

A new colubroid snake (Serpentes) from the early Pleistocene of Sardinia, Italy

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ABSTRACT - We herein describe *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.*, a new snake taxon from the early Pleistocene of Monte Tuttavista VI, Sardinia, Italy. *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* possesses a distinct vertebral anatomy and is diagnosed by a unique combination of features. The new Sardinian taxon is further compared in detail and differentiated from all extant European and North African snake species. Although the affinities of *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* with colubroids are clear, its more inclusive relationships within that clade cannot be resolved with certainty. Being an insular form, *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* adds significantly to our so far poor knowledge of island endemic snakes. An overview of the fossil record of snakes from the Mediterranean islands is provided. The new species increases the number of reptile taxa that went extinct in Sardinia during the late Neogene and Quaternary.

RIASSUNTO - [Un nuovo serpente colubroide (Serpentes) del Pleistocene inferiore della Sardegna, Italia] - Viene qui descritto *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.*, un serpente proveniente dai livelli fossiliferi del Pleistocene inferiore di Cava IV (Monte Tuttavista, Orosei, Sardegna). *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* è rappresentato da numerose vertebre caratterizzate da una combinazione di caratteri unica. Di particolare importanza nel distinguerlo da tutte le specie viventi o estinte dell'area europea e nordafricana sono la presenza di carena emale nelle vertebre del tronco e la sua ampiezza (tale da ospitare una convessità nel caso delle vertebre del tronco posteriori); la neurospina relativamente bassa che aggetta sia anteriormente sia posteriormente; l'arco neurale piuttosto depresso; i processi prezigapofisari relativamente lunghi, apicalmente ottusi, e provvisti di un margine posteriore leggermente convesso se osservati in norma dorsale; la presenza di una cavità nel margine dorsale dello zigantro. La lunghezza del centro delle vertebre del tronco non supera i 5 mm. Sebbene sia chiara l'affinità di *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* con i colubroidi sprovvisti di ipoapofisi nelle vertebre del tronco, non è possibile risolvere i suoi rapporti filogenetici di dettaglio. Tuttavia, l'epiteto specifico indica una affinità apparente con le specie appartenenti al genere *Elaphe s.l.* La descrizione di questa nuova specie amplia le conoscenze relative ai serpenti insulari del Mediterraneo di cui viene presentata una sintesi. L'estinzione di *Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.* testimonia ulteriormente che durante il tardo Neogene e il Quaternario la Sardegna ha perduto un numero significativo di rettili (geomydidi a tartarughe dal guscio molle, anfisbene, agamidi, lacertidi di taglia relativamente grande appartenenti al genere *Timon* e vipere, oltre alla specie qui descritta) e che quindi la sua erpetofauna attuale è notevolmente impoverita se confrontata con quella del suo recente passato.

INTRODUCTION

Insular environments are well known to represent laboratories of evolution, characterised by rapid species diversification, high levels of endemism, minimum or maximum size extremes, and peculiar morphologies (among others, Van der Geer et al., 2010). Documented cases of unique taxa, as well as extreme forms characterised by both dwarfism and gigantism are known in the fossil record already since the Mesozoic, with principal examples the Cretaceous dwarf dinosaurs of the Hațeg Island in modern day Romania (Benton et al., 2010), the Neogene and Quaternary flightless birds of numerous oceanic islands (Steadman, 2006; Worthy et al., 2016; Pavia et al., 2017), the Neogene and Quaternary giant rodents of the Mediterranean islands (Van der Geer et al., 2010), the Neogene and Quaternary dwarf hippos, deers, and peculiar “artiodactyls” of the Mediterranean islands (Palombo et al., 2006, 2012b, 2013; Van der Geer et al., 2010), the small carnivorans from the Mediterranean

islands (Rook et al., 2004, 2018; Abbazzi et al., 2005; Van der Geer et al., 2010), the Sardinian Plio-Pleistocene macaque (Rook & O'Higgins, 2005; Zoboli et al., 2016), and, most principally, the Quaternary dwarf elephants and mammoths of the Mediterranean islands, the Philippines, and Indonesia (Major, 1883; Van der Geer et al., 2010; Herridge & Lister, 2012; Palombo et al., 2012a; Zoboli et al., 2018). Insular extinct Cenozoic reptile taxa are not so well known as their co-occurring mammal species; however, there are known interesting cases of large-sized lacertids and giant tortoises in the late Neogene and Quaternary of the Mediterranean (Leith Adams, 1877; Böhme & Zammit-Maempel, 1982; Bailon et al., 2014; Rhodin et al., 2015; Luján et al., 2017), as well as peculiar terrestrial crocodylians, large iguanians, and bizarre chelonians in the remote islands of Oceania (Pregill & Dye, 1989; Mead et al., 2002; Pregill & Worthy, 2003; Pregill & Steadman, 2004; White et al., 2010). The fossil record of insular snakes is even more poorly known, with most cases simply recognizing extant taxa in Pleistocene

localities (e.g., Kotsakis, 1977a, b; Nakamura et al., 2013; Bochaton et al., 2019), although interesting forms have been rarely also described, e.g., from the Late Cretaceous of Hațeg, Romania (Vasile et al., 2013), the Neogene of the Balearic Islands (Bailon et al., 2002, 2010), the Miocene of the Canary Islands (Barahona et al., 1998), and the Quaternary of the Caribbean Islands (Bochaton & Bailon, 2018).

Being one of the largest Mediterranean islands, and remaining relatively isolated from the European mainland at least since the Oligocene (Masini et al., 2008; Mennecart et al., 2017), Sardinia offers a nice opportunity to study the evolution of insular environments during the Quaternary. Indeed, insular elephants are well known from the Pleistocene of Sardinia, where the endemic species of dwarf mammoth *Mammuthus lamarmorai* (Major, 1883) is well known (Major, 1883; Van der Geer et al., 2010; Palombo et al., 2012a; Zoboli et al., 2018), while a large array of other, unique endemic mammals have also been described from the island (Rook et al., 2004, 2018; Abbazzi et al., 2005; Rook & O'Higgins, 2005; Palombo et al., 2012b, 2013; Zoboli et al., 2016; Angelone et al., 2018). The area of Monte Tuttavista, Orosei (northeastern Sardinia), has yielded a large number of vertebrate fossils from 19 different fissure fillings, spanning from the late Pliocene up to the latest Pleistocene or Holocene (Abbazzi et al., 2004, 2005; Rook et al., 2004, 2018; Palombo et al., 2006, 2012b, 2013; Delfino et al., 2008; Angelone et al., 2018; Tschopp et al., 2018). Snake finds from Monte Tuttavista were so far confined only to brief descriptions of indeterminate “colubrines”, the natricine *Natrix* Laurenti, 1768, and the viperid *Vipera* Laurenti, 1768; however, only the latter has been partially figured (Abbazzi et al., 2004). In order to fill this gap of knowledge, here we describe a new species of snake, originating exclusively from one of these fissure fillings, Monte Tuttavista VI, pertaining to an early Pleistocene age.

MATERIALS AND METHODS

All fossil specimens described herein originate from the early Pleistocene locality of Monte Tuttavista VI, Orosei, Sardinia, and are permanently curated at the Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Sassari e Nuoro (Nuoro local operational headquarters), Sardinia, Italy. Photographs of the fossil material were taken with a Leica M205 microscope at the Dipartimento di Scienze della Terra, Università di Torino, Italy, using the software Leica Application Suite V4.10.

Comparative material of extant species includes a large number of skeletons from the collections of HNHM, MDHC, MNCN, MNHN, NHMW, NNHC-HUJ, UWr, and ZZSiD, pertaining to multiple taxa. The material included mainly adult specimens but also younger individuals, as ontogenetic differences are known in vertebrae of snake species (see Georgalis & Scheyer, 2019). See Appendix for a complete list of comparative extant specimens.

Institutional abbreviations

HNHM: Hungarian Natural History Museum, Budapest, Hungary; MDHC: Massimo Delfino

Herpetological Collection, Università di Torino, Italy; MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN: Muséum national d'Histoire naturelle, Paris, France; NHMW: Naturhistorisches Museum, Vienna, Austria; NNHC-HUJ: National Natural History Collection, Hebrew University of Jerusalem, Israel; UWr: University of Wrocław, Wrocław, Poland; ZZSiD: Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences, Krakow, Poland.

GEOLOGICAL AND PALAEOECOLOGICAL SETTINGS

The geology of Monte Tuttavista is described in great detail by Abbazzi et al. (2004). All specimens described in this paper originate exclusively from the fissure filling Monte Tuttavista VI, which pertains to an early Pleistocene age.

Associate fauna of this fissure filling includes the insular (mostly endemic) mammal taxa *Praemegaceros cazioti* (Depéret, 1897), *Cynotherium sardous* Studiat, 1857, *Prolagus cf. sardus* (Wagner, 1829), *Rhagamys orthodon* (Hensel, 1856), *Tyrrhenicola henseli* (Major, 1905), and a species of the genus *Nesiotites* Bate, 1945. The herpetofauna was so far represented in Monte Tuttavista VI by plethodontids, alytids, bufonids, hylids, indeterminate anurans, gekkotans, agamids, lacertids, amphisbaenians, “colubrines”, natricines, viperids, and indeterminate snakes (Abbazzi et al., 2004; Delfino et al., 2008; Tschopp et al., 2018).

SYSTEMATIC PALAEOONTOLOGY

SQUAMATA Oppel, 1811

SERPENTES Linnaeus, 1758

CAENOPHIDIA Hoffstetter, 1939

COLUBROIDEA Oppel, 1811 (sensu Lawson et al., 2005)

?COLUBRIDAE Oppel, 1811

Sardophis Georgalis & Delfino n. gen.

Type species *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp., the type and only known species.

Diagnosis - As for the type and only known species.

Etymology - The genus name *Sardophis* originates from the Greek words “Sardo” (“Σαρδῶν”), the most widespread name of the island of Sardinia during Antiquity, and “ophis” (“ὄφις”), meaning snake. Gender is masculine.

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. (Figs 1-8)

Holotype - MT-S-VI-01, an almost completely preserved posterior trunk vertebra (Fig. 1).

Type locality - Monte Tuttavista VI, Orosei, Sardinia, Italy; early Pleistocene.

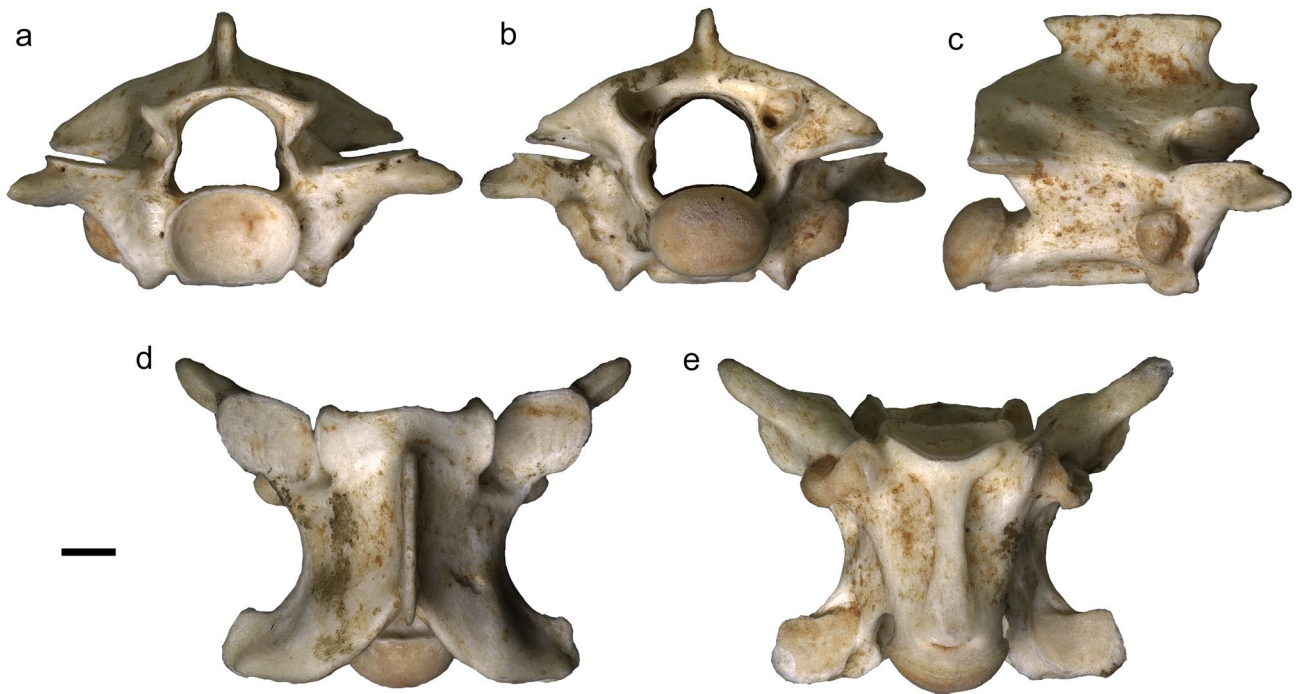


Fig. 1 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Holotype posterior trunk vertebra (MT-S-VI-01) in anterior (a), posterior (b), right lateral (c), dorsal (d), and ventral (e) views. Scale bar corresponds to 1 mm.

Diagnosis - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. can be differentiated from all other known colubroid taxa by the unique combination of features: small vertebral size (centrum lengths ranging between 3.4 and 4.5 mm), presence of a relatively wide haemal keel in mid- and posterior trunk vertebrae, which in the posteriormost trunk vertebrae becomes wider and possesses a distinct groove inside its ventral surface across large portion of its length; presence of a marked concavity on the dorsolateral rim of the zygantrum in posterior view; dorsoventrally short neural spine in lateral view, overhanging both anteriorly and posteriorly; low, dorsoventrally depressed neural arch; prezygapophyses only slightly dorsally inclined in anterior view and protruding much anteriorly in lateral view; neural spine crossing around two thirds of the midline of the neural arch; deep interzygapophyseal constriction; prominent and moderately long prezygapophyseal accessory processes; thin and arched zygosphenes in anterior view; presence of paracotylar foramina; robust diapophyses; parapophyses mediolaterally compressed forming a sharp parasagittal edge pointing downwards; presence of distinct foramina, situated within deep depressions in the zygantrum; presence of small foramina on the lateral edges of the postzygapophyses in posterior view; presence of a distinct foramen on prezygapophyseal accessory processes; presence of dorsal tubercles near the edges of the postzygapophyses (visible in anterior, posterior, and lateral views); cotyle and condyle sub-oval, wider than long, except for the posteriormost trunk vertebrae where these elements are almost circular; presence of small subcotylar tubercles (in some vertebrae). See below for further differences with European and Mediterranean species of snakes.

Referred specimens - The holotype MT-S-VI-01 was selected from a group of vertebrae and ribs coming from a single block of matrix - the same matrix also contained other 33 trunk vertebrae and numerous ribs and vertebral fragments. Due to the morphological uniformity of most of the vertebrae it is likely, but it is not possible to demonstrate, that they belong to a single individual. These remains of the block of matrix are as follows: 33 trunk vertebrae (MT-S-VI-02 to MT-S-VI-05 and MT-S-VI-08, MT-S-VI-09, MT-S-VI-19 [two vertebrae], MT-S-VI-20, MT-S-VI-21 [11 vertebrae and several vertebral fragments], MT-S-VI-23 [nine vertebrae and two pairs of two articulated vertebrae]) and numerous ribs and various other vertebral fragments (MT-S-VI-22). Other specimens from Monte Tuttavista VI, but not from the same block of matrix as the above: ten trunk vertebrae (MT-VI-07, MT-VI-10 to MT-VI-18) plus 535 trunk vertebrae (MT-S-VI-24).

Distribution - Known exclusively from the type locality. Early Pleistocene, Monte Tuttavista VI, Orosei, Sardinia, Italy.

Etymology - The species epithet “elaphoides” originates from the word *Elaphe* and the Greek ending “-oides” (“-οειδής”), meaning “like” or “similar to”. The name denotes a certain degree of resemblance of the new extinct taxon with members of the genus *Elaphe* Fitzinger in Wagler, 1833 (sensu lato). The name “*elaphoides*” (“ελαφοειδής”) means also in Greek “deer-like” - rather amusingly, this may allude also to the large and long prezygapophyseal accessory processes of the new taxon. Gender is masculine.

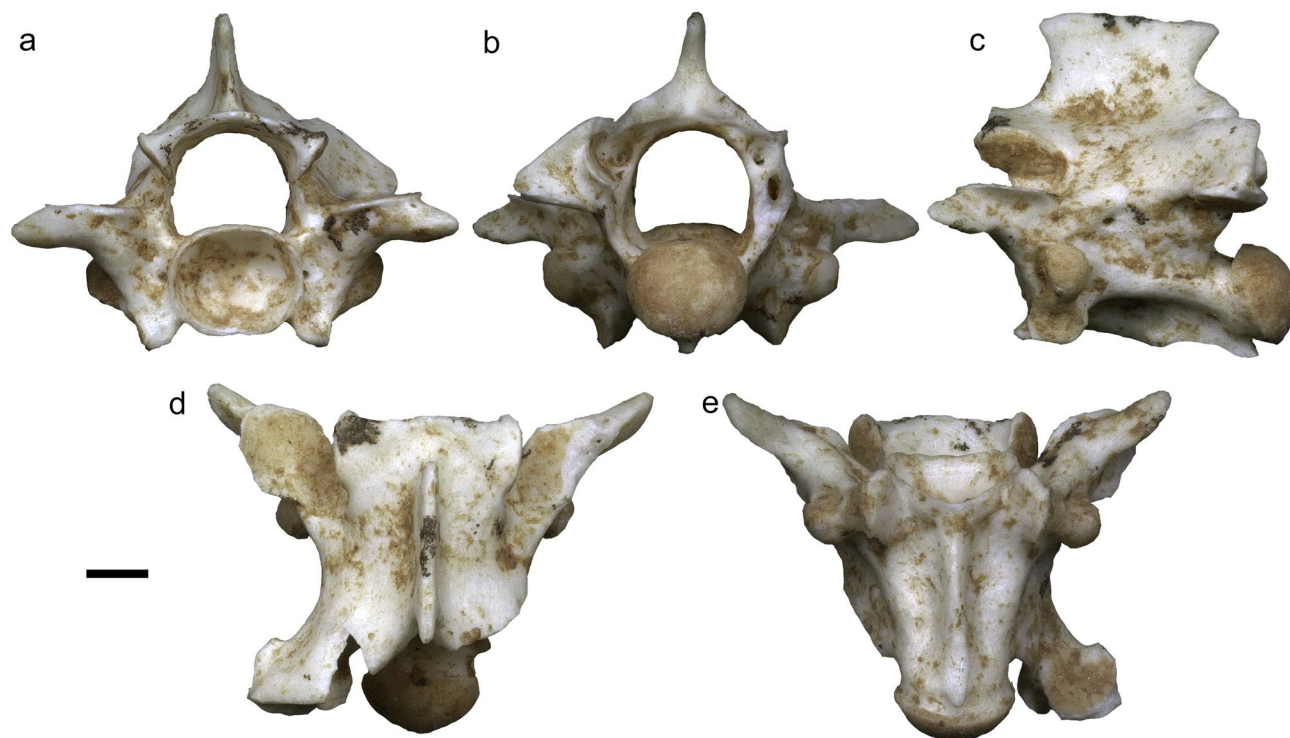


Fig. 2 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Anterior trunk vertebra (MT-S-VI-10) in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views. Scale bar corresponds to 1 mm.

Description of the holotype - MT-S-VI-01 is an almost perfectly preserved vertebra. The vertebra is relatively small, with a centrum length of 4.4 mm and a neural arch width of 3.8 mm, i.e., a ratio of centrum length to neural arch width approximately equal to 1.16 (Fig. 1). In anterior view (Fig. 1a), the zygosphe is rather thin; it is convex, with two distinct lateral lobes bending dorsally. The neural spine is dorsoventrally short. The neural canal is moderately high and there is a constriction of its width at approximately around its mid-height level. The prezygapophyses are only slightly dorsolaterally inclined. One distinct foramen is situated at the “base” of each of both prezygapophyseal accessory processes. The cotyle is large, larger than the ventral part of the neural canal; the shape of the cotyle is elliptical and its ventral level is relatively flattened. Two paracotylar foramina, one large and one smaller, are present, in each side of the cotyle. The parapophyses are pointed and extend ventrally from the level of the cotyle. In posterior view (Fig. 1b), the neural arch is depressed. Two large foramina are situated within deep depressions inside the zygantrum. There is an unusual, marked concavity on the dorsolateral rim of the zygantrum in both its edges. Small foramina are present at the edges of both postzygapophyses. The condyle is large, wider than the ventral part of the neural canal, and is elliptical in shape (with a horizontal main axis). The diapophyses are large. In lateral view (Fig. 1c), the neural spine is moderately low. It distinctly overhangs both anteriorly and posteriorly, with the posterior overhanging being more prominent. The dorsal edge of the neural spine is straight. The zygosphenal articular facets are large and their shape is ovoid. The interzygapophyseal ridges appear to be slightly convex. A large, deep

foramen is present from both lateral sides, situated below the interzygapophyseal ridge. The diapophyses and parapophyses are clearly separated. The subcentral ridges are convex. The haemal keel is prominent, extending ventrally from the level of the centrum. The condylar neck is relatively long. In dorsal view (Fig. 1d), the zygosphe is slightly trilobate, with two main lateral lobes and one incipient median one. The interzygapophyseal constriction is deep. The prezygapophyses extend anterolaterally. The prezygapophyseal articular facets are massive and oval-shaped. The prezygapophyseal accessory processes are prominent, elongated, very slightly curved in anteromedial direction, and relatively distally blunt. The neural spine is thin and its base crosses around two thirds of the midline of the neural arch. The posterior median notch of the neural arch is deep. In ventral view (Fig. 1e), the centrum is longer than wide. The haemal keel is rather prominent and thick. It crosses throughout most of the midline of the centrum, commencing at the ventral level of the cotyle and terminating prior to the condylar neck. The width of the haemal keel is not uniform throughout its length, as there is a slight constriction at around 1/4 of its length anteriorly; as such, the haemal keel reaches its maximum broadness at its posterior portion and its anteriormost tip. One moderately large subcentral foramen is present on the left side of the haemal keel. The subcentral grooves are wide. The postzygapophyseal articular facets are large and square-shaped. Judging from the width of its haemal keel and the depth of the subcentral grooves, we can assume that the holotype vertebra MT-S-VI-01 pertains to the posterior (but not posteriormost) trunk region of the column.

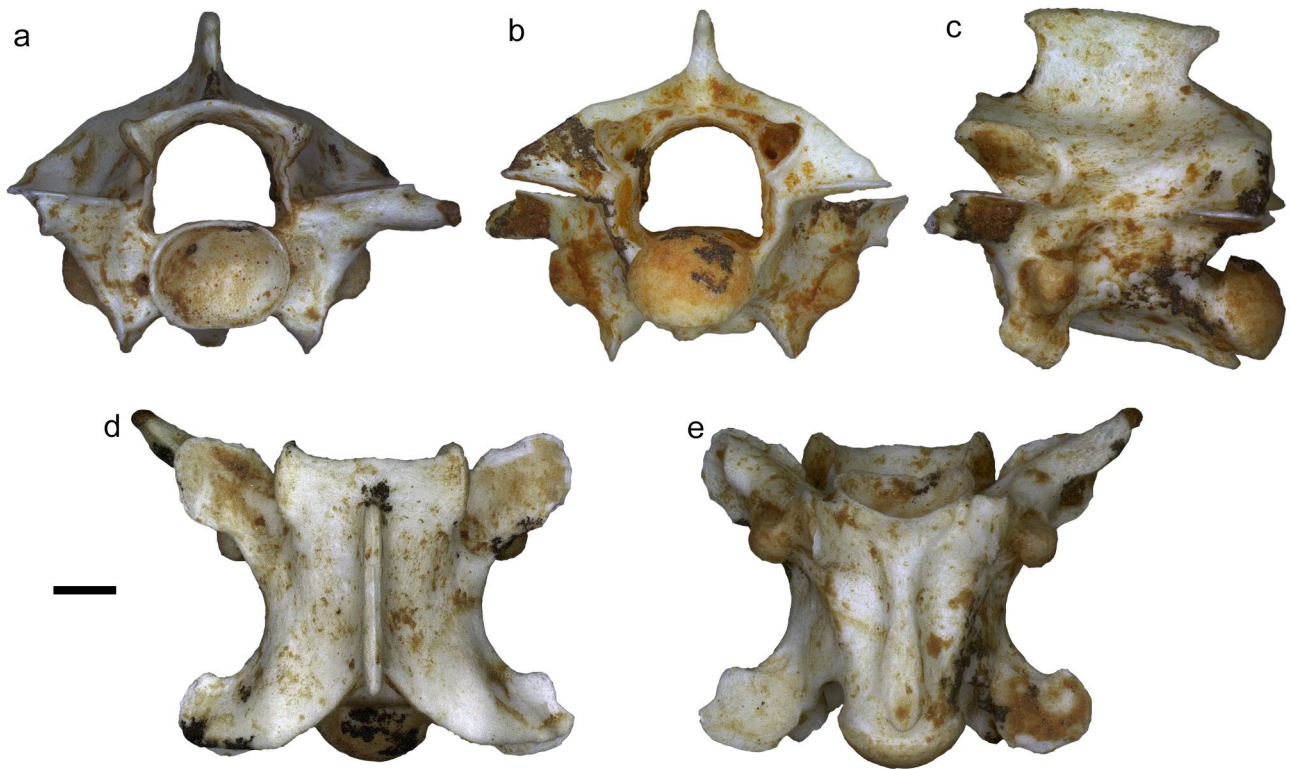


Fig. 3 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Mid-trunk vertebra (MT-S-VI-11) in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views. Scale bar corresponds to 1 mm.

Description of referred specimens: intracolumnar variation - The majority of referred vertebrae of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. is of moderate size, with centrum lengths ranging between 3.4 and 4.5 mm, therefore indicating a total body length of around 100 cm, probably slightly less than that. Ratios of centrum length to neural arch width range between 1.08 and 1.2, though in most specimens this number is (similarly to the holotype) around 1.16. The large available number of vertebrae that is referred to this taxon documents that there are not significant changes in morphology across the vertebral column (Figs 2-8). As such, all vertebrae are characterised by a dorsoventrally low neural spine in lateral view, overhanging both anteriorly and posteriorly, deep interzygapophyseal constriction, rather prominent and long prezygapophyseal accessory processes, low neural arch, thin and arched zygosphene in anterior view (except for the posteriormost trunk region), paracotylar foramina, distinct robust diapophyses and parapophyses acute and with a sharp edge situated ventrally, prominent foramina inside the zygantrum, prezygapophyses only slightly dorsally inclined in anterior view and protruding much anteriorly in lateral view, a marked concavity on the dorsolateral rim of the zygantrum, foramina above the zygantrum in the edges of the postzygapophyses, foramina on prezygapophyseal accessory processes, dorsal tubercle near the edges of the postzygapophyses, and a constriction prior to the condyle (condylar neck).

Some minor typical differences nevertheless are present: anterior trunk (i.e., cervical) vertebrae (Fig. 2) have also a similar morphology to the holotype, with only principal differences being the presence of a moderately

thin hypapophysis instead of a wide haemal keel, a somewhat more vaulted neural arch, and a neural spine that is slightly higher but still being dorsoventrally short. The length and dorsoventral extent of these hypapophyses cannot be evaluated as these elements are much damaged.

Mid-trunk vertebrae (Figs 3-4) are of also practically the same morphology as the holotype, except for a thinner haemal keel, which is still though relatively wide (and not sharp), a neural arch that is slightly more vaulted but still being relatively depressed and a higher neural spine, which is still dorsoventrally short in any case. In the transition between mid-trunk and posterior trunk vertebrae, i.e., in the posterior mid-trunk ones (Fig. 5), the neural arch becomes more depressed and the neural spine lower in comparison with the preceding ones.

In the posterior trunk region of the column (Fig. 6), the vertebral morphology approaches to a high degree that of the holotype (which is also a posterior trunk vertebra).

The posteriormost trunk vertebrae, however, pose a relative “challenge” to this morphological “continuum” (Fig. 7). In these vertebrae, the haemal keel becomes even wider than the preceding ones. Notably, in MT-S-VI-13 (Fig. 7a-e) and MT-S-VI-14 (Fig. 7f-j), the haemal keel possesses a constriction in the anterior part, it is strongly wide in the anteriormost part and rather wide uniformly in the posterior half; almost surprisingly, in this posterior half, a distinct groove is present in the haemal keel that is delimited by two “thick ridges” (Fig. 7d, i). In these two latter specimens, the haemal keel is also prominent in lateral and, especially, ventral views - there are almost tubercle-like structures (Fig. 7d-e, i-j). Another feature of the posteriormost trunk vertebrae is that the neural

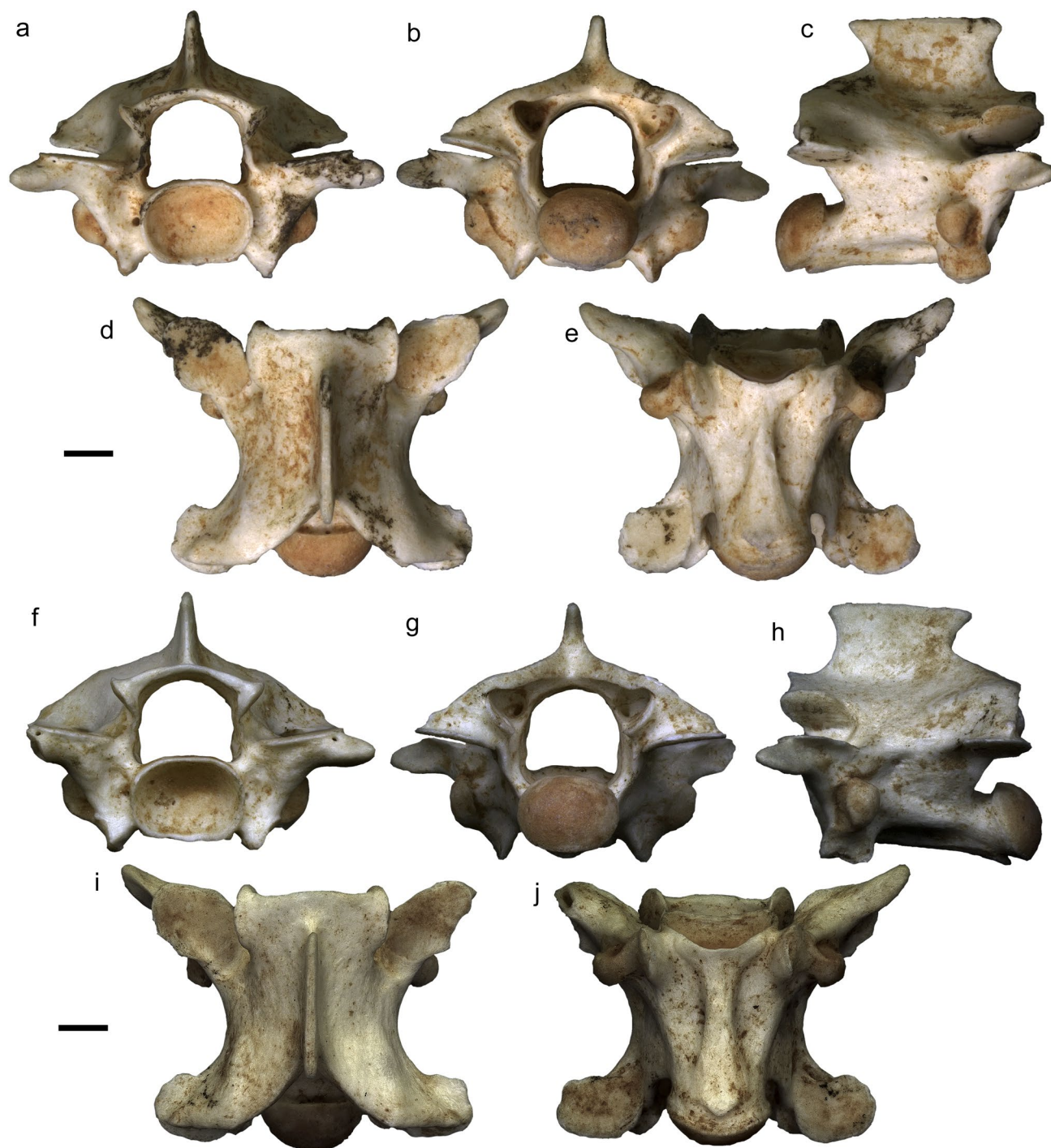


Fig. 4 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. a-e) Mid-trunk vertebra (MT-S-VI-02) in anterior (a), posterior (b), right lateral (c), dorsal (d), and ventral (e) views. f-j) Mid-trunk vertebra (MT-S-VI-09) in anterior (f), posterior (g), left lateral (h), dorsal (i), and ventral (j) views. Scale bars correspond to 1 mm.

spine becomes exceedingly dorsoventrally short, while it is anteroposteriorly elongated and its overhanging edges are not so apparent (Fig. 7e, j). Also in these vertebrae, a strange bump is evident in the subcentral ridges, visible in ventral view (most prominent in MT-S-VI-14; Fig. 7i). Both cotyle and condyle are rather small and almost circular and the former also possesses subcotylar tubercles (Fig. 7a-b, f-g). The interzygapophyseal constriction is also rather deep (Fig. 7c, h). The zygosphene is straight in anterior view and proportionally thicker (Fig. 7a, f),

instead of convex and thin as in the preceding ones. Finally, further interesting differences of these posteriormost trunk vertebrae are their proportionally thicker neural spine, prezygapophyses, postzygapophyses, and parapophyses and their proportionally smaller neural canals (Fig. 7). Despite all such differences of these posteriormost trunk vertebrae that seemingly deviate from the morphological bauplan norm of the preceding anterior, mid- and posterior trunk vertebrae, we still choose to treat them as pertaining to the same species.

Growth rings on the prezygapophyses are clearly visible in certain specimens (e.g., MT-S-VI-13). Cloacal and caudal vertebrae attributable to this species are not known with certainty.

REMARKS

Affinities of Sardophis elaphoides Georgalis & Delfino n. gen. n. sp.: comparison with extant and extinct taxa

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. can be assigned to colubroid snakes on the basis of its vertebral morphology, with a longer than wide centrum, long prezygapophyseal accessory processes, and paracotylar foramina (Rage, 1984; Szyndlar, 1984; Smith, 2013). Note that here for Colubroidea we follow the definition of Lawson et al. (2005), which is the most widespread in modern literature, and according to which this lineage includes colubrids and their relatives along with elapoids and viperoids, i.e., all caenophidians to the exception of acrochordids. In the traditional palaeontological sense, *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. might be referred to “Colubrinae” on the basis of its lightly built vertebrae and the absence of continuous hypapophyses throughout the vertebral column (Rage, 1984; Szyndlar, 1984, 1991a, b, 2012). However, recent advances in molecular phylogenetics of snakes, supported also by morphological data, have demonstrated that certain groups, such as psammophiids, lamprophiids, dipsadids, and certain atractaspidids, that have an overall similar vertebral anatomy, in fact lie outside colubrids and pertain instead to much distantly related clades (Lawson et al., 2005; Vidal et al., 2007, 2008; Kelly et al., 2008, 2009; Zaher et al., 2019).

Among extant European colubrines, *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. can be differentiated: from *Coronella austriaca* Laurenti, 1768, and *Coronella girondica* (Daudin, 1803), by its larger size, more distally pointed prezygapophyseal accessory processes, less dorsally inclined prezygapophyses, larger postzygapophyseal articular facets, higher neural spine, more vaulted neural arch, wider haemal keel, and different shapes of zygosphene, cotyle and condyle; from *Dolichophis caspius* (Gmelin, 1789) by its smaller size, broader centrum, thicker haemal keel, prezygapophyses more anteriorly directed in dorsal view, thinner zygosphene, more depressed neural arch, and different shape of neural spine, prezygapophyseal articular facets, cotyle and condyle; from *Dolichophis jugularis* (Linnaeus, 1758), by its smaller size, more depressed neural arch, shorter neural spine, more anteriorly oriented prezygapophyses, broader centrum, thicker haemal keel, and shape of neural spine, zygosphene, zygantral articular facets, prezygapophyseal articular facets, cotyle, and condyle; from *Eirenis modestus* (Martin, 1838), by its larger size, broader centrum, more anteriorly directed prezygapophyseal accessory processes, higher neural spine that overhangs both anteriorly and posteriorly, and different shape of zygosphene and zygantrum; from *Elaphe quatuorlineata* (Lacépède, 1789), *Elaphe sauromates* (Pallas, 1814), and *Elaphe dione* (Pallas, 1773), by its considerably smaller size, more anteriorly oriented prezygapophyseal accessory processes, thinner zygosphene, lower neural spine, and less concave zygosphene; from *Hemorrhoids hippocrepis* (Linnaeus, 1758), and *Hemorrhoids ravergeri* (Ménétriés, 1832), by its wider haemal keel, more anteriorly directed prezygapophyseal accessory processes, more depressed neural arch, and less convex zygosphene; from *Hemorrhoids*

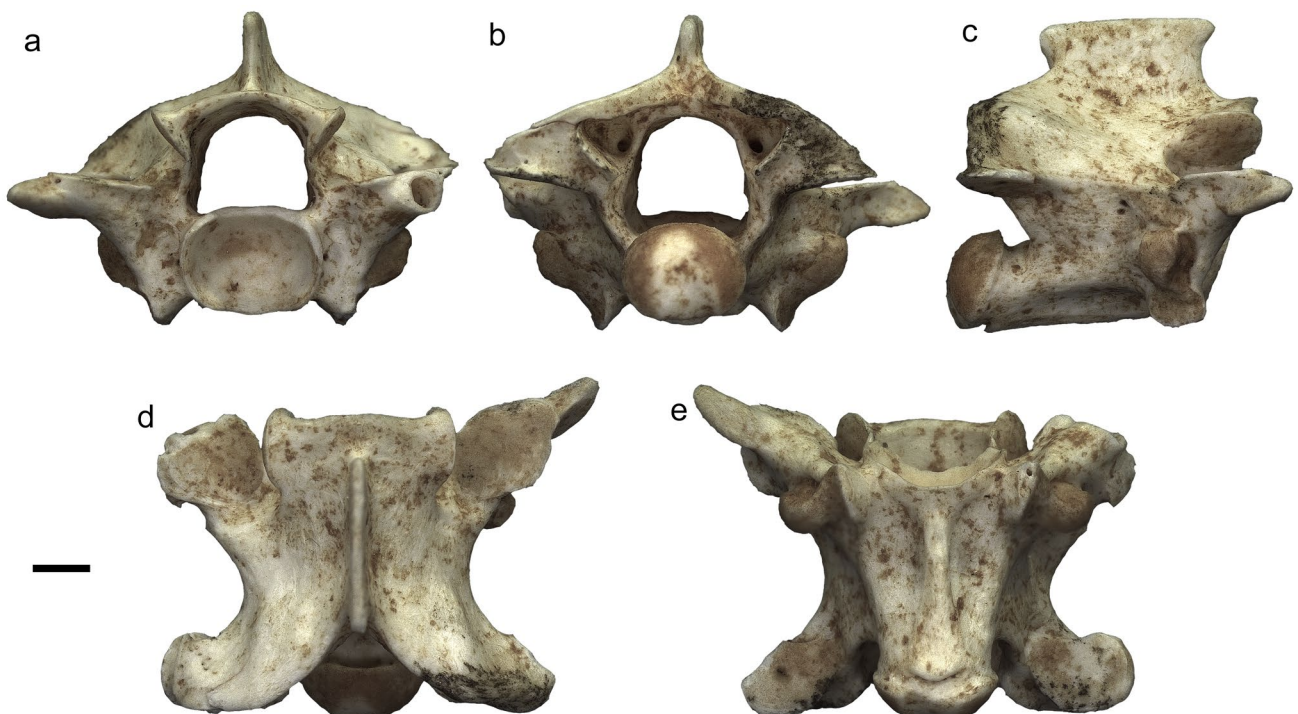


Fig. 5 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Posterior mid-trunk vertebra (MT-S-VI-08) in anterior (a), posterior (b), right lateral (c), dorsal (d), and ventral (e) views. Scale bar corresponds to 1 mm.

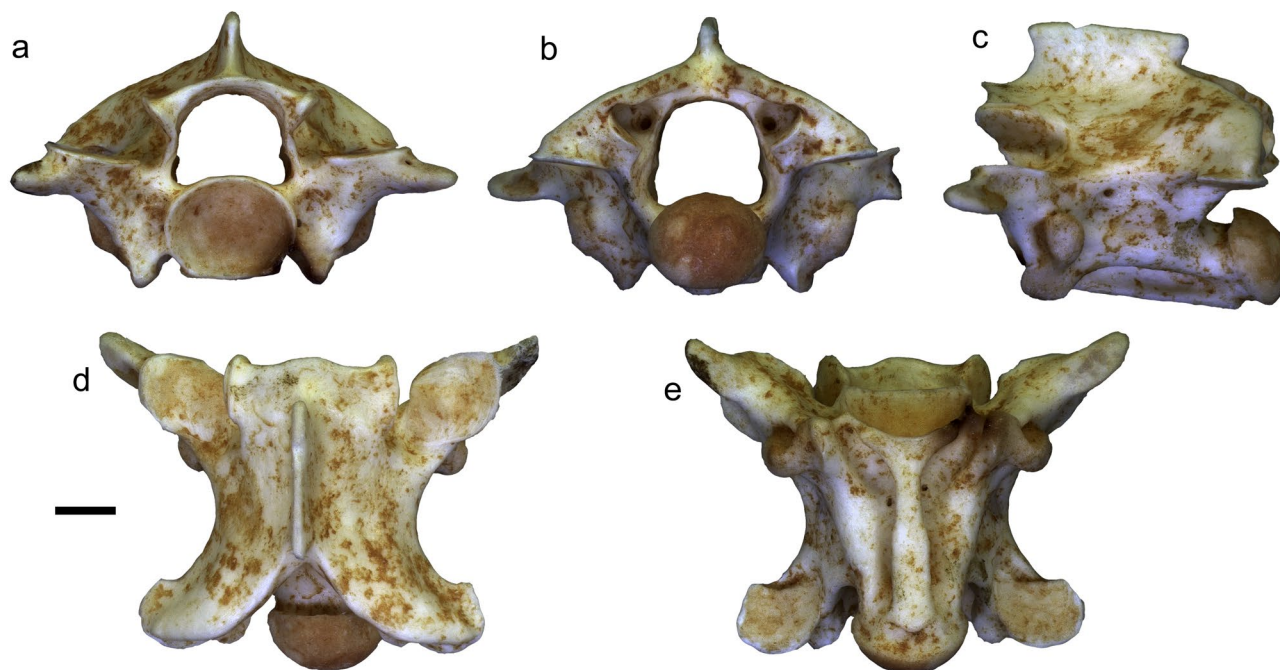


Fig. 6 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Posterior trunk vertebra (MT-S-VI-20) in anterior (a), posterior (b), left lateral (c), dorsal (d), and ventral (e) views. Scale bar corresponds to 1 mm.

nummifer (Reuss, 1834), by its more depressed neural arch, less dorsally inclined prezygapophyses, and differently shaped neural spine and zygantrum; from *Hierophis gemonensis* (Laurenti, 1768), by its shorter centrum, more anteriorly directed prezygapophyseal accessory processes, wider haemal keel, much wider cotyle and condyle, shorter neural spine, and more expanded postzygapophyses; from *Hierophis viridiflavus* (Lacépède, 1789), by its shorter centrum, more anteriorly directed prezygapophyseal accessory processes, wider haemal keel, much wider cotyle and condyle, shorter and differently shaped neural spine, and less extended prezygapophyses; from *Macroprotodon brevis* (Günther, 1862) by its larger size, more anteriorly oriented prezygapophyseal accessory processes, much wider cotyle and condyle, less prominent lateral lobes on the zygosphenes, wider haemal keel, and different-shaped neural spine; from *Platyceps najadum* (Eichwald, 1831), by its larger size, broader and shorter centrum, larger prezygapophyseal articular facets, thicker prezygapophyseal accessory processes, wider haemal keel, wider cotyle and condyle, and taller neural spine; from *Telescopus fallax* (Fleischmann, 1831) by its larger size, more vaulted neural arch, different shape of zygosphenes with not so prominent lateral and median lobes, larger and more anteriorly directed prezygapophyseal accessory processes, wider haemal keel, and wider cotyle and condyle; from *Zamenis lineatus* (Camerano, 1891) and *Zamenis longissimus* (Laurenti, 1768) by its anteroposteriorly shorter centrum, thicker haemal keel, more anteriorly directed prezygapophyseal accessory processes, thinner zygosphenes, and shorter neural arch and neural spine; from *Zamenis situla* (Linnaeus, 1758), by its prezygapophyseal accessory processes being more elongated, more pointed, and more anteriorly directed; from *Zamenis scalaris* (Schinz in Cuvier, 1822) by a wider haemal keel, more anteriorly directed prezygapophyseal

accessory processes, smaller prezygapophyseal articular facets, less pronounced diapophyses and parapophyses, shorter and different shaped neural spine, and more depressed neural arch, while also lacks a much ventrally expanded haemal keel in posterior trunk vertebrae.

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. can be further differentiated from the two European psammophiids, i.e., *M. insignitus* (Geoffroy Saint-Hilaire, 1827), and *Malpolon monspessulanus* (Hermann, 1804), by its much smaller size, shorter and broader centrum, wider haemal keel, thinner zygosphenes, shorter and more anteriorly directed prezygapophyseal accessory processes, wider cotyle and condyle, more depressed neural arch, and shorter neural spine.

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. can be also differentiated from the following extant North African colubrids: from *Macroprotodon cucullatus* (Geoffroy Saint-Hilaire, 1827) by its more anteriorly directed and less dorsally inclined prezygapophyseal accessory processes; from *Spalerosophis diadema* (Schlegel, 1837) by its much shorter neural spine, more anteriorly directed prezygapophyseal accessory processes, larger and more elongated prezygapophyseal articular facets, wider haemal keel, and differently-shaped neural arch; from *Dasyplectis scabra* (Linnaeus, 1758), by its not so dorsally inclined prezygapophyses, absence of the peculiar, characteristic hypapophyses in the anterior trunk vertebrae that are present in the African taxon, much shorter neural spine, more depressed neural arch, and a generally totally different morphology (see figs in Gans, 1952).

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. can be also differentiated from the following North African psammophiids and lamprophiids: from *Boaedon fuliginosus* (Boié H. in Boié F., 1827) by its much greater extent of prezygapophyseal accessory processes, wider

cotyle and condyle, more depressed neural arch, and most principally the absence of hypapophyses in the posterior trunk vertebrae; from *Lycophidion capense* (Smith, 1831), by the absence of hypapophyses in its mid- and posterior trunk vertebrae (see Bogert, 1940; Malnate, 1972); from *Psammophis schokari* (Forskål, 1775), and *P. sibilans* (Linnaeus, 1758), by its shorter and broader centrum, less curved postzygapophyses, and different shape, orientation,

acuteness, and inclination of the prezygapophyseal accessory processes; from *Rhagerhis moilensis* (Reuss, 1834) by its shorter centrum and the wider haemal keel (see figs in Böhme & de Pury, 2011).

Among North African taxa, we were unable to directly compare *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. to the following: *Lytorhynchus diadema* (Duméril, Bibron, & Duméril, 1854), as well as few species of

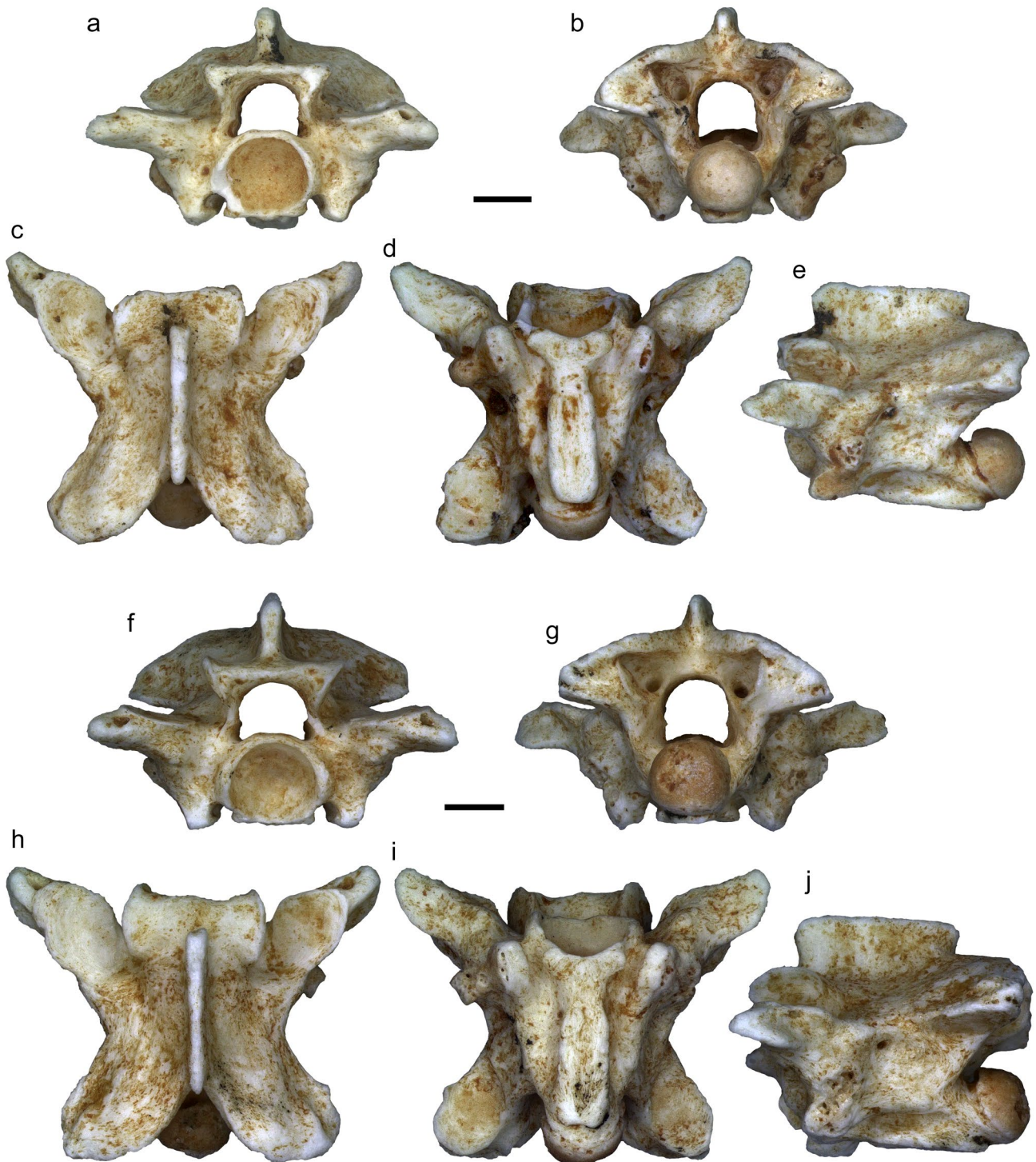
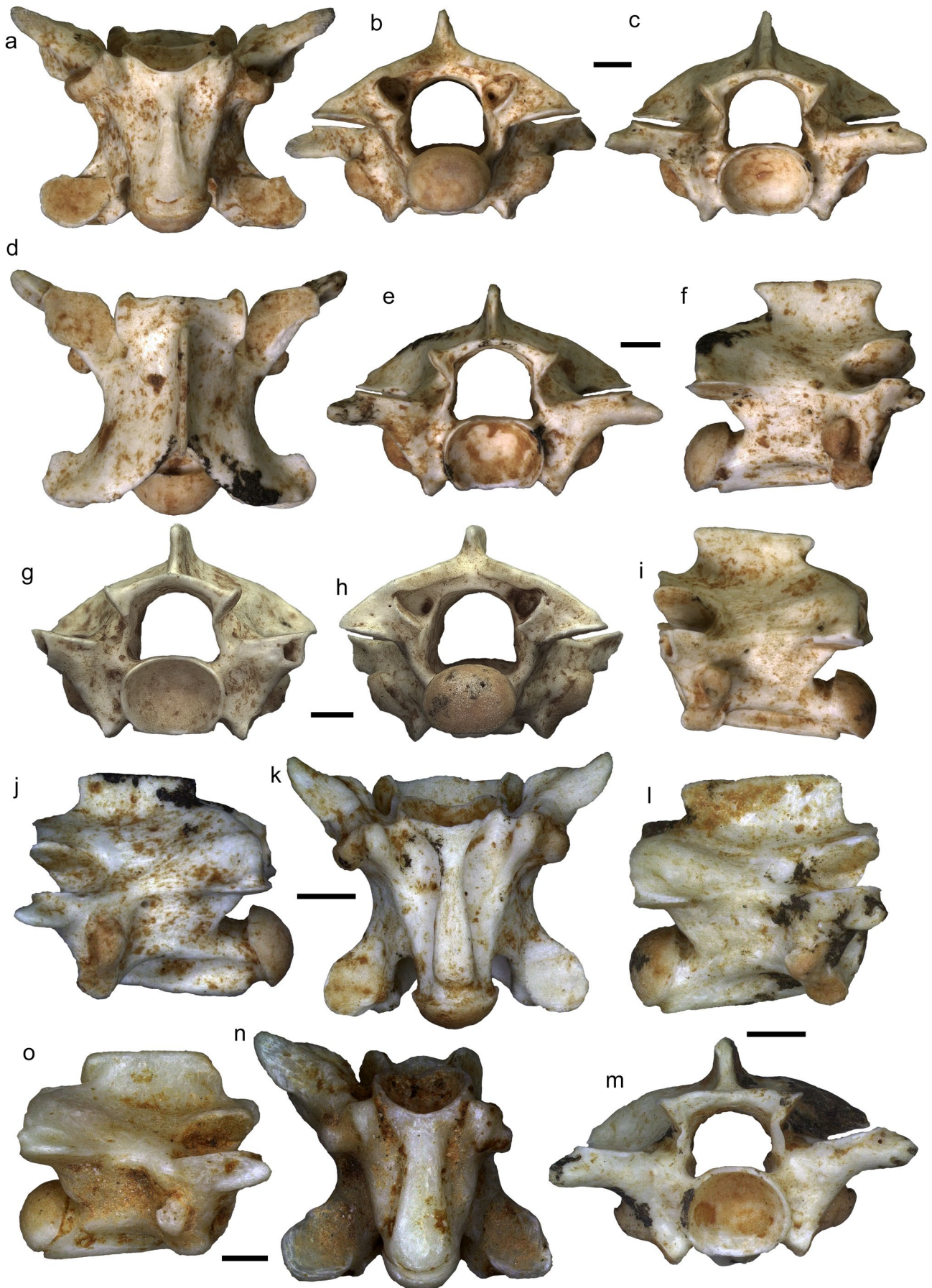


Fig. 7 - *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. a-e) Posteriormost trunk vertebra (MT-S-VI-13) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views. f-j) Posteriormost trunk vertebra (MT-S-VI-14) in anterior (f), posterior (g), dorsal (h), ventral (i), and left lateral (j) views. Scale bars correspond to 1 mm.



the genera *Eirenis* Jan, 1863, *Hemorrhoids* Boié, 1826, *Platyceps* Blyth, 1860, *Psammophis* Boié in Fitzinger, 1826, *Spalerosophis* Jan in Filippi, 1865, and *Telescopus* Wagler, 1830, due to the fact that there was not such material available for direct study and comparisons and their vertebral anatomy has not been described/figured in the literature. Among these inadequately known taxa, we consider that *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. possesses a different morphology from the African species of *Eirenis*, *Hemorrhoids*, *Platyceps*, *Spalerosophis*, and *Telescopus*, as the new Sardinian taxon was extensively compared with other congeneric species of these genera and its vertebral anatomy was much different (see above). The colubrid *Lytorhynchus diadema* is present in northern Africa (Wallach et al., 2014). Its vertebral anatomy has not been described, however, the genus *Lytorhynchus* Peters, 1862, is known to be the sister taxon and genetically rather close to the Indian *Wallaceophis* Mirza, Vyas, Patel, Maheta & Sanap, 2016, vertebrae of which have been figured (Mirza et al., 2016: fig. 2). Judging from that single known figure of a mid-trunk vertebra of *Wallaceophis gujaratensis* Mirza, Vyas, Patel, Maheta & Sanap, 2016, that is nevertheless only depicted in posterior and lateral views, the Sardinian taxon can be differentiated by its slightly more vaulted neural arch, dorsoventrally taller and differently-shaped neural spine, wider haemal keel, and larger and more elliptical condyle, so we can (at least tentatively) assume that it can be also differentiated from *Lytorhynchus* spp. by similar features.

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. can be readily differentiated from natricines, viperids, and elapids, by the absence of hypapophyses in its mid- and posterior trunk vertebrae. Nevertheless, the distinct anterior and posterior overhanging of the neural spine of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. is a typical feature for natricines (e.g., Szyndlar, 1991b; Ivanov, 2002), however, we have to highlight that this feature is observed also in many colubrids as well.

It is thus evident that *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. is different from all extant European and relevant North African snake species. The wide haemal keel that is characteristic of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. is a feature that is also present in *Elaphe quatuorlineata*; these two taxa also share a similar ratio of centrum length to neural arch width. However, as mentioned above, the two forms possess a number of differences that suffice generic separation. Besides *E. quatuorlineata*, the closest similarity of the new Sardinian form with European taxa is with *Zamenis scalaris* and *Z. situla*, in terms of several features, such as overall size, degree of anteroposterior compression of the centrum, shape of zygosphenes and vaultness of the neural arch. Interestingly, *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. bears certain resemblance with vertebrae of the extant African and Middle East genera *Atractaspis* Smith, 1849, *Crotaphopeltis* Fitzinger,

1843, and *Grayia* Günther, 1858 (see figs in Thireau, 1967 and Zaher et al., 2019). However, that resemblance is only confined to few sporadic characters, while, at the same time, there are important features that can enable distinction among these distantly related forms and *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp.

Among extinct taxa from Europe, *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. bears certain features in common, especially the wide haemal keel, with "*Coluber*" *planicarinatus* (Bachmayer & Szyndlar, 1985) from the Miocene of Austria, *Texasophis bohemicus* Szyndlar, 1987, from the Miocene of the Czech Republic, and mostly, *Telescopus bolkayi* Szyndlar, 2005, from the Miocene of Hungary; nevertheless, all these three extinct taxa can be differentiated from *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp., by a number of features, including the ratio of centrum length to neural arch width, the orientation and length of the prezygapophyseal accessory processes, the shape and height of the neural spine, and the zygosphenes convexity and thickness (see figs in Bachmayer & Szyndlar, 1985, and Szyndlar, 1987, 2005). *Paleoheterodon arcuatus* Rage & Holman, 1984, from the Miocene of France, the sole so far named dipsadid from Europe, shares a wide haemal keel with *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp., however, the two forms can be readily differentiated by important differences in the elongation of the centrum, vaultness of the neural arch, orientation of the prezygapophyseal accessory processes and shape of zygosphenes (see figs in Rage & Holman, 1984). Additionally, the tubercle-like structures of the posteriormost trunk vertebrae of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. are slightly reminiscent of the recently described *Periergophis micros* Georgalis, Villa, Ivanov, Vasilyan & Delfino, 2019, from the latest Miocene/earliest Pliocene of Maramena in northern Greece, but still in the Sardinian new taxon they are not so prominent and besides, it has a much larger size and an overall radically different morphology than the Greek form (see figs in Georgalis et al., 2019b).

In fact, certain vertebral features of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. appear to be unique for the new Sardinian species. Notably, the groove present in the haemal keel of the posteriormost trunk vertebrae is a feature that is not present in any other extinct and extant form. Similarly, the unusually marked concavity on the dorsolateral rim of the zygantrum in *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. appears to be a unique feature as well; a kind of concavity on the dorsolateral rim of the zygantrum can be variably observed in some extant colubrids (e.g., *Coronella austriaca*, *Dolichophis caspius*), though this is not so prominent as in *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp., neither so consistent throughout the vertebral column as in the new Sardinian taxon. Such features, along with the above mentioned combination of vertebral characters, enable the taxonomic distinctiveness

Fig. 8 - Additional vertebrae of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. a-c) Mid-trunk vertebra (MT-S-VI-03) in ventral (a), posterior (b), and anterior (c) views. d-f) Mid-trunk vertebra (MT-S-VI-07) in dorsal (d), anterior (e), and right lateral (f) views. g-i) Mid-trunk vertebra (MT-S-VI-04) in anterior (g), posterior (h), and left lateral (i) views. j-k) Posterior trunk vertebra (MT-S-VI-15) in left lateral (j) and ventral (k) views. l-m) Posterior to posteriormost trunk vertebra (MT-S-VI-16) in right lateral (l) and anterior (m) views. n-o) Posterior to posteriormost trunk vertebra (MT-S-VI-12) in right lateral (n) and ventral (o) views. Scale bars correspond to 1 mm.

of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. Nevertheless, its exact phylogenetic affinities among caenophidians are difficult to disentangle due, on one side, to the absence of a comprehensive data matrix based on the vertebral morphology of snakes (whose precise phylogenetic value has still to be demonstrated) and, on the other side, to the above mentioned fact that recent phylogenetic approaches using both molecular data and external morphology revealed a new image of disparate partitioning in the traditional concept of “Colubrinae”. Accordingly, we cannot further determine whether this new insular endemic taxon evolved locally, or represents the product of a dispersal event from Europe or Africa to Sardinia, or even a relic survivor of an ancient lineage (still undetected elsewhere) that was present in the island since the early Neogene or Paleogene.

Insularity and snake diversity: Mediterranean fossil snakes

Although a not so popular fact as the respective unique island turtle and lizard forms, extant faunas demonstrate high degrees of snake species endemism across insular environments of the planet (e.g., Wallach et al., 2014). This speciation and unique diversity of insular snake forms can be observed even in the most remote oceanic islands. Typical examples are the adaptive radiation of scolecophidians from the Caribbean and Micronesia, candioids from the Pacific Islands, boids, tropidophiines, and dipsadids from the Caribbean, crotalines from the California Islands, and elapids from the Archipelagos of Papua New Guinea (Thomas & Hedges, 2007; Wynn et al., 2012; Reynolds et al., 2013; Wallach et al., 2014; Meik et al., 2018; O’Shea & Kaiser, 2018; Bochaton et al., 2019; Ruiz-Sanchez et al., 2019). Insular snakes also include taxa with extreme morphologies, such as the Mascarenian bolyeriids, which are known to possess a divided into two-parts maxilla, a totally unique feature among all tetrapods (Frazetta, 1970; Maisano & Rieppel, 2007). Despite this abundance, high diversity, and uniqueness of extant forms, fossil snakes from islands are only scarcely known.

Interestingly, snakes in the extant herpetofauna of the Mediterranean islands have not reached high levels of endemism such as those of their sympatric lizards. As such, most Mediterranean islands are inhabited by snake species that are also present in mainland Europe and/or Anatolia, with the only exception of the viperid *Macrovipera schweizeri* (Werner, 1935), that is endemic to Milos and three other nearby islands in Cyclades in the Aegean Sea (Werner, 1935; Sindaco & Jeremčenko, 2008). The identification of further endemic species, *Dolichophis cypriensis* (Schätti, 1985) from Cyprus, and *Elaphe rechingeri* Werner, 1932, from Amorgos Island in the Aegean Sea, has not met wide acceptance in ophidian literature, while, “*Coluber*” *gyarosensis* Mertens, 1968, a purported endemic in Gyaros Island in the Aegean Sea, is now considered to be conspecific with *Hierophis viridiflavus*, being probably simply the product of human transportation during Antiquity (Utiger & Schätti, 2004; but see Wallach et al., 2014). At the subspecies level, more supposed endemic taxa have been named, such those of the species *Natrix natrix* (Linnaeus, 1758) from Cyprus, Corsica, and Kephallonia (Ionian Sea) (Hecht, 1930), and of the species *Elaphe quatuorlineata* from Skyros and

various Cyclades Islands in the Aegean Sea (Cattaneo, 1999), however, these are all currently considered as junior synonyms of the mainland nominal taxa (Wallach et al., 2014). Snake fossil finds from the Cenozoic of the Mediterranean islands are only poorly documented.

The islands of the Aegean Sea have yielded snake fossil remains spanning from the early Neogene up to the Quaternary. There are early Miocene snake finds from the localities Kymi (?MN 3) and Aliveri (MN 4) in Euboea Island (Römer, 1870; Georgalis et al., 2019a), Lapsarna (?MN 3) in Lesbos Island (Vasileiadou et al., 2017), however, these islands are so geographically proximate to the mainland that were apparently part of it during that time. The same applies for much younger records from the Pliocene of Maritsa and Apollakia in Rhodes Island (Szyndlar, 1991a), the Pleistocene of Laghada B in Kos Island (Szyndlar, 1991b), the indeterminate Quaternary of Pili B, also in Kos Island (Szyndlar, 1991a, b), and the Middle Pleistocene of Latomi in Chios Island (Schneider, 1975), as these islands are also too close from the adjacent Anatolia that probably were in fact part of it during the Neogene or Quaternary. It seems thus that the oldest Aegean Islands true insular snake find is a colubrid (?natrixine) from the late Miocene (MN 9) of Plakias, Crete Island (Georgalis et al., 2016b). Nevertheless, even on this occasion, it is not fully clear whether Crete at that time was indeed an isolated island or somehow connected with the Greek mainland (Georgalis et al., 2016b). In the Pleistocene of Crete, snake finds probably corresponding to extant forms have been described from Bate (*Hierophis* cf. *gemonensis*) and Gerani (*Natrix* cf. *tessellata*) caves (Kotsakis, 1977a; Szyndlar, 1991b), while undescribed mentions of additional taxa (cf. *Zamenis longissimus* and *Zamenis situla*) have been reported from Gerani cave, Rethymno, Sitia 1, and Sitia 2 (Szyndlar, 1991a, b).

Cyprus has yielded only relatively recent fossil snake records, as all such known occurrences are of Holocene age. Nevertheless, an array of different taxa pertaining to *Dolichophis jugularis*, *Telescopus fallax*, *Natrix natrix*, and large-sized “Oriental vipers” are known from the localities Aetokremnos, Khirokitia, and Kisonerga-Mylioudia (Watson et al., 1977; Bailon, 1999; Croft et al., 2017).

In the Balearics, the oldest find is an indeterminate viperid from the middle Miocene of Punta Nati 2, in Minorca (Bailon et al., 2002). An indeterminate viperid has been also described from the nearby younger, early Pliocene locality of Punta Nati 3 (Bailon et al., 2002). However, the most diverse assemblage from Minorca is known from the early Pliocene of Punta Nati 12, which yielded a “colubrine” as well as the so far only named Mediterranean extinct insular snake species, *Vipera natiensis* Bailon, Garcia-Porta & Quintana-Cardona, 2002 (Bailon et al., 2002). Mallorca has also interesting snake finds: the early Pliocene locality of Caló den Rafelino has yielded “colubrines” and at least two viperid taxa, one with probable affinities with the Minorcan *Vipera natiensis* and a large-sized “Oriental viper” (Bailon et al., 2010; Bover et al., 2014). Na Burguesa-1, another Pliocene (MN 15/16) Mallorcan locality, has yielded an interesting assemblage, with scolecophidians, “colubrines”, and large-sized “Oriental vipers” (Bover et al., 2014; Torres et al., 2014). Notably these Mallorcan “Oriental vipers”

from Caló den Rafelino and Na Burguesa-1 were of exceptional sizes (centrum lengths more than 12 mm) and rank among the largest viperids, though still smaller than their contemporary European mainland giant relatives (Georgalis et al., 2016a).

In Sicily, snakes are known from the early Middle Pleistocene of Spinagallo, being represented by a form probably related to *Hierophis viridiflavus* and an indeterminate form of the genus *Natrix* Laurenti, 1768 (Kotsakis, 1977b). Additionally, material from the Pleistocene of Monte Pellegrino, that was originally referred to rodents (De Gregorio, 1887), pertains in fact to snakes, probably “colubrines” (see Delfino, 2002). The same applies also for supposed rodent material from the Pleistocene of Castellana (De Gregorio, 1925) that apparently pertains to snakes (see Delfino, 2002). Recently, Forgia et al. (2013) reported the presence of *Elaphe* cf. *quatuorlineata*, *Vipera* gr. *V. aspis*, and undetermined snakes in the Holocene of Vallone Inferno (Scillato), however, no figure or description of that material was provided.

Sardinia has apparently yielded the so far oldest insular remains of snakes from the Mediterranean, known from the early to early middle Miocene (MN 1-5) of Oschiri (Venczel & Sanchíz, 2006). This locality yielded *Eoanilius oligocenicus* Szyndlar, 1994, an indeterminate natricine, and a viperid of the *Vipera aspis* complex; however, this material was only rather briefly described with none accompanied figure that could confirm such taxonomic allocations (Venczel & Sanchíz, 2006). A more diverse snake fauna from the island is known from the early Pliocene (MN 15) of Capo Mannu D1 Local Fauna, comprising indeterminate “colubrines” and natricines, an erycine with potential affinities with the extant *Eryx jaculus* (Linnaeus, 1758), and the viperid *Vipera* Laurenti, 1768 (Delfino et al., 2011). The Plio-Pleistocene fissure fillings of Monte Tuttavista have yielded so far a viperid of the *Vipera aspis* complex, while reports of *Natrix* and indeterminate “colubrines” also occur (Abbazzi et al., 2004); to these, we here now add, *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp., known exclusively from the fissure VI of Monte Tuttavista. Finally, the early Middle Pleistocene Grotta di Dragonara has yielded a “colubrine” (probably related to *Hierophis*) and the natricine *Natrix* (Kotsakis, 1980). It is here worth noting that the supposed Sardinian endemic pythonid *Palaeopython sardus* Portis, 1901b, from the middle Miocene of Monte Albu (= Monte Alvu), has been recently demonstrated to represent not even a reptile but instead a fish (Delfino et al., 2014).

Furthermore, besides the now existing islands, palaeogeographic reconstructions have shown that other islands have also existed in the Mediterranean, that are now only part of the European mainland. An interesting such case is the so called Gargano palaeoisland, which was formed during the Neogene in the area of modern day Apulia, Italy, and possessed a unique endemic mammal fauna (e.g., Van der Geer, 2014). From the late Miocene-early Pliocene of Gargano “Terre Rose”, there have been described three “colubrines”, one with probable affinities with *Zamenis*, another with *Telescopus*, and another with the Austrian Miocene species “*Coluber*” *planicarinatus*, plus a viperid of the “Oriental vipers” group (Delfino, 2002).

CONCLUSIONS

Sardophis elaphoides Georgalis & Delfino n. gen. n. sp. is a new colubroid taxon from the early Pleistocene of Monte Tuttavista VI in Sardinia, based on abundant postcranial material, including complete vertebrae. Detailed comparisons with extant and extinct European and northern African forms reveal that the new Sardinian species can be diagnosed by a unique combination of vertebral features. The precise affinities of *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. within colubroid snakes remain unresolved, as are also its exact origins. *Sardophis elaphoides* Georgalis & Delfino n. gen. n. sp. represents the second only known Cenozoic extinct insular endemic named snake taxon from Europe, the other being *Vipera natiensis*, from the Pliocene of Minorca (Bailon et al., 2002), implying that not only mammals, turtles, and lizards reached high degrees of insular endemism in the proximate geologic past of the Mediterranean islands. This discovery further adds to the known fossil record of reptiles in Sardinia (Portis, 1901a; Comaschi Caria, 1959; Kotsakis, 1980; Abbazzi et al., 2004, 2008; Venczel & Sanchíz, 2006; Chesi et al., 2007; Delfino et al., 2008, 2011; Georgalis et al., 2017; Tschopp et al., 2018; Zoboli et al., 2019), that testifies for a significant loss of taxa (geomydids and soft-shelled turtles, agamid lizards, worm lizards, the large lacertid *Timon* Tschudi, 1836, and vipers) and indicates that the current assemblage is significantly impoverished if compared even only to the late Neogene and early Quaternary ones.

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APPENDIX

List of comparative skeletal material of extant species

Colubridae

Boiga sp. (MDHC 137); *Coelognathus helena* (UWr uncat.); *Coronella austriaca* (MDHC 41, MDHC 412, NHMW 22628); *Coronella girondica* (MDHC 203, MNCN 16325); *Dolichophis caspius* (HNHM 2004.70.1, HNHM 2004.72.1.b, MDHC 266, MDHC 289); *Dolichophis jugularis* (NHMW 29055.1, ZZSiD 326); *Eirenis modestus* (MDHC 290, MDHC 291); *Elaphe dione* (ZZSiD 417); *Elaphe quatuorlineata* (MDHC 169, MDHC 383, MDHC 401, ZZSiD 248); *Elaphe sauromates* (ZZSiD 231); *Hemorrhois hippocrepis* (MNCN 16316, MNCN 16319, ZZSiD 354); *Hemorrhois nummifer* (NNHC-HUJ- Z-432, NNHC-HUJ- Z-435, NNHC-HUJ- Z-446, NNHC-HUJ- Z-449); *Hemorrhois ravergieri* (ZZSiD 406); *Hierophis gemonensis* (MDHC 399, NHMW 22535.1); *Hierophis viridiflavus* (MDHC 219, MDHC 306, MNCN 16321, NHMW 22563, ZZSiD 278); *Lampropeltis getula* (UWr uncat.); *Macroprotodon brevis* (MNCN 16344 [juvenile], MNCN 16345); *Macroprotodon cucullatus* (ZZSiD 351); *Orthriophis taeniurus* (UWr uncat.); *Pantherophis guttatus* (UWr

uncat.); *Platyceps najadum* (MDHC 248); *Spalerosophis diadema* (IRSNB 92.048.R.0052, ZZSiD 485); *Telescopus fallax* (MDHC 303, NHMW 22632, ZZSiD 412); *Zamenis lineatus* (MDHC 382); *Zamenis longissimus* (HNHM 2004.57.1.b, MDHC 92, NHMW 22534.1, ZZSiD 20); *Zamenis scalaris* (MNCN 16328, MNCN 16333, MNCN 16343); *Zamenis situla* (MDHC 21).

Dipsadidae

Heterodon platirhinos (ZZSiD 247).

Lamprophiidae

Boaedon fuliginosus (MNHN 1967-149); *Boaedon lineatus* (MNHN 1967-85).

Psammophiidae

Malpolon insignitus (MDHC 400, NHMW 22629); *Malpolon monspessulanus* (MNCN 16357, MNCN 41034); *Psammophis lineolatum* (ZZSiD 484); *Psammophis schokari* (MDHC 278, MNHN uncat., ZZSiD 413); *Psammophis sibilans* (MNHN 1966-209).