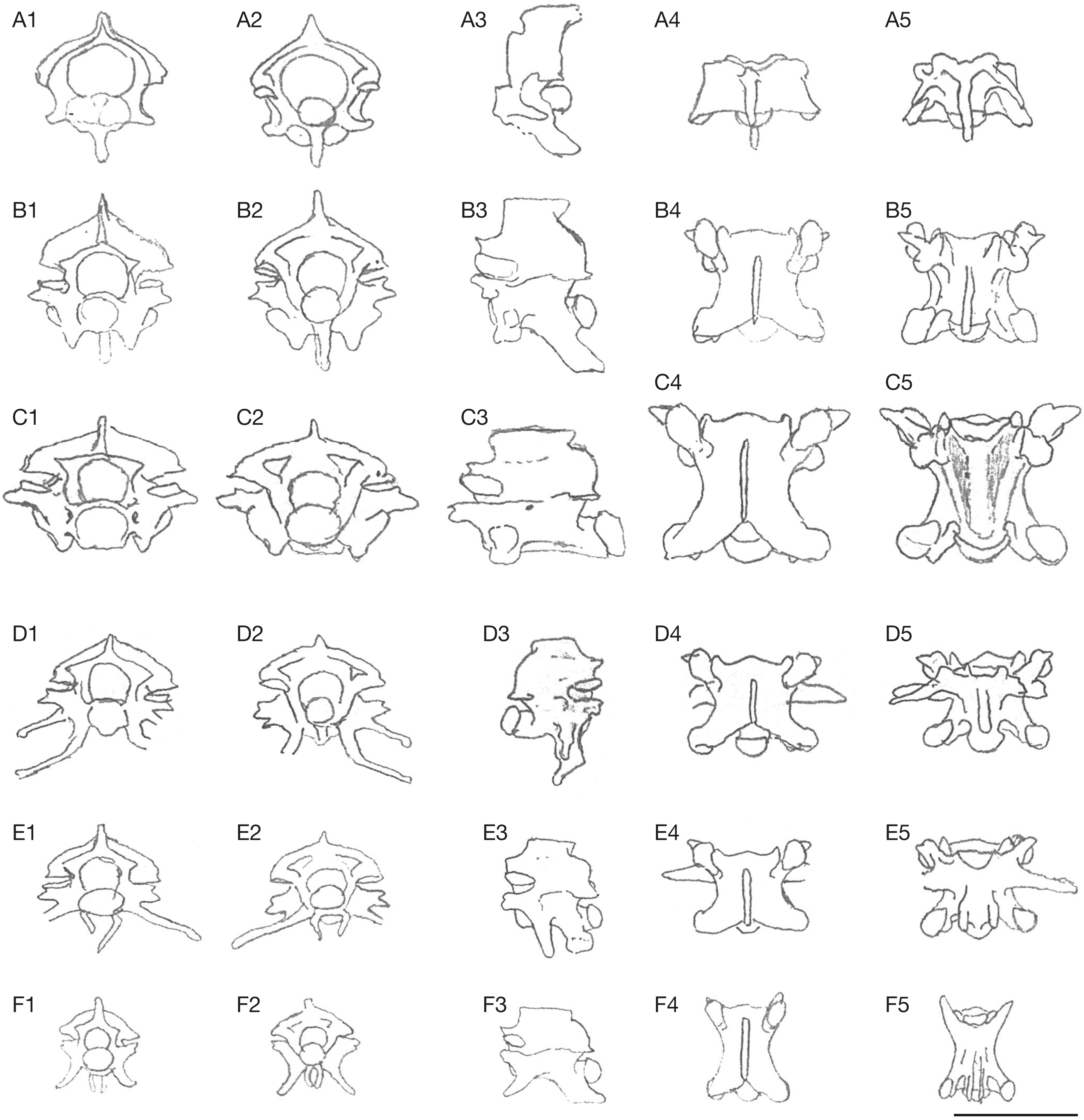

Fig. 4. — Intracolumnar variation of extant *Zamenis situla* (Linnaeus, 1758) (ISEA R/349): **A**, axis (V 2); **B**, anterior trunk vertebra (V 10); **C**, mid-trunk vertebra (V 100); **D**, cloacal vertebra (V 173 = S 2); **E**, anterior caudal vertebra (V 180 = C 5); **F**, posterior caudal vertebra (V 210 = C 35). All vertebrae in each row appear in anterior (**1**), posterior (**2**), lateral (**3**), dorsal (**4**), and ventral (**5**) views. All lateral views shown are left, except for **D3**, which is right. Scale bar: 2 mm.

widens, in the posterior portion of the tail. The neural arch gets more vaulted. The prezygapophyseal and postzygapophyseal articular facets progressively become more oval in shape (in dorsal and ventral views respectively) and oriented more anterodorsally than laterally. Paired haemapophyses emerge from the ventral surface of the centrum; these are more or less parallel to each other in anterior caudal vertebrae (Fig. 4E) but towards the posterior caudal series, their distal ends approach closer to each other (Fig. 4F).

DISCUSSION

The Cretan fossil specimens can be assigned to Colubridae (commonly known as "colubrines" in palaeontological literature), because of the following features: vertebrae longer than wide; presence of a developed hypapophysis only on the anterior trunk vertebrae; presence of haemal keel in mid- and posterior trunk vertebrae; presence of elongated and prominent prezygapophyseal accessory processes; presence of paracotylar foramina; paradiapophyses clearly divided into diapophyses and parapophyses (Szyndlar 1984, 1991a; Zaher *et al.* 2019). Moreover, the anterior trunk vertebrae from our sample differ from Natricidae in their vertebral structures. In *Natrix tessellata* (i.e., the only natricid currently inhabiting Crete), the neural spine possesses more acute posterior overhanging, and its hypapophysis is less straight in anterior trunk vertebrae than in our fossil specimens (see figures in Szyndlar 1984, 1991b; Venczel 2000); moreover, the anterior trunk vertebrae described here further differ from *N. tessellata* in terms of their shape of the zygosphene and their prezygapophyseal accessory processes (see figures in Szyndlar 1984; Venczel 2000; Ratnikov & Mebert 2011).

Among the extant Cretan colubrids, *Hierophis gemonensis* is characterised by an almost straight (to only slightly convex) zygosphene in dorsal view (unlike our specimens, where the zygosphene is triangular, with distinct lobes), and long and acute prezygapophyseal accessory processes (see Szyndlar 1991a). *Telescopus fallax* has highly distinctive trunk vertebrae, which also do not match the specimens in our sample; more specifically, in *T. fallax* the parapophyses are twice as long as the diapophyses, and the neural spine is very low (see figures in Szyndlar 1991a, 2005).

The third colubrid from Crete, *Zamenis situla*, is primarily characterized by a triangular zygosphene, short and acute prezygapophyseal accessory processes, and the relative shortness of the centrum (see descriptions above for Figure 4). The morphology of our fossil specimens matches the morphology and variation observed in extant *Z. situla*, including both anterior trunk, mid-trunk, and caudal vertebrae (Fig. 4). Some differences, however, observed in our fossil material cannot be attributed to intracolumnar variation with certainty. For example, the shape and width of the haemal keel of the trunk vertebrae of our fossil specimens approaches somehow the morphology of another Mediterranean insular form, the endemic *Sardophis elaphoides* Georgalis & Delfino *in* Georgalis *et al.*, 2019 from the Early Pleistocene of Sardinia, as well as some extant members of *Elaphe* (e.g. *Elaphe dione* [Pallas, 1773] or *Elaphe schrenckii* [Strauch, 1873]); nevertheless these forms differ significantly in the shape and height of the neural spine, prezygapophyses accessory processes, cotyle and condyle (Georgalis *et al.* 2019). Our fossil material also does not fully match another characteristic of *Zamenis situla* that was highlighted by Ratnikov (2004), i.e., the long prezygapophyseal accessory processes. However, as Ratnikov (2004) had pointed out, his observation on long prezygapophyseal accessory processes in *Z. situla* did not match with those of Szyndlar (1991a); this may suggest intraspecific variation in that structure in *Zamenis situla*. In account of such differences, but also taking into consideration the high diversity of now extinct endemic vertebrates in the Pleistocene of Crete, we here prefer to refer the material as cf. *Zamenis situla*, in agreement with the original mention of these specimens by Szyndlar (1991a).

Several recent studies, based on both morphological evidence and molecular data, have dealt with the intrageneric affinities of *Zamenis* species, as well as the placement of the genus within other colubrids, often yielding conflicting results (e.g., Helfenberger 2001; Utiger *et al.* 2002; Pyron *et al.* 2011, 2013; Zaher *et al.* 2012; Figueroa *et al.* 2016; Zheng & Wiens 2016). Helfenberger (2001) used independent morphological and molecular approaches, which recovered different topologies for European rat snakes; based on molecular data, he suggested that *Zamenis situla*, alongside *Zamenis hohenackeri* (Strauch, 1873), and *Zamenis persica* (Werner, 1913), was the sister group of *Zamenis longissimus* (Laurenti, 1768) (at that time all these aforementioned species were still classified under the genus *Elaphe*). Using molecular evidence, Utiger *et al.* (2002) suggested that *Zamenis situla* is closely related to other *Zamenis* species. The relationships within the genus were not fully resolved, but still, Utiger *et al.* (2002) suggested a close relationship between *Zamenis situla*, *Zamenis longissimus*, and *Zamenis lineatus* (Camerano, 1891), which together formed a sister group to *Zamenis hohenackeri*. A similar, though not identical, topology was retrieved in the molecular analysis of Figueroa *et al.* (2016), who recovered *Z. situla* as the sister group of the grouping comprising *Z. lineatus*, *Z. longissimus*, but also *Ptyas korros* (Schlegel, 1837), which was also deeply nested within *Zamenis*. According to most molecular studies (Pyron *et al.* 2011; Zaher *et al.* 2012; Zheng & Wiens 2016), *Zamenis situla* is the sister taxon to *Zamenis scalaris* (Schinz, 1822) (for a long time placed in its own genus *Rhinechis* Michahelles *in* Wagler, 1833). Zheng & Wiens (2016) placed the split between *Z. situla* and *Z. scalaris* at around 8.42 Ma. Zaher *et al.* (2019), using both molecular and morphological evidence, recovered the same topology but with a slightly younger divergence date, at 5.87 Ma. In contrast, Salvi *et al.* (2018) relying on molecular data suggested that *Zamenis scalaris* is the sister group to all other *Zamenis* species, while *Zamenis situla* is more closely related to a clade consisting of *Zamenis longissimus* and *Zamenis lineatus*. In the same study of Salvi *et al.* (2018), the divergence of *Zamenis situla* was suggested to have occurred during around the Late Miocene (*c.* 7 Ma) or during the Pliocene (*c.* 4 Ma), in the area of western Anatolia and the southern Balkans (Salvi *et al.* 2018). Further diversification has been also proposed to have occurred in *Z. situla*, which during the Pleistocene, split into two distinct clades: one associated with populations from Crete, the Peloponnese, and Thera, and the other with populations from Anatolia, northern continental Greece, and the eastern Aegean islands (Kyriazi *et al.* 2013). Nevertheless, the available fossil record of the species can neither support nor refute these divergence estimates, as it is particularly limited. In fact, so far, fossils attributed to *Zamenis situla* have been exclusively described from the Middle Pleistocene of Tourkobounia 2, Greece (Szyndlar 1991a). Interestingly though, fossil material of cf. *Elaphe* sp. described by Ivanov (2002) from the Early Miocene of Merkur Nord in Czech Republic, was suggested to bear much resemblance with *Z. situla*; indeed, this record was subsequently interpreted by Helfenberger & Schultz (2013) as representing the oldest find of *Zamenis situla* (*sensu lato*). Further, non-documented occurrences have also been mentioned from the Middle Pleistocene of Varbeshnitsa, Bulgaria (Szyndlar 1991a), the Late Pleistocene of Bacho Kiro cave, Bulgaria (Szyndlar 1991a), the Late Pleistocene-Holocene of Emine-Bair-Khosar, Crimea (Vremir & Ridush 2005), the Late Pleistocene of Kalamakia Cave, Greece (Roger & Darlas 2008), the indeterminate Quaternary of Pili B in Kos Island, plus another record from Crete, originating from the Late Pleistocene of Gerani Cave (Szyndlar 1991a).

If our identification of this fossil material from the Rethymnon fissure is correct, it confirms that *Zamenis situla* has been present in Crete since the Late Pleistocene. This further supports the molecular evidence, which suggested that the species already inhabited Crete during this epoch (Kyriazi *et al.* 2013). Nevertheless, due to the scarcity of the snake fossil record from Crete, it is not possible to determine if the Late Pleistocene record of *Zamenis situla* has continuously inhabited the island since then, or whether at one point the species went extinct and was subsequently later reintroduced to the Island.

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