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# The rise and fall of the Iberian cobras (Elapidae, *Naja*) in the context of their European and global fossil record

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Running title: Cobras in the Iberian Miocene

**Abstract:** Very few remains of elapid snakes are known from the Iberian Peninsula, but these include a probable endemic extinct species of cobra, *Naja iberica* from the Late Miocene. We here describe isolated vertebrae of cobras from several Middle to Late Miocene localities in the Vallès-Penedès Basin (Catalonia, Spain). All these fossils are herein referred to an indeterminate species of the genus *Naja*. These remains are the first conclusive evidence that cobras were present in Iberia before the Messinian Salinity Crisis, and that they persisted there throughout the Miocene (and ultimately until the Pliocene). Recently, a phylogeny of extinct *Naja* based on cranial and vertebral morphology recognized *N. iberica* as a distinct lineage separate from the Central European one, represented mainly by *Naja romani*. However, due to taxonomic uncertainties, it is still unclear whether Iberian cobras were all part of a single lineage or several *Naja* lineages inhabited the Iberian Peninsula. They went finally extinct in Iberia before the end of the Pliocene. In the Vallès-Penedès Basin, cobras were living in a mosaic environment, surviving through different phases characterized by different environmental features.

**Key words:** Europe; Iberian Peninsula; Miocene Climatic Optimum; Neogene; Pyrenees; Serpentes

Snakes are a group of diverse and iconic squamate reptiles, whose unique morphology and behaviour have had—and still have—a particular influence on humans. In this context, cobras figure prominently among the snake groups that most attracted the human interest. These animals gained significant cultural relevance, to the level of even becoming readily recognisable also by non-specialists thanks to noticeable features such as the ability to raise the anterior part of their body in a vertical stance, that of spitting venom to long distances, and their typical hood. There are other snakes capable of enacting a standing behavior (Pokrant *et al.* 2017) and of producing a hood (e.g. Pitman 1965; León *et al.* 2013; Pokrant *et al.* 2017), and on the opposite hand, not all cobra species share the spitting behaviour (Berthé 2011; Kazandjian *et al.* 2021). Nevertheless, these features became emblematic of cobras, and these animals were featured in several cultures and religions as part of folk tales (both in positive and negative roles) or as embodiments of deities (Crump 2015). Cobras are also often used in popular media, either in a symbolic way or more directly to straightforwardly communicate the image of a menacing snake.

From a herpetological point of view, cobras are venomous snakes, members of the family Elapidae. They mostly belong to the genus *Naja* Laurenti, 1768 (the “true cobras” with 34 extant species; Uetz *et al.* 2023), but a few species commonly referred to as cobras are allocated to other genera: *Aspidelaps* Fitzinger, 1843 ( “shield cobras”, two species); *Hemachatus* Fleming, 1822 (rinkhals, or “ring-necked spitting cobras”; one species); *Ogmodon* Peters, 1864 (“Fiji cobra”, one species); *Ophiophagus* Günther, 1864 (“King cobra”, one species); *Pseudohaje* Günther, 1858 (“tree cobras” or “forest cobras”, two species); and *Walterinnesia* Lataste, 1887 (“desert cobras”, two species). However, the relationships of these genera with true cobras are complex. *Hemachatus* is robustly recovered as sister to *Naja* in recent large scale-molecular phylogenies (e.g. Zaher *et al.* 2019, 2021), and the clade composed by these two genera plus *Aspidelaps* and *Walterinnesia* is also strongly supported. *Ophiophagus* is less closely related with true cobras, being an early branching offshoot of the clade including *Naja* and the above-mentioned related genera (Zaher *et al.* 2019, 2021), whereas *Ogmodon* is more closely related to sea snakes and sea kraits than to other elapids (Vitt & Caldwell 2009; Zaher *et al.* 2019, 2021; Uetz *et al.* 2023). The affinities of *Pseudohaje* are still obscured by its omission from large scale published phylogenies, but recent work by Plettenberg Laing (2019) and Major *et al.* (2023) supported it as sister to *Naja* in a closer position than *Hemachatus*. Regarding *Naja*, four different clades were recognised in recent phylogenetic analyses (Wüster *et al.* 2007; Wallach *et al.* 2009; Zaher *et al.* 2019, 2021; Major *et al.* 2023), which were either treated as subgenera (Wallach *et al.* 2009) or genera (Wallach *et al.* 2014) in recent literature: *Afronaja* Wallach et al., 2009; *Boulengerina* Dollo, 1886; *Naja* s.s.; and *Uraeus* Wagler, 1830.

Nowadays, true cobras have a broad range, encompassing Africa, the Arabian Peninsula, the Middle East, and Southern Asia (Sindaco *et al.* 2013; Uetz *et al.* 2023). Asian and Afro-Arabian true cobras make up two different clades (Wüster *et al.* 2007; Wallach *et al.* 2009; Pyron *et al.* 2013; Zaher *et al.* 2019), with the Asian one corresponding to the *Naja* s.s. and the Afro-Arabian one comprising the remaining subgenera. These elapids independently evolved the ability to spit venom with pain-enhancing toxins in three different lineages (African cobras, Asian cobras, and *Hemachatus*), maybe as a defensive adaptation against hominins (Kazandjian *et al.* 2021). The fang morphology of spitting cobras is sensibly different from that of non-spitting cobras (among others, Bogert 1943; Young *et al.* 2004; Berthé 2011), and therefore fossils can be positively identified. However, with the single exception of an isolated maxilla from South Africa (potentially representing either a rinkhal or a true cobra; Vilakazi *et al.* 2018), there are no fossil maxillae or isolated fangs disclosing the presence of spitting cobras in the fossil record yet.

Cobras also inhabited Europe during the Neogene (Rage 1984, 2013; Szyndlar & Rage 1990; Szyndlar & Zerova 1990; Szyndlar 1991a; Pokrant *et al.* 2017; Ivanov 2022), and a few occurrences testify their past presence in the Iberian Peninsula (Alberdi *et al.* 1981; Alférez Delgado & Brea López 1981; Jaen & Sanchiz 1985; Szyndlar 1985, 1988; Szyndlar & Rage 1990; Bailon, 1992; Carmona *et al.* 2010; Luján 2015). These occurrences even include a potentially endemic extinct species, *Naja iberica* Szyndlar, 1985 from Algora (Late Miocene, MN13). As currently known, however, the Neogene fossil record of snakes in Iberia is largely dominated by other snake clades, mainly colubroids, constrictors, and viperids. Thus, available information on the history of cobras in the area is scarce. To provide new data and contribute to this topic, here we thoroughly describe and identify elapid vertebrae from the Vallès-Penedès Basin (VPB), in Catalonia, further providing an overview of all known fossil cobras and discussing the role of these snakes as palaeoenvironmental proxies.

# GEOLOGICAL SETTING

The material described in this paper comes from various sites of the VPB (Fig. 1), a small and elongate half-graben parallel to the coastline and bounded by the Catalan Coastal (Littoral and Prelittoral) Ranges, near the city of Barcelona (Catalonia, Spain). This basin formed during the latest Oligocene in the context of a larger rifting process that affected the Western Mediterranean (Roca *et al.* 1999). The sedimentary infill of the Vallès-Penedès spans almost the entire Miocene (~20–7 Ma; see Casanovas-Vilar *et al.* 2016a, 2022a, for recent reviews) and mostly consists of alluvial fan deposits that were sourced from the bounding reliefs. However, during the Middle Miocene various marine transgressions affected the basin, the most important one during the Langhian, when the southeastern half of the basin was covered by a shallow sea (Cabrera & Calvet 1996; Casanovas-Vilar *et al.* 2016a, 2022a). The VPB is a reference area for the study of European Miocene terrestrial vertebrates and has been intensely sampled for more than a century, so that hundreds of localities (which combined have yielded tens of thousands of remains) are now known. However, most studies have focused on fossil mammals, with little attention to other groups, such as fossil snakes, which are present at most sites.

The oldest material described here comes from the site of Sant Mamet (SM), within the municipality of Sant Cugat del Vallès. Although new fossiliferous levels (Sant Mamet 1 and 2) have been sampled recently (Jovells-Vaqué 2020), the remains described here come from the classical Sant Mamet site, sampled during previous decades, which was located in a clay quarry (Crusafont *et al.* 1955) and was subsequently destroyed in the 1990s by construction works (Casanovas i Vilar *et al.* 2021). The fossiliferous layers were located just below an ostreid coquina that crops out at the church of Santa Maria de Campanyà (formerly also referred to as Ermita de Sant Mamet), and which correspond to the oldest Langhian marine units in this sector of the basin (Casanovas-Vilar *et al.* 2016a; Jovells-Vaqué 2020; Casanovas i Vilar *et al.* 2021). Before the classical outcrops were destroyed, the Sant Mamet and Rubí sectors were sampled for magnetostratigraphy. Magnetostratigraphic results just revealed one long reverse magnetozone which was correlated to chron C5Br, the long reverse chron that characterizes the base of the Langhian (Garcés Crespo 1995). Such correlation would imply an age between 15.97 and 15.16 Ma (Ogg 2020). Recent biostratigraphic results based on the rodent fauna from Sant Mamet favor a correlation with Aragonian subzone Cb of the Calatayud-Montalbán Basin (Jovells-Vaqué 2020; Jovells-Vaqué & Casanovas-Vilar 2021), which ranges from 16.3–16.0 Ma. Considering all available data, an age of ~16.0 Ma can be estimated for Sant Mamet.

Most of the material described in this paper comes from the fossiliferous area of els Hostalets de Pierola, which includes multiple localities that were traditionally grouped (e.g. Agustí *et al.* 1985) into Hostalets Inferior (supposedly pre-Vallesian levels, based on the lack of hipparionin equids) and Hostalets Superior (Vallesian levels), as well as several localities included within the Abocador de Can Mata macrosite (ACM; Alba *et al.* 2006, 2017, 2022). Recent magnetostratigraphic work at ACM, however, has shown that some localities from the area of els Hostalets traditionally correlated to the latest Aragonian, such as Can Mata 1 (Agustí *et al.* 1985; Moyà-Solà *et al.* 2009), actually postdate the earliest record of hipparionins elsewhere in the basin at 11.2 Ma (Garcés *et al.* 1996; Casanovas-Vilar *et al.* 2016b; Alba *et al.* 2019) and must be hence considered earliest Vallesian (Alba *et al.* 2022). The sediments recorded at ACM span from ~12.6 to ~11.1 Ma (latest MN6 to earliest MN9), although other outcrops from the same area (such as some localities from Ecoparc de Can Mata) have a younger MN9 age (Alba *et al.* 2022). Thus, the remains from els Hostalets de Pierola indeterminate have a wide uncertainty range from latest MN6 to the end of MN9 (~12.6–10.3 Ma), while those from Hostalets Inferior probably range from latest MN6 to earliest MN9 (~12.6–11.1 Ma). In contrast, the remains from various ACM localities can be accurately dated thanks to detailed litho-, bio-, and magnetostratigraphic correlation (Alba *et al.* 2017, 2022). Estimated ages for the sites, to the accuracy of at least 100 ka, can be computed based on interpolated ages for each subchron. The three localities that have yielded cobra remains are correlated to chron C5r.3r, with interpolated ages of 12.0 Ma (ACM/C3-A7), 11.9 Ma (ACM/C5-

C3), and 11.7 Ma (ACM/C4-A1) according to Alba *et al.* (2017, 2022). All these ACM localities are correlated to MN7+8, but while ACM/C3-A7 is correlated on biostratigraphic grounds to the *Megacricetodon crusafonti – Democricetodon crusafonti* interval subzone of the VPB, the two other localities are correlated to the *Democricetodon crusafonti – Hippotherium* interval subzone, the boundary between the two subzones being placed at 11.88 Ma (Casanovas-Vilar *et al.* 2016b).

Finally, the youngest material described in this paper comes from the site of Santiga (SA), in the municipality of Santa Perpètua de Mogoda. The site was initially discovered during excavation works related to the building of an industrial area (current Polígon Industrial de Santiga) near the church of Santa Maria de Santiga (Crusafont-Pairó & Golpe-Posse 1972), being originally referred to as Santiga, and subsequently renamed as Santiga 1 when micromammals were subsequently sampled from a new locality in that area (Santiga 2) during the 1990s. A rich rodent sample is available from the site, which allows for a correlation to detailed local rodent zonation for the VPB. The site is unambiguously correlated to the *Cricetulodon hartenbergeri* range subzone of the VPB, which spans from 10.3 to 10.0 Ma (Casanovas-Vilar *et al.* 2016b), thus corresponding to the early Vallesian (MN9).

## MATERIAL AND METHODS

All fossils herein described were found after a careful review of the VPB collections housed at the ICP Museum (Sabadell, Spain) during the last two decades. Studied specimens from ACM were either recovered after sediment screen-washing or excavated. For screen-washing, we used a special sieving equipment similar to that described in Daams & Freudenthal (1988) and originally designed to collect small mammals. This is a large structure that contains four sieves with mesh sizes of 10 mm, 2.5 mm, 1 mm, and 0.5 mm, which are mounted in series. The fraction under 0.5 mm is discarded since practice has shown that it barely contains any vertebrate remains and these are often too fragmentary to be confidently identified. Material from Sant Mamet (SM) was collected on the surface of the site. Material from SA was recovered during excavations following the discovery of the site during the building of an industrial area, but no further information is available to us on how the cobra vertebrae were collected. Precise information is also not available for the vertebrae from the old collections of Hostalets de Pierola (HP, HPI), for which both surface collection and excavation are possible options. Part of the vertebrae from ACM were preliminary reported by Carmona *et al.* (2010). Osteological terminology follows the one defined by Auffenberg (1963), as reported by Szyndlar (1984) and recently updated by Szyndlar & Georgalis (2023). Measurements were taken with a digital caliper to the nearest 0.01 mm and are provided in Appendix S1). Statistical parameters reported in Appendix S1 and in the following text are based on the specimens for which the related measurements or ratios can be measured and calculated to the most complete level. Photos of selected specimens were mainly taken with a Leica M80 stereomicroscope and a Nikon D7500 camera. Detailed photos of IPS43553 and IPS87398 used to show the epizygapophyseal spine were taken with a Nikon d7500 equipped with a Laowa 25 mm Ultra Macro 2.5X-5X lens and a Sigma 105 mm Macro lens, mounted on a MJKZZ-MFB Stack and Stich system (automated focus rail); the Helicon software was used for stacking. We here follow Uetz *et al.* (2023) in considering *Naja* in a broad sense: that is, without raising to genus rank subgenera such as *Afronaja* as done by Wallach *et al.* (2014).

*Abbreviations*: ACM, Abocador de Can Mata; CL, centrum length; HP, els Hostalets de Pierola; HPI, Hostalets Inferior; ICP, Institut Català de Paleontologia Miquel Crusafont; IPS, acronym of the collections of the ICP (formerly "Institut de Paleontologia de Sabadell"); MCO, Miocene Climatic Optimum; NAW, centrum width; PR-PO, length from the anterior edge of prezygapophyseal articular surface to the posterior edge of postzygapophyseal articular surface; PR-PR, width between the outer edges of prezygapophyseal articular surfaces; SA, Santiga; SM, Sant Mamet; VPB, Vallès-Penedès Basin; ZW, zygosphene width.

## SYSTEMATIC PALAEONTOLOGY

Suborder SERPENTES Linnaeus, 1758

Infraorder ALETHINOPHIDIA Nopcsa, 1923

Clade CAENOPHIDIA Hoffstetter, 1939

Family ELAPIDAE Boie, 1827

Genus *Naja* Laurenti, 1768

*Naja* sp.

### Remains

Two precloacal vertebrae from SM (~16.0 Ma): IPS128035, IPS128036.

27 precloacal vertebrae from ACM: IPS50956 from ACM/C3-A7 (12.0 Ma); IPS29786, IPS48059, IPS48060, IPS48064, IPS48066 from ACM/C4-A1 (11.7 Ma); IPS42218, IPS42237, IPS42252, IPS42253, IPS42258, IPS42296, IPS42375, IPS42390, IPS42392, IPS42393, IPS42445, IPS42461, IPS42472, IPS42501, IPS42503, IPS43553, IPS43580, IPS43595, IPS43688, IPS48045, IPS127501 from ACM/C5-C3 (11.9 Ma).

Five precloacal vertebrae from HP (~12.6–10.3 Ma): IPS87398, IPS127510, IPS127511, IPS127512, IPS127513.

Four precloacal vertebrae from HPI (~12.6–11.1 Ma): IPS128029, IPS128030, IPS128031, IPS128034.

Seven precloacal vertebrae from SA (10.3–10.0 Ma): IPS128022, IPS128023, IPS128024, IPS128025, IPS128026, IPS128027, IPS128028.

## Description

SM (Fig. 2): The two precloacal vertebrae from SM are robust and large. The centrum is anteroposteriorly elongated (CL/NAW = 1.3 in the best-preserved specimen, IPS128035) and procoelous, with a flat ventral surface marked laterally by low and blunt subcentral ridges. In the middle of the centrum, a sharp hypapophysis is present. The distal end of the latter is broken in both specimens. Para- and diapophyses are well separated. The presence/absence or development of a prezygapophyseal accessory process cannot be evaluated because of poor preservation. The cotyle is wide and subcircular. The zygosphene is missing in both specimens, but an inner cast of the neural canal made by consolidated sediment infilling evidences that the sides were constricted at least in IPS128035 (Fig. 2A). The neural arch is low and moderately to distinctly vaulted in posterior view (vaulting ratio is 0.46 for IPS128035 and 0.53 for IPS128036). The interzygapophyseal constriction is shallow. The zygapophyses show a light dorsal tilt. The neural spine is broken off.

ACM (Figs 3–6): These precloacal vertebrae are robust and large. The CL reaches up to 10.46 mm in IPS42445 (lowest value = 5.76 mm in IPS29786; mean = 8.89 mm, n = 18). The procoelous centrum is anteroposteriorly elongated (the CL/NAW ratio varies from 1.05 to 1.45; mean = 1.18, n = 12) and displays large and circular cotyle and condyle. Ventrally, there is a sharp hypapophysis, whose distal portion is generally missing. It was originally complete in IPS42390 (Carmona *et al.* 2010: fig. 4B; Fig. 5A–F), but it is now broken in this specimen as well. The hypapophysis was posteroventrally developed and short, with a slightly sigmoid anterior margin and a rounded end. The posterior end did not extend over the posterior condyle in lateral view. IPS29786 (Fig. 3A–F) also preserves a similar hypapophysis. The ventral surface of the centrum is defined laterally by marked and blunt subcentral ridges. Between the hypapophysis and the ridges the surface is flat, with no subcentral grooves. Paracotylar foramina are absent in all specimens with a preserved and exposed (i.e. not covered by sediment) anterior cotyle, except for IPS42296, in which they are present. The subcotylar tubercles are generally present as small or very small bumps, but they can also be absent (e.g. IPS43553). The paradiapophyses are clearly divided into para- and diapophyseal portions. The parapophyseal portion is longer than the diapophyseal one and bears a short parapophyseal process, which is however preserved only in a few cases. This process is laminar, broad, anteriorly directed and distally rounded. Posterodorsal to the diapophyses, a wide lateral foramen is present at midlength on the lateral surface of the neural arch walls, in at least some vertebrae (e.g. IPS43553). In anterior view, the neural canal is subpentagonal in cross section, with constricted lateral margins. The neural arch is depressed, with a moderately to distinctly vaulted shape in posterior view (vaulting ratio ranges from 0.41 to 0.54 in the seven specimens for which it can be calculated; mean = 0.46). The zygosphene is robust. In anterior view, it has a horizontal roof and strongly dorsally inclined (>45° from the base of the prezygapophyses) zygosphenal facets. In dorsal view, the anterior margin is slightly wavy, with multiple very small convexities. There are three convexities (a median one and two lateral ones) on IPS42237, IPS42390 (Fig. 5C), IPS42445, IPS48060, and likely also on IPS43580 and IPS48064. Five convexities are displayed by IPS42218, IPS43553 (Fig. 6A), IPS42461, and maybe also IPS42375 and IPS43688. The neural spine is narrow and long, almost reaching the anterior end of the zygosphene. Its dorsal portion is incomplete in almost all cases, but it was rather high (but still longer than tall) at least in IPS42375, IPS42393 (Fig. 4C–F), IPS42461, and IPS42472 (Fig. 4I–L). IPS42393 (Fig. 4E–F) and IPS42472 (Fig. 4K–L) also show that the spine slightly overhangs at least posteriorly. A very small epizygapophyseal spine is present (Fig. 7A). The zygapophyses are suboval and very slightly inclined dorsally. Prezygapophyseal accessory processes were present, but they are missing in all cases. When at least partially preserved, the base of these processes is broad. In dorsal view, the interzygapophyseal constriction is very weak, thus giving a wide appearance to the whole vertebra.

HP (Fig. 8): Precloacal vertebrae from HP are similar in morphology to those from ACM, but they are less well preserved. Three of them are large sized, but IPS127510 and IPS127511 are much smaller. The vertebrae are robustly built, with an elongated and procoelous vertebral centrum. For none of the vertebrae we can calculate the CL/NAW ratio, but the best-preserved one, IPS87398, has a CL of 7.92 mm. Ventrally, there is an hypapophysis, which is however incomplete in all specimens. Lateral to the hypapophysis, the ventral surface of the centrum is flat, with very shallow to absent subcentral grooves. The lateral margins of the centrum are represented by low and robust subcentral ridges. Cotyle and condyle are wide and circular. Subcotylar tubercles are either absent (e.g. IPS127512) or present (e.g. IPS127511). The paradiapophyses are well developed, with clearly-separated para- and diapophyseal portions. The two portions are equally long anteroposteriorly. IPS127512 preserves a short, slender and blunt parapophyseal process (Fig. 8K–L). The neural arch is low, moderately to distinctly vaulted in posterior view. The vaulting ratio can be calculated only for IPS127511 (0.51) and IPS127512 (0.46). Anteriorly, there is a robust zygosphene. At least in IPS127512, the latter has two distinct lateral convexities and a more or less straight anterior margin with two small accessory convexities (Fig. 8I). IPS127511 shows very small lateral convexities, together with a small median one. In anterior view, the dorsal margin of the zygosphene is straight. The neural spine is low (three times longer than high in IPS127512; Fig. 8K–L), and it starts from the posterior end of the zygosphene. Pre- and postzygapophyses are well extended laterally and very poorly inclined dorsally. Prezygapophyseal accessory processes are partially present, because only their bases are preserved. There are no epizygapophyseal spines (Fig. 7B). In dorsal view, the vertebrae are rather wide. A distinct interzygapophyseal constriction is present.

HPI (Fig. 9): These vertebrae are large and robustly built. The CL/NAW ratio can be calculated only for IPS128030 and is 0.98 in this specimen. The procoelous centrum is provided with an hypapophysis ventrally, which in no case is completely preserved. Small subcotylar tubercles are present only in IPS128034 (Fig. 9K). The hypapophysis is ventrally flat in its anterior part, becoming sharper posteriorly. The distal end is always missing, but it was most likely not strongly extended in ventral direction based on the preserved portion. The only exception to this is IPS128034, whose hypapophysis displays a very robust base and was likely more extended ventrally (Fig. 9K–L). This vertebra is most probably an anterior trunk vertebra (i.e. a cervical). Lateral to the hypapophysis, the ventral surface of the centrum is flat, with no subcentral grooves. The subcentral ridges are low and blunt. The wide cotyle is subcircular. On the lateral surfaces, the para- and diapophyses are clearly separated and individualized. The preservation is not sufficient to evaluate the possible presence and morphology of parapophyseal processes. The zygapophyses are slightly tilted dorsally. The zygosphene is preserved only in IPS128031. It is wide and robustly built. In anterior view, the lateral sides are constricted and the roof is straight. In dorsal view, the anterior margin is straight; very small convexities are visible, but poor preservation prevents us from confidently count them. The neural arch of these vertebrae is low. It is moderately vaulted in posterior view (the vaulting ratio is 0.44 in the only specimen for which it can be calculated, IPS128029). The interzygapophyseal constriction is poorly marked. The neural spine is broken off in all cases.

SA (Fig. 10): Vertebrae from SA are also large and robust, with an elongated procoelous centrum (CL/NAW ranges from 0.97 to 1.14 in the four specimens sufficiently preserved to allow calculation, with a mean of 1.06) provided with an hypapophysis. The ventral surface of the centrum is flat, with no distinct subcentral grooves and low and blunt subcentral ridges. The hypapophysis misses the distal tip in all specimens, but the anterior portion is either gently convex or rather sharp in cross section. IPS128024 (Fig. 10H–L) bears the best-preserved hypapophysis; based on the preserved portion, the latter was not much extended in ventral direction. There are no subcotylar tubercles, except for very small ones in IPS128028. The anterior cotyle is wide and subcircular. The para- and diapophyses are clearly individualized. Short and laminar parapophyseal processes are present, being slightly anteroventrally directed and with a rounded end. The zygosphene is wide and robustly built. It has constricted lateral walls and a straight roof in anterior view. In dorsal view, its anterior margin is wavy, with several small convexities. The zygapophyses are wide, elliptical and slightly tilted dorsally. The bases of robust prezygapophyseal accessory processes are visible in the specimen preserving the prezygapophyses. The neural arch is low, moderately to distinctly vaulted in posterior view (mean vaulting ratio = 0.49, n = 3; minimum and maximum are 0.45 and 0.51 respectively). The interzygapophyseal constriction is shallow. The only specimen preserving the neural spine is IPS128022 (Fig. 10A–C), which is represented by the dorsal portion of the neural arch only. In this vertebra, the spine is low and rather slender. In lateral view, it is subtrapezoidal, only slightly overhanging anteriorly and posteriorly.

## DISCUSSION

### Identification of the cobra vertebrae from the Vallès-Penedès Basin

The referral to elapids of isolated vertebrae is complicated by similar vertebral features shared by these and other large snakes formerly included in the clade Colubridae sensu lato—as currently intended, Colubridae is a much less inclusive clade, with several former members even placed within elapoid snakes (Zaher *et al.* 2019)—and especially large representatives of those groups historically gathered together as “colubrines” (or “Colubrinae”; e.g. Szyndlar 1984, 1991b). Like elapids, these snakes have elongated vertebrae with a vaulted neural arch and well-developed neural spines, but they significantly differ in displaying a haemal keel instead of an hypapophysis in the middle and posterior trunk portions of the vertebral column. Elapids, on the other hand, retain the hypapophysis throughout the column (Hoffstetter 1939; Szyndlar 1991a). To discriminate between “colubrines” and elapids when dealing with isolated vertebrae, it is thus of primary importance to exclude their belonging to the anterior (i.e. cervical) region of the vertebral column. This can be stated with confidence for almost all of the considered VPB vertebrae due to their elongation, moderately narrow neural canal, and low neural spine, whereas anterior precloacal vertebrae of snakes are generally shorter and provided with a broad neural canal and a higher neural spine. Only IPS128034 (Fig. 9K–L) from HPI is likely a cervical vertebra, but it shares similar general morphology with the other herein-described vertebrae from the same locality and is therefore attributed to the same taxon. There are two other European snake clades with hypapophyses in postcervical precloacal vertebrae: Natricidae and Viperidae. The VPB vertebrae differ from natricids and most viperids, being more comparable with elapids instead, because of the larger size, the higher degree of robustness, and the lower neural spine (Szyndlar 1984, 1991a, b). They further differ from all viperids because of the shorter hypapophysis (at least based on what could be originally observed on IPS42390), the not tilted prezygapophyseal (and postzygapophyseal) facets, and the vaulted, not roof-shaped, neural arch (Szyndlar 1991a). Taking all of this into consideration, the described isolated vertebrae from the VPB can be referred to elapid snakes. Within elapids, they further agree with *Naja* in the shallow interzygapophyseal constriction, large cotyle and condyle, triangular centrum, and well-marked subcentral ridges (Rage & Bailon 2011). Attribution to *Naja* is also supported by the large size and the low CL/NAW ratio (Ivanov 2000). According to Meylan (1987), *Naja* displays small or absent epizygapophyseal spines, PR-PR/PR-PO ratio between 1.15 and 1.35, and ZW/NAW ratio between 0.71 and 1.00. PR-PR/PR-PO can be calculated only for IPS127512 from HP and IPS128023 from SG, being 1.29 and 1.34, respectively, and thus fitting within the range reported by Meylan (1987). This is not always the case for ZW/NAW, though: in four out of seven vertebrae for which this ratio can be calculated (see Appendix S1), it is lower than 0.71 (e.g. 0.66 in IPS43553 from ACM/C5-C3). However, a similar low range is reported for other fossil *Naja* from Europe (e.g. 0.61–0.75, mean 0.69 ± 0.03 in Kohfidisch, Austria; Bachmayer & Szyndlar 1985). It is thus possible that either European extinct *Naja* were characterized by a lower width ratio between zygosphene and centrum or that some sort of variation, missed by Meylan's (1987) dataset, is implicated. Thus, an attribution to *Naja* of the VPB vertebrae is well supported. At least one vertebra in each locality can be confidently identified at genus rank. IPS128028, IPS128031, and IPS128034 do not show a set of diagnostic characters, but they are referred to the same genus on the basis of general morphological congruence with the diagnostic vertebrae from the respective localities.

Identification at the species rank appears trickier, mainly due to the overall similarity that *Naja* vertebrae, especially those of European extinct species, display (Szyndlar 1995: 42). High intraspecific variation in axial morphology is also evident in the vertebral column of *Naja romani* (Hoffstetter, 1939) (Szyndlar 2005), whose holotype is an almost complete individual. Despite this, it is still worth comparing the VPB vertebrae with other *Naja* fossils. The presence of supernumerary convexities on the zygosphene in addition to the median and lateral ones is uncommon in *N. romani* (Hoffstetter 1939; Bachmayer & Szyndlar 1985; Szyndlar & Schleich 1993; Ivanov 2000; Miklas-Tempfer 2003; Syromyatnikova *et al.* 2021), with only some vertebrae from Kohfidisch figured by Bachmayer & Szyndlar (1985: fig. 5; previously referred to *Naja austriaca* Bachmayer & Szyndlar, 1985) and a single vertebra from Fălciu-Prut 1 (identified as *Naja* cf. *romani*; Codrea *et al.* 2022) clearly displaying two small convexities medial to the lateral ones. Having no more than three convexities on the anterior margin of the zygosphene is also the general condition in *Naja iberica* and all *Naja* sp. vertebrae described and/or figured in the literature (see references reported in Appendixes S2 and S3). *Naja depereti* (Hoffstetter, 1939) has underdeveloped lateral convexities of the zygosphene (Bachmayer & Szyndlar 1985; Ivanov 2000). The depression of the neural arch of the VPB vertebrae recalls *N. iberica* (see Szyndlar 1985), but also *Naja antiqua* Rage, 1976 and *Naja haje* (Linnaeus, 1758) (Rage 1976). The neural arch is more vaulted in posterior view in *Naja* vertebrae from Grund (Miklas-Tempfer 2003), Kohfidisch (Bachmayer & Szyndlar 1985), Solnechnodolsk (Syromyatnikova *et al.* 2021), and maybe also Ravin de la Pluie (Georgalis *et al.* 2018a), Rudabánya (Szyndlar 2005), and Çalta (Rage & Şen 1976). However, variation in the degree of depression of the neural arch is clear in the *N. romani* vertebrae figured by Hoffstetter (1939) and Szyndlar & Schleich (1993: fig. 7). Therefore, similarities and differences between the VPB vertebrae and those from other localities are most likely simply due to the portion of the column from which the vertebrae come. The depressed neural arch, together with the higher neural spine, observed in the VPB specimens indicate that at least some of them are probably mid-trunk vertebrae (Hoffstetter 1939; who also mentioned lowering of the neural spine posteriorwards, as is the rule in snakes in general). The height of the neural spine seems to be similar to what is seen in vertebrae identified as *Naja* cf. *romani* from Vieux-Collonges

(Ivanov 2000: fig. 12). Syromyatnikova *et al.* (2021) refuted the identification as *N. iberica* for a vertebra from Solnechnodolsk based on more obtuse prezygapophyseal accessory processes and distally-pointed hypapophysis. Following this line of reasoning, the VPB vertebrae could be linked to *N. iberica* because of the rounded distal end of the hypapophysis. However, data related to this feature are very limited in the material available to us, and thus this possibility must be taken with caution. Following Ivanov (2000), affinities with *N. iberica* may be also found in the CL/NAW ratio, which for the VPB vertebrae is more comparable with his *Naja* sp. 1 from Vieux-Collonges than with his *Naja* cf. *romani*. Ivanov (2000) stated that the CL/NAW range observed in the vertebrae he identified as *Naja* sp. 1 resembles *N. iberica*, a species with narrower vertebrae than *N. romani* according to Szyndlar (1985). Nevertheless, CL/NAW in the VPB vertebrae is comparable with at least some other vertebrae attributed to *N. romani*, such as those from Petersbuch 2 (Szyndlar & Schleich 1993). Ivanov (2001) himself later stated that *Naja* sp. 1 and *Naja* cf. *romani* from Vieux-Collonges may actually be conspecific. Thus, intracolumnar variation should be considered when it comes to the discriminating potential at specific rank of this feature. The same applies to the condition observed in the African species *Naja robusta* Meylan, 1987: this species also has a lower CL/NAW, but it is based only on very few vertebrae (Meylan 1987; Rage & Bailon 2011). *Naja robusta* is further characterized by a slightly higher ZW/NAW than the VPB specimens, as well as more developed subcentral ridges.

In our opinion, a confident referral to any of the known extinct *Naja* species is not advisable for the VPB specimens at the moment. This is mainly due to insufficient diagnostic potential and high variation of the vertebral morphology of these snakes, but also to the poor preservation of most of the Catalan fossils. Significant features, such as the morphology of the distal tip of the hypapophysis (possibly suggesting affinities with *N. iberica*) and the peculiar anterior margin of the zygosphene provided with multiple small convexities, may still provide support to a future identification, though, when and if better preserved material and especially cranial bones are found in the VPB. Vertebrae from the seven localities herein considered do not present significant differences and may thus represent the same species. They are all attributed to an indeterminate species of *Naja* here. In terms of largest size reached, the VPB specimens are roughly equivalent to vertebrae of *N. romani* from Kohfidisch (Bachmayer & Szyndlar, 1985, 1987) and Solnechnodolsk (Syromyatnikova *et al.* 2021), *Naja* cf. *romani* from Ravin de la Pluie (Georgalis *et al.* 2018a), and *Naja* sp. from Altıntaş (Syromyatnikova *et al.* 2022) and Gratkorn (Böhme & Vasilyan 2014), figuring among the largest known fossil cobras.

## An overview of the global fossil record of *Naja* snakes

Currently, the elapid genus *Naja* includes 34 extant species distributed throughout Africa and Asia (Uetz *et al.* 2023; see also Appendix S4), but its scarce fossil record is largely skewed towards Europe (Figs 11, 12). Recently, Pokrant *et al.* (2017) gave an account of this record, but several reports were missing from their list. We here provide an updated overview. Of the 48 known fossil occurrences of *Naja* (see Appendix S2), 71% (34) correspond to European localities and only about 15% to African and Asian ones (seven occurrences both). When it comes to the age of the findings, 33 records (69%) are from the Miocene, a single one (2%) is dated to the Miocene/Pliocene boundary, nine (19%) are Pliocene in age, and only five (10%) are from the Pleistocene.

*Naja* was present in Europe since the Early Miocene. Confidently identified remains from the MN4 of Petersbuch 2, in southern Germany, are one of the oldest known not only from the continent, but also from the whole world. Petersbuch 2 yielded cranial remains, one isolated fang, and several vertebrae that Szyndlar & Schleich (1993) referred to *Naja romani*, an extinct species with a widespread record in Europe. Hoffstetter (1939) originally described this species based on an almost complete single individual from La Grive-Saint-Alban (Middle Miocene, MN7+8), further establishing the genus *Palaeonaja* Hoffstetter, 1939 on its basis as well as two other European extinct species. Later on, Bogert (1943) criticized the erection of a separate genus for these species, reporting insufficient differences with *Naja* when a wider sample of the intrageneric variation is considered. Similar criticism was pointed out by Szyndlar & Rage (1990). *Palaeonaja* is thus considered a junior subjective synonym of *Naja*. In any case, *N. romani* survived in Europe until the Late Miocene. Apart from the above-mentioned occurrence in Petersbuch 2, it was reported from Grund (late MN5, Austria; Miklas-Tempfer 2003; Daxner-Höck *et al.* 2004), Rudabánya (MN9, Hungary; Bernor *et al.* 2004; Szyndlar 2005), Hrytsiv (MN9, Ukraine; Szyndlar & Zerova 1990; Szyndlar 1991a), and Kohfidisch (MN11, Austria; Bachmayer & Szyndlar 1985, 1987; Szyndlar & Zerova 1990; Szyndlar 1991a; Tempfer 2005). The mentioned occurrences include the type localities of both *Palaeonaja crassa* Hoffstetter, 1939 (La Grive-Saint-Alban) and *Naja austriaca* (Kohfidisch). The first is one of the two other elapid species named by Hoffstetter (1939), based on isolated vertebrae, which is a junior synonym of *N. romani* according to Szyndlar & Rage (1990). *Naja austriaca*, on the other hand, was described by Bachmayer & Szyndlar (1985), who referred to this species several cranial bones and vertebrae from Kohfidisch. Further material was later added by Bachmayer & Szyndlar (1987). Szyndlar & Zerova (1990) synonymized *N. austriaca* with *N. romani* in the light of strong similarities, but a revision in progress of the material supports its status as a distinct species (Quadros 2022). There are few other localities where *N. romani* was tentatively identified in Europe: Echzell (MN4, Germany; Vasilyan *et al.* 2022), Vieux-Collonges (MN4–MN5, France; already mentioned by Hoffstetter, 1939, and later studied by Ivanov, 2000), Ravin de la Pluie (MN10, Greece; Georgalis *et al.* 2018a; Georgalis & Delfino 2022), and Fălciu-Prut 1 (MN11–MN12, Romania; Codrea *et al.* 2022). In all these cases, however, only isolated fangs and vertebrae were found, and thus we agree with the respective authors in the need of taking the referral at species rank with caution. A similar degree of uncertainty may be applied to the Grund and Rudabánya records, also represented by vertebrae alone. Ivanov (2000) further described other vertebrae from Vieux-Collonges that he originally thought pertained to a second species of *Naja* different from *Naja* cf. *romani* from the same locality. However, he later suggested that all this material may actually be conspecific (Ivanov 2001). The easternmost, and youngest, known occurrence of *N. romani* is a single vertebra from Solnechnodolsk (MN13, Russia) published by Syromyatnikova *et al.* (2021).

Two other extinct species of *Naja* are known from Europe, both currently reported from their respective type localities only. Cobras were cursorily mentioned from Algora (Late Miocene, MN13), in Spain, by Alberdi *et al.* (1981). This snake was later described as a new species, *Naja iberica*, by Szyndlar (1985), who pointed out clear differences from other cobras in the several cranial and postcranial bones from the site. The slightly younger *Naja depereti* was described by Hoffstetter (1939) as the third species included in his *Palaeonaja*. The few vertebrae referred to this elapid come from Serrat d'en Vaquer (also spelled as Vacquer in the literature; Early Pliocene, MN15), in southern France, and were previously part of the type material of Depéret's (1890–1897) *Coelopeltis laurenti* Depéret, 1897. Hoffstetter (1939) recognised that the species, as conceived by its original author, was a chimaera, including remains of psammophiid (referred to *Malpolon laurenti*), elapid (*N. depereti*), and viperid (*Vipera* Laurenti, 1768) snakes (for a detailed discussion on the chimaera status of *C. laurenti*, see also Georgalis & Szyndlar 2022: 3274). Szyndlar (1985) and Szyndlar & Rage (1990) questioned the identification as *Palaeonaja* aff. *depereti* of elapid remains from Librilla (Late Miocene, MN13, Spain) by Alberdi *et al.* (1981). These remains were referred to *Naja* sp. by Szyndlar & Rage (1990). A recent phylogenetic analysis of fossil *Naja* based on morphology recognized *N. depereti* as a distinct species (Quadros 2022).

Other remains of *Naja* from Europe are all indeterminate to species. Adding to the occurrences mentioned in the paragraphs above and the Middle to Late Miocene fossils from the VPB described herein, *Naja* sp. was present or possibly present in the Iberian Peninsula from the Early Miocene to the Pliocene; in central Europe during the Early–Middle Miocene; in southern France during the Early–Middle Miocene and the Early–Late Pliocene; and in the southern Balkans during the Miocene/Pliocene boundary and the Late Pliocene. At least some of the Iberian records outside of Catalonia are either questionable or poorly documented. Córcoles (Early Miocene, MN4) only yielded isolated fangs (Alférez Delgado & Brea López 1981) and two poorly-preserved elapid vertebrae, whose diagnostic value at genus rank is feeble (Szyndlar 1985; Szyndlar & Alférez 2005). Fossils from Venta del Moro (Late Miocene, MN13; Alberdi *et al.* 1981; Marquina *et al.*

2016) and Layna (Early Pliocene, MN15; Jaen & Sanchiz 1985; Szyndlar 1988; Szyndlar & Rage 1990) were never properly described, and so their precise identification should be treated with caution. Referral of two vertebrae from Moreda (Pliocene, MN15–MN16), on the other hand, is better substantiated (Bailon 1991, 1992). In central Europe, few vertebrae were described and referred to *Naja* from Rothenstein 1/13 and Sandelzhausen in Germany (Middle Miocene, MN5; Szyndlar 2009), as well as Gratkorn in Austria (Middle Miocene, MN7+8; Böhme & Vasilyan 2014). Vertebrae from Sandelzhausen and Rothenstein 1/13 are comparable with *N. romani* according to Szyndlar (2009). Čerňanský *et al.* (2017) also published six vertebrae of a possible cobra from Hambach 6C (Middle Miocene, MN5, Germany), but they treated their identification as only tentative. The most interesting material from France is likely that found in Sète (Early Pliocene, MN15), among which there are both cranial and postcranial elements. These fossils were mentioned by Szyndlar & Rage (1990) and subsequently described by Bailon (1991) in his PhD dissertation. The Sète material represents the only occurrence of fossil cobras with cranial bones available that still remains unassigned at species rank, despite the potential taxonomic value of the preserved remains (see Appendix S2). According to Bailon (1991), trunk vertebrae from this locality show characters different from both *N. romani* and *N. iberica*, being more similar to the extant *Naja nigricollis* Reinhardt, 1843. The cervical vertebrae, however, share long prezygapophyseal accessory processes with *N. romani*. The cranial material also approaches more closely the morphology of *N. romani* than that of *N. iberica*, and African species (especially *N. haje*) among extant taxa. This material is certainly worth of a redescription under modern osteological knowledge and taxonomy. The only vertebra coming from the locality of Balaruc 2 (Late Pliocene, MN16) was tentatively assigned to *Naja* by Bailon (1989, 1991), whereas there is no detailed information on the remains from Isle d'Abeau (Middle Miocene, MN7+8) reported by Szyndlar & Rage (1990: fig. 1) in their map of western Palaearctic cobras. In Greece, indeterminate *Naja* vertebrae were found in Maramena 1 (Miocene/Pliocene boundary, MN13/MN14) and Tourkobounia 1 (Late Pliocene, MN16) (Szyndlar & Zerova 1990; Szyndlar 1991a, 1995; Georgalis *et al.* 2019; Georgalis & Delfino 2022). Szyndlar (1991a) mentioned only two fragments of large vertebrae as cf. *Naja* sp. from Maramena 1, but subsequent recovery of better-preserved material confirmed the generic assignment (Szyndlar, 1995; Georgalis *et al.* 2019). Szyndlar & Zerova (1990) asserted that the *Naja* sp. from Tourkobounia 1 could represent a species different from *N. romani*. Further small vertebrae referred to indeterminate elapids from Vieux-Collonges (Elapidae B) and Devínska Nová Ves (Elapidae C; Middle Miocene, MN6, Slovakia) also may belong to *Naja* according to Ivanov (1998, 2000, 2001).

As already highlighted earlier, fossil cobras are far less represented in non-European countries (Fig. 12). In addition to the occurrence of a single vertebra referred to *N. romani* from the Northern Caucasus (Syromyatnikova *et al.* 2021), four other *Naja* species were identified or tentatively identified from localities in Africa and Asia. In Africa, two extinct species were described, both from Neogene assemblages. The oldest one of these two is *Naja antiqua*, known from the Middle and tentatively Late Miocene of Morocco (Bailon *et al.* 2017). *Naja antiqua* was named by Rage (1976) in his study of the squamates from Beni Mellal (early Middle Miocene, ca. 14 Ma; Benammi *et al.* 1996; Werdelin 2010; but see Hugueney *et al.*, 1996, for a slightly older [15 Ma] estimate based on the evolutionary stage of Beni Mellal small mammals). The species is represented by cranial material, isolated fangs, and elements of the vertebral column, being thus the best-known fossil cobra from outside Europe. According to Rage (1976), it is related to the extant *N. haje*, but not displaying the paradiapophyseal morphology indicating the presence of a hood. Blain *et al.* (2013) tentatively assigned few cranial remains from Guefaït-1 (Late Miocene, MN10; Agustí *et al.* 2023) to the same species, extending its possible survival in Morocco until the Late Miocene at least. Another extinct species, *Naja robusta*, is known based on five precloacal vertebrae of, probably, a single individual from the Upper Laetolil Beds (Late Pliocene, 3.6–3.8 Ma; Su & Harrison 2015) in Tanzania. These fossils were originally described by Meylan (1987) and more recently further commented on by Rage & Bailon (2011). Despite the very limited material available, all these authors agreed on possible relations of the extinct species with the *N. nigricollis* complex, including among others the extant African species *N. nigricollis* and *Naja mossambica* Peters, 1854. The only records of extant species are the mentions of *Naja naja* (Linnaeus, 1758) and *Naja* cf. *naja* from caves in India and the Philippines, respectively, and that of *Naja* cf. *nigricollis* from Tanzania. Lydekker (1886) attributed a vertebra found in caves with Pleistocene deposits in the Indian district of Karnul (today Kurnool) to *Naja tripudians* Merrem, 1820, which is a junior synonym of the extant *N. naja*. Nevertheless, he gave no description or figure. More recently, Reis & Garong (2001) listed *Naja* cf. *naja* among the vertebrates identified in the Taurung-tung cave (Late Pleistocene) in the Philippines. Again, the authors did not describe the findings or made any comments on the material, and thus this attribution cannot be verified at the moment based on the literature available. Vertebrae of an indeterminate species of *Naja* were briefly reported by Rage (1973) from Bed I at Olduvai (Early Pleistocene, 1.84–1.78 Ma), in Tanzania. He provided no descriptions or figures of them, but commented that they were identical to those of *N. nigricollis*. Subsequently, Rage (1979: 329) referred to the same occurrence more directly as *Naja* cf. *nigricollis* in a list of snakes from Olduvai.

The genus *Naja* was further reported from Arrisdrift (late Early Miocene; Rage 2003) in Namibia, locality 21 at Al-Sarrar (late Early Miocene; Rage 1982) in Saudi Arabia, Altıntaş (Late Miocene, MN9; Syromyatnikova *et al.* 2022) and Çalta (Early Pliocene, MN15; Rage & Şen 1976) in Turkey, locality DIK-1 at Dikika (Late Pliocene; Wynn *et al.* 2006) in Ethiopia, Irhoud Ocre (Early Pleistocene; Bailon *et al.* 2017) in Morocco, and layer XIX at Qafzeh Cave (early Late Pleistocene; Biton & Bailon 2023) in Israel. Only Rage & Şen (1976), Rage (2003), Syromyatnikova *et al.* (2022), and Biton & Bailon (2023) gave clear descriptive comments and (except for Rage, 2003) figures of the cobra remains. Fossils from Çalta were originally referred to *Palaeonaja* sp. (Rage & Şen 1976), whereas those from Qafzeh Cave were assigned to a large viperid by Biton & Bailon (2022). The same authors later corrected their attribution and identified the remains as pertaining to a cobra (Biton & Bailon 2023). The single vertebra confidently assigned to elapids from Arrisdrift is referred to *Naja* only tentatively (Rage 2003). Rage (1982) and Bailon *et al.* (2017) simply gave general mentions of the presence of this snake in the assemblages. The occurrence from Al-Sarrar was originally referred to as *Naja-Palaeonaja* group by Rage (1982). In their list of taxa associated with the DIK-1 hominin locality, Wynn *et al.* (2006) mentioned one specimen identified by Rage (cited as author of the identification in their acknowledgements; Wynn *et al.* 2006: 336) and referred to cf. *Naja* sp., but there is no further detail (no descriptions, no figures, and no mention of the nature of this specimen, if a vertebra or other). Detailed information is also missing about undescribed fossils from the Miocene of Kenya mentioned by Meylan (1987). *Naja* vertebrae may also be present among fossils described by Lapparent de Broin *et al.* (2020) from Afghanistan, more specifically from the Sherullah 9 locality (Late Miocene, equivalent to MN10/MN11). However, these vertebrae are too poorly preserved for a confident identification, as pointed out by the authors already, and they may also pertain to natricids instead. Vilakazi *et al.* (2018) described an isolated fossil maxilla from Locus X Cave in the Cradle of Humankind (late Early Pleistocene, South Africa), that they referred to a venom-spitting elapid belonging to either *Hemachatus* or *Naja*. The maxilla alone, however, is not sufficient to refine the identification.

Snake fossils that were at first identified as cobras, but later rethought as pertaining to different taxa, exist as well. The species *Naja suevica* Fraas, 1870 was described by Fraas (1870) from Steinheim am Albuch (Middle Miocene, MN7+8, Germany). The description was based on several vertebrae, some of which still articulated, but Fraas (1870) failed to provide figures and a diagnosis. This led Hoffstetter (1939) to consider *N. suevica* as a nomen nudum. Rage (1984) considered the name to be available and the species to be taxonomically valid, further designating a lectotype among the several syntype vertebrae. However, he transferred it to colubrids and even tentatively within the genus *Coluber* Linnaeus, 1758 (back then considered in a broad sense, not limited to the Eastern racer, *Coluber constrictor* Linnaeus, 1758, as in modern taxonomy; Wallach *et al.* 2014; Uetz *et al.* 2023). This generic ascription was later followed by other authors as well (e.g. Szyndlar & Böhme 1993; Ivanov 2002), but Wallach *et al.* (2014) tentatively transferred the species to the genus *Hierophis* Fitzinger in Bonaparte, 1834. In France, fossils from the Middle Pleistocene of

Coudes were referred to *Naja* first by Bravard (in Gervais 1859) and later by Rochebrune (1880). The latter also named the species *Naja sauvagei* Rochebrune, 1880 based on a single vertebra from the locality. Subsequent authors reassigned all the fossils from Coudes to colubroidean snakes, most likely either colubrids or natricids (Hoffstetter 1939; Rage 1984; Holman 1998). The holotype vertebra of *N. sauvagei* belongs to a juvenile individual and it is thus difficult to confidently assign it to a precise taxon. Rage (1984) and Holman (1998) suggested it probably pertains to an extant species. Therefore, *N. sauvagei* should be considered a nomen dubium, potentially being a junior subjective synonym of an extant European colubroidean species. Schneider (1975) described and figured *Naja* vertebrae from the Middle Pleistocene of Chios Island in Greece. Szyndlar (1991a) considered this material not to represent a cobra, highlighting natricine features of a vertebra figured by Schneider (1975). Subsequently, both Holman (1998) and Georgalis *et al.* (2018a) further supported the probable reidentification as a natricine snake.

## Palaeoenvironment and palaeobiogeography of European and Iberian cobras

Despite the clear scarcity of the record, especially for Africa and Asia (which still host extant species), fossil cobras provide useful insights into the evolutionary history of these snakes. The estimated diversification of crown elapids was dated to the late Oligocene by Zaher *et al.* (2019). Uncertainty still covers their centre of origin, but at least *Naja* possibly originated in Africa and later dispersed outside of the continent (Ineich 1995; Wüster *et al.* 2007). This agrees with the finding of a posterior trunk vertebra sharing morphological affinities with *Naja* in the late Oligocene Nsungwe Formation in Tanzania (McCartney *et al.* 2014) and of a single, poorly-preserved mid-trunk vertebra tentatively assigned to *Naja* by Rage (2003) from the late Early Miocene of Namibia. The lack of more informative African fossils confidently attributed to *Naja* predating the Middle Miocene hinders any further comments on their early evolution, but their presence in Europe already in the late Early Miocene speaks for a rapid dispersal as soon as Afro-Arabia and Eurasia became connected (permanent connections in the Neogene were first established by 19 Ma; Rögl 1999; Harzhauser *et al.* 2007). As a matter of fact, the age of the oldest cobra occurrences from Europe (from Petersbuch 2 and Echzell in Germany, and potentially Córcoles in Spain; Alférez Delgado & Brea López 1981; Szyndlar & Schleich 1993; Szyndlar & Alférez 2005; Vasilyan *et al.* 2022) is comparable with the one of the oldest known occurrences from both Africa (Arrisdrift in Namibia; Rage 2003) and Asia (Al-Sarrar in Saudi Arabia; Rage 1982), which is considered to be late Early Miocene. This rapid dispersal of cobras in Europe parallels the pattern seen for other reptiles that entered and quickly dispersed into the European continent after the onset of the so-called *Gomphotherium* land bridge during early MN3 (e.g. chameleons, monitor lizards, and pythons; Georgalis *et al.* 2016, 2020, 2023; Villa *et al.* 2018). Potential future findings of Early Miocene cobras in eastern Europe, and the Balkan Peninsula in particular, could help confirm whether at least some of these snakes used this route to enter the continent, likely favoured by hyperthermal conditions during the MCO (~16.9–14.7 Ma; see Steinthorsdottir *et al.* 2021, and references therein) as suggested by Rage (2013) and Ivanov (2022). In any case, cobras seem to have appeared in Europe slightly later than other small elapids (Elapidae A of Ivanov, 2000, 2001, or Elapidae gen. et sp. indet. according to Ivanov, 2002), the latter being already present at Merkur-North (MN3), Czech Republic, where *Naja* is apparently lacking.

The most widespread Miocene European cobra, *N. romani*, was considered part of an Euroasiatic lineage by Szyndlar (1985), Szyndlar & Rage (1990), and Szyndlar & Zerova (1990). According to Szyndlar (1991a), it could even be a possible early offshoot of the Asian clade, in contrast to *N. antiqua* and *N. iberica*, which would be part of an African group (perhaps polyphyletic). This would suggest the presence of two different lineages in Europe during the Miocene, one in Iberia and the other in the rest of the continent (except for Italy, which, according to current data, was never inhabited by cobras; Fig. 13A). An African origin was recently suggested by Georgalis & Szyndlar (2022) for another Late Miocene Iberian snake, *Psammophis odysseus* Georgalis & Szyndlar, 2022 from Salobreña (MN13), whose lineage likely took advantage of the environmental consequences of the Messinian Salinity Crisis to enter the Iberian Peninsula. However, *Naja* remains, even though unassigned to species, are present in Iberia already since way before the Late Miocene (see also Appendix S2), and there is no evidence of direct African-Iberian faunal dispersals before about 6.2 Ma (Agustí *et al.* 2006; Gibert *et al.* 2013). Therefore, even though the age of *N. iberica* would agree with a Messinian arrival into the Iberian Peninsula for this species, the same does not hold for other Iberian *Naja*. An alternative explanation could be that a single European *Naja* lineage passed through the continent reaching Iberia (Fig. 13B), where it later gave origin to an endemic species (at odds with the two lineages hypothesis) or was either flanked or substituted by a different species of African origin in the Late Miocene. The Iberian *Naja* would have never dispersed back into the rest of Europe, like other (African-related) snakes living in the peninsula during the Miocene (Szyndlar, 2012). The reasons behind this, if any, still need to be clarified, though, given that the most obvious potential geographical barrier, the Pyrenees, had a lower elevation that started to increase only in the Late Miocene (at least in their eastern portion; Pérez Vila *et al.* 2001; Suc & Fauquette 2012; Huyghe *et al.* 2020; but see Tosal *et al.* 2021, for a discordant estimate). An ecological barrier could be involved instead: the Iberian cobras could have adapted to the transitional environments present in the peninsula and were prevented from dispersing again into the rest of Europe by the more densely forested environment that developed there during the second part of the Miocene (Kovar-Eder 2003; Pound *et al.* 2012). A similar pattern has been described for mammals (Casanovas-Vilar *et al.* 2005; Eronen *et al.* 2010) and potentially also for the psammophiid snake *P. odysseus* (Georgalis and Szyndlar 2022). Competition with species better adapted to those environments may also have played a role. In contrast with the Eurasian hypothesis suggested by the other authors, Bogert (1943) allied *N. romani* with African cobras, because of the presence of two teeth on the posterior end of maxilla (vs. one or no teeth behind the fang in the Asiatic *N. naja*). This line of reasoning was recently followed by Wallach *et al.* (2014), who included all extinct *Naja* species into *Afronaja*.

The possible presence of cobras in the MN4 of Córcoles (Alférez Delgado & Brea López 1981; Szyndlar & Alférez 2005) and, more confidently, in the early MN5 of SM (this work) situates them not just among the earliest in Europe, but also considering the worldwide record of the genus. Sant Mamet has not yielded palaeobotanical remains, but both rich macrofloras as well as pollen samples have been recovered from nearby, almost time-equivalent sites in the same basin (Bessedik 1985; Bessedik & Cabrera 1985; Sanz de Síria Catalán 2001, Jiménez-Moreno & Suc 2007). These indicate a warm tropical to subtropical climate with clear rainfall seasonality. In macrofloral assemblages, herbaceous plants and leguminous trees (such as acacias) are the most common elements (Sanz de Síria Catalán 2001). However, both macrofloral and pollen assemblages indicate more humid evergreen broad-leaf forests close to freshwater bodies and at moderate elevations. In any case, mega- and mesothermic taxa are abundant and indicate warm temperatures. This reconstruction meets well the requirements for the genus *Naja* as reported by Tempfer (2005): the genus would favour dry places in flat areas with high grass and scattered groves of trees, even though at least some extant *Naja* species can live and even thrive in forests as well (e.g. *Naja melanoleuca* Hallowell, 1857; Luiselli & Angelici 2000; Luiselli 2002). The presence of open and dry areas in early Aragonian sites of the VPB is also supported by the presence of two testudinids (*Titanochelon richardi* (Bergounioux, 1938) and *Testudo catalaunica* Bataller, 1926; Luján *et al.* 2014a, 2016), as well as the composition of the micromammal assemblage, with diverse and abundant glirids and sciurids with a preference for an arid environment (Casanovas-Vilar *et al.* 2016a; Jovells-Vaqué 2020). On the other hand, other herpetofaunal components recovered from either SM (*Latonia* Meyer, 1843 frogs; Villa *et al.* 2019) or other sites of comparable age (frogs and crocodylians from els Casots, and geoemydid turtles from ACM and Can Pallars i Llobateres: Luján *et al.* 2014b; Díaz Aráez *et al.* 2017; Alba *et al.* 2018; Casanovas-Vilar *et al.* 2022b) sustain the presence of permanent water bodies in the VPB during the early Aragonian.

Plant data for late Aragonian and Vallesian sites of the VPB are scarce. Large mammals of the same age and, more clearly, the entire mammal assemblage of late Aragonian and early Vallesian localities in the VPB seem to point to a more forested environment and a subtropical to warm-temperate climate (Casanovas-Vilar & Agustí 2007; Casanovas-Vilar *et al.* 2008a, 2016a). At

ACM, the composition of the rodent fauna (Casanovas-Vilar *et al.* 2008a) agrees with the presence of dense forests, as it includes flying squirrels and diverse arboreal dormice. A recent study of C and O stable isotopes focused on the small ruminant *Micromeryx* Lartet, 1851 (DeMiguel *et al.* 2021) from ACM in the interval between 12.6 and 11.4 Ma shows overall warm temperatures (17–23 ºC), but important variations in humidity. DeMiguel et al. (2021) recognised three different phases, with decreasing humidity and increasing habitat heterogeneity. ACM/C3-A7 pertains to the first phase, which is the most humid and characterised by long-standing forests with bushy and woody vegetation. ACM/C5-C3 and ACM/C4-A1 belong to the second and third phases, respectively, seeing a progressive opening of the environment (even though still in the range of tropical seasonal forests). The third phase, in particular, is interpreted as a mosaic environment with trees growing in sparser formations and interspersed and restricted gallery forests. Evidence of permanent water bodies is present in this phase, in the shape of aquaphilous mammals (Alba *et al.* 2011; DeMiguel *et al.* 2021) or freshwater turtles such as *Ptychogaster batalleri* (Bergounioux, 1931) (Luján *et al.* 2014b), but also, to a lower extent, in the second one, with the very rare occurrence of beavers (Casanovas-Vilar *et al.* 2008b).

The site of SA deserves special attention as its small mammal fauna includes some dormice clearly associated to forested environments as well as two different species of semiaquatic beavers (*Chalicomys jaegeri* Kaup, 1832, *Euroxenomys minutus* (Meyer, 1838); Casanovas-Vilar *et al.* 2016b). SA is very close to the locality Can Llobateres 1, which is only slightly younger (9.76 Ma; Casanovas-Vilar *et al.* 2016b). The latter site corresponds to a wetland environment and includes a wealth of forest-dwelling taxa, such as flying squirrels (Casanovas-Vilar *et al.* 2015) and hominoid primates (Alba *et al.* 2012)—(for an updated review see Arranz *et al.* 2023), besides the two same species of beavers and abundant remains of the frog *Latonia* (Villa *et al.* 2019). Furthermore, recent excavations at the Can Llobateres 1 site yielded a rich (but not diverse) plant assemblage that consists of abundant reeds, palms, evergreen laurels, and figs, which grew next to a marshy area close to the deposition site (Marmi *et al.* 2012). The absence of deciduous elements, coupled with the occurrence of some mega-mesothermal taxa is consistent with a warm climate. However, based on palaeobotanical evidence from older (late Middle Miocene) sites of the VPB and nearby areas, Marmi *et al.* (2012) concluded that more arid and open woodlands, likely populated by leguminous trees and herbaceous plants occurred far from the wetlands. Indeed, the slightly younger (9.7–9.6 Ma, MN10) flora from the geographically close Empordà Basin (NE Catalonia) shows the occurrence of open woodlands (dominated by *Paliurus*) far from freshwater bodies in the lowlands (Tosal *et al.* 2022). Therefore, this kind of mosaic environment would have been also adequate for *Naja*, which consistently is a rare faunal element throughout different phases characterised by different environmental features in the VPB.

*Naja* persisted in Europe for the entire Neogene, surviving only in the circum-Mediterranean area during the Pliocene. As observed in a plot of occurrences in Europe and circum-Mediterranean North Africa (Fig. 13A), its northernmost distribution was reached by the end of the Early Miocene (MN4) coinciding with the onset of the MCO. However, the subsequent cooling during the Middle Miocene Climatic Transition (~14.7–13.8 Ma; see Steinthorsdottir *et al.* 2021, and references therein) was not enough to exclude cobras from northern Europe, suggesting that conditions were still suitable for them for some time after the MCO. After that, the genus started a steady geographical range contraction towards the south, Late Miocene and Pliocene occurrences being restricted to more southern regions. *Naja* finally disappeared from Europe prior to the Pliocene/Pleistocene boundary, Pleistocene circum-Mediterranean records being restricted to norther Africa and the Levant (Fig. 13A). This pattern fits that of many other thermophilous taxa, whose distribution contracted towards what are interpreted as southern climatic refugia in parallel to climate cooling through the Pliocene and Quaternary (e.g. Delfino 1997; Böhme 2003; Bailon & Blain 2007; Rage 2013; Blain *et al.* 2016; Georgalis *et al.* 2017, 2018b; Blain & Bailon 2019; Villa & Delfino 2019; Ivanov 2022; Macaluso *et al.* 2023). In contrast to other taxa, however, it seems that *Naja* never entered Italy because it has never been recorded from well-known Neogene faunas from the region (Fig. 13A), and the same might be true for Mediterranean islands such as the

Balearic Islands and Sardinia (Neogene herpetofaunas are not known from Sicily). Its absence from other regions may just be due to a general poor knowledge of their Neogene herpetofaunas, especially regarding small members of the assemblages. Its extirpation is roughly contemporaneous with that of other tropical groups like varanids or “anilioids” (end of the Ruscinian, ca 3.2 Ma, according to Bailon & Blain, 2007, and Blain *et al.,* 2016). *Naja* was outlived in the Iberian Peninsula by other “exotic” taxa like agamids, non-*Anguis* anguids, and scolecophidian and erycid snakes that would disappear at different moments during the Pleistocene (Blain *et al.* 2014, 2016; Blain & Bailon 2019).

The very few occurrences in Asia, half of which are poorly documented, do not allow a thorough exploration of the past history of cobras in this continent, which most likely had an important role in its evolution considering the current diversity of Asian species. The vertebra found in Solnechnodolsk (Russian Caucasus; presumably equivalent to MN13) could testify that *N. romani* expanded eastwards by the very end of the Miocene, and the *Naja* fossils from Al-Sarrar (Saudi Arabia; late Early Miocene) and Altıntaş (Turkey; MN9) speak for the presence of cobras at least in western Asia throughout the Miocene. However, the absence of other evidence restrains at the moment to ascertain when and how other species evolved and spread in Asia. The absence of cobras in rich and diverse Miocene assemblages such as those from the Pakistani Siwaliks (Head 2005), Kazakhstan (Ivanov *et al.* 2019), and India (Singh *et al.* 2022a, 2022b) is noteworthy, and further studies and data would be required to uncover their Asian history.

## CONCLUSION

According to the available molecular and palaeontological evidence, true cobras arose in Africa. However, their fossil record in the African continent is meagre. The same holds true for Asia as well. Thus, the evolutionary history of these snakes in the areas they still inhabit nowadays is largely unknown. In Europe, cobras were present since the late Early Miocene. Their oldest presence in the Iberian Peninsula may be comparably as old as the oldest one in the rest of the continent, but this is based on remains of uncertain taxonomic value. Nevertheless, they were undisputedly present at least in the northeasternmost part of Iberia starting from the early Middle Miocene (MN5), as demonstrated by the vertebrae from SM. The material we described from the VPB highlights a persistence of these snakes in this area throughout the Middle and the early Late Miocene. All the VPB fossils can be referred to the genus *Naja* with confidence, but the absence of cranial material hinders a more precise attribution at the moment. The few remains available suggest an overall rarity of cobras in the faunas of the localities where they are found. General preference for open and dry habitats by extant *Naja* would agree with the presence of mosaic environments in the VPB sites. Nevertheless, they were able to survive in the area throughout different phases with different environmental features, implying a certain degree of ecological flexibility. Moreover, they support a warm palaeoclimate for the VPB localities where their remains are found, given that a mean annual temperature lower than 20 °C seems to act as a northern barrier for present-day elapids (Bailon & Blain 2007).

Apart for the Early Miocene and doubtful material from Córcoles, all other, non-VPB *Naja* fossils from Iberia postdate the Messinian Salinity Crisis. This includes a possibly endemic species, *N. iberica*, of hypothesized African affinities, and other occurrences of indeterminate species. Previous authors suggested that the Iberian Miocene snake faunas were of African affinities and included taxa that never dispersed into the rest of Europe. *Naja iberica* would fit this scenario, potentially having entered the Iberian Peninsula taking advantage of the effects of the Messinian Salinity Crisis and being blocked by the Pyrenees in the north. However, Middle and early Late Miocene cobras (as well as late Early Miocene ones, if the occurrence from Córcoles is supported by more diagnostic fossils in the future) from Iberia are puzzling in this context. Before the Late Miocene, the Pyrenees were apparently not the geographical barrier they would have been at later times. So, it is still an open question whether early representatives of cobras in the Iberian Peninsula may have been ancestral to the *N. iberica* lineage that reached Europe prior to the Messinian and then never dispersed northwards for some still unknown reason or they were part of a different lineage colonizing the area in older times from Central Europe (being thus at odds with the idea of a completely independent ophidiofauna in the Iberian Miocene). Resolving this question would require finding additional cobra fossils (including cranial remains) from pre-Messinian Miocene localities in the Iberian Peninsula as well as performing a detailed phylogenetic analysis to resolve the relationships among extinct cobras.

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## AUTHOR CONTRIBUTIONS

**Conceptualization** AV, ÀHL, AB, ICV; **Data Curation** AV, MD, ÀHL, JMR, DMA; **Funding Acquisition** AV, ÀHL, ICV, DMA; **Investigation** AV, ABQ, MD, ÀHL, AB; **Resources** ICV, JMR, DMA; **Supervision** MD, ICV, DMA; **Validation** MD, ICV, DMA; **Visualization** AV, ÀHL, AB, ICV; **Writing – Original Draft Preparation** AV, AB; **Writing – Review & Editing** AV, ABQ, MD, ÀHL, AB, ICV, DMA.

## DATA ARCHIVING STATEMENT

Data for this study [including Appendixes S1 to S4] are available as Supplementary Information **[please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]**

## SUPPLEMENTARY INFORMATION

**Appendix S1.** Measurements and related statistical parameters for the *Naja* sp. vertebrae from the Vallès-Penedès Basin.

**Appendix S2.** Fossil record of the genus *Naja*.

**Appendix S3.** References related to the fossil record presented in Appendix S2.

**Appendix S4.** Fossil record and current distribution (in light blue) of the genus *Naja*. For locality numbers, see Fig. 11 and 12 in the main text. The current distribution is based on data available on

RepFocus (https://repfocus.dk/Naja.html), except for the circum-Mediterranean area, which follows Pokrant *et al.* (2017) as in Fig. 13.

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# FIGURES:

**Fig. 1.** Geological map of the Vallès-Penedès Basin within the Iberian Peninsula, indicating the location of the localities with cobra remains. Map modified from Casanovas-Vilar *et al.*, 2016a. Abbreviations: ACM, Abocador de Can Mata; HP, els Hostalets de Pierola; HPI, Hostalets Inferior; SA, Santiga; SM, Sant Mamet.

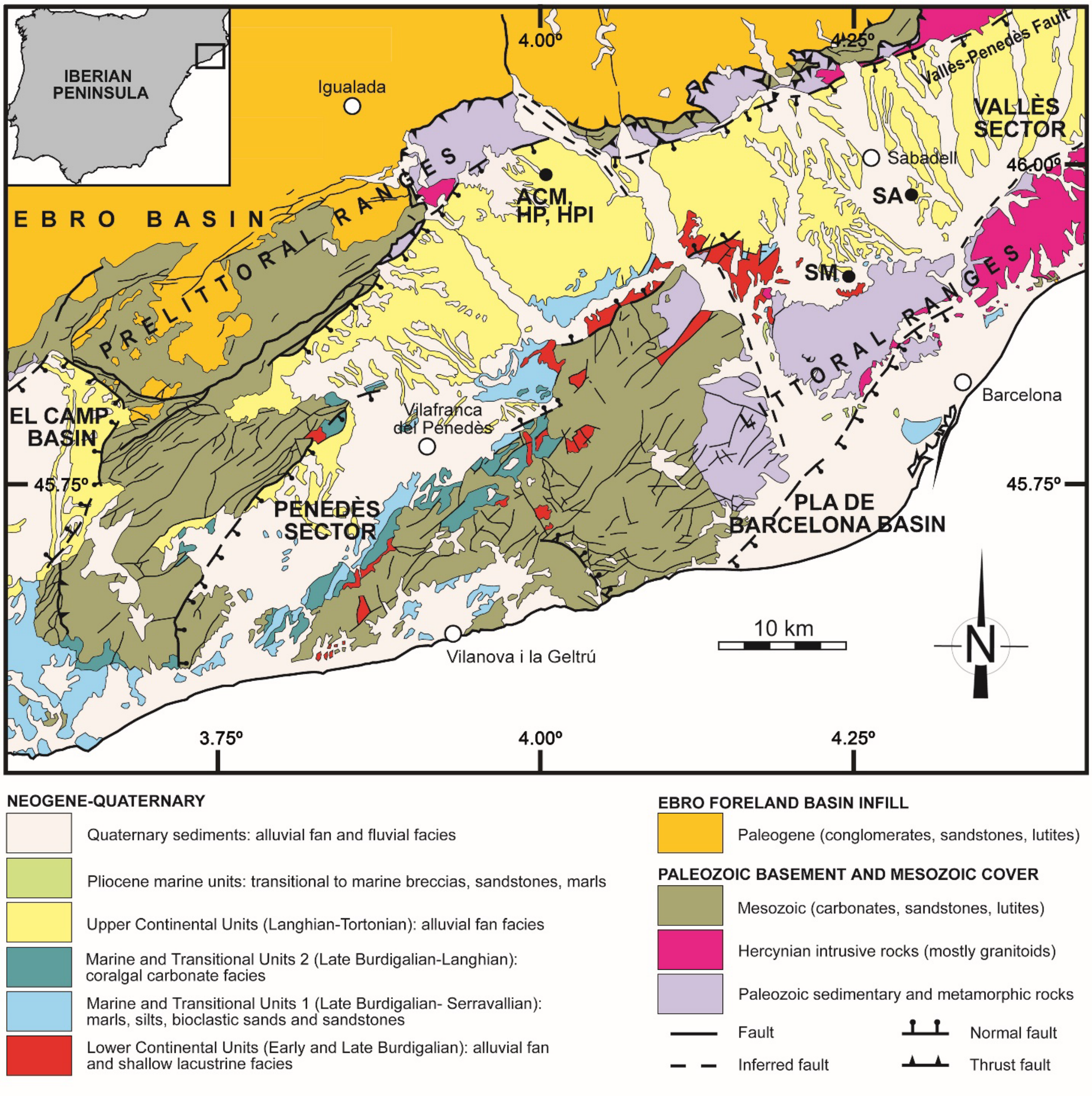

**Fig. 2.** *Naja* sp. from SM: precloacal vertebra (IPS128035) in anterior (A), posterior (B), ventral (C), dorsal (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS128036) in dorsal (G), ventral (H), anterior (I), posterior (J), right lateral (K) and left lateral (L) views. All scale bars represent 1 mm.

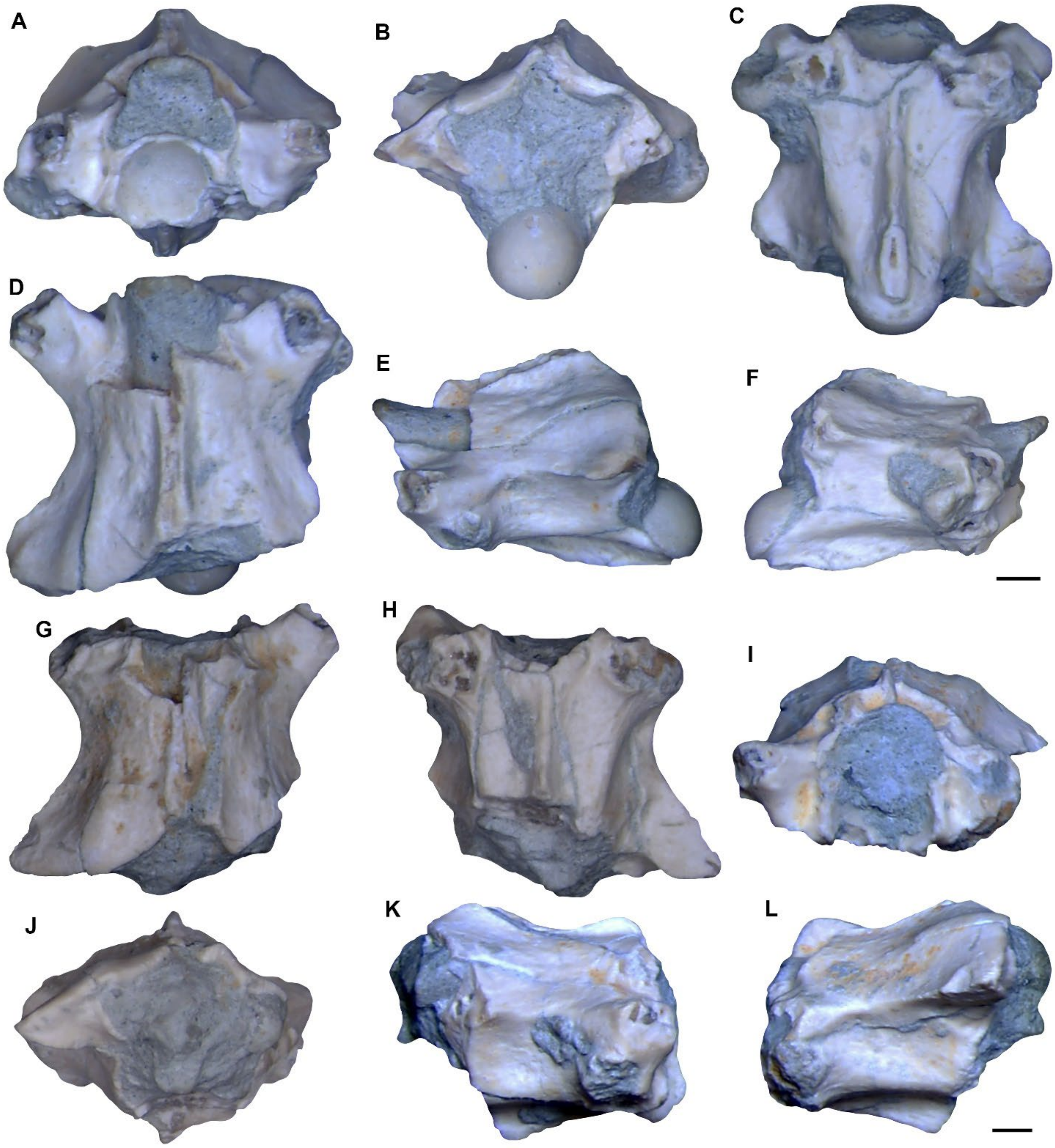

**Fig. 3.** *Naja* sp. from ACM/C4-A1 and ACM/C3-A7: precloacal vertebra (IPS29786) from ACM/C4-A1 in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS50956) from ACM/C3-A7 in dorsal (G), ventral (H), anterior (I), posterior (J), left lateral (K) and right lateral (L) views. All scale bars represent 2 mm.

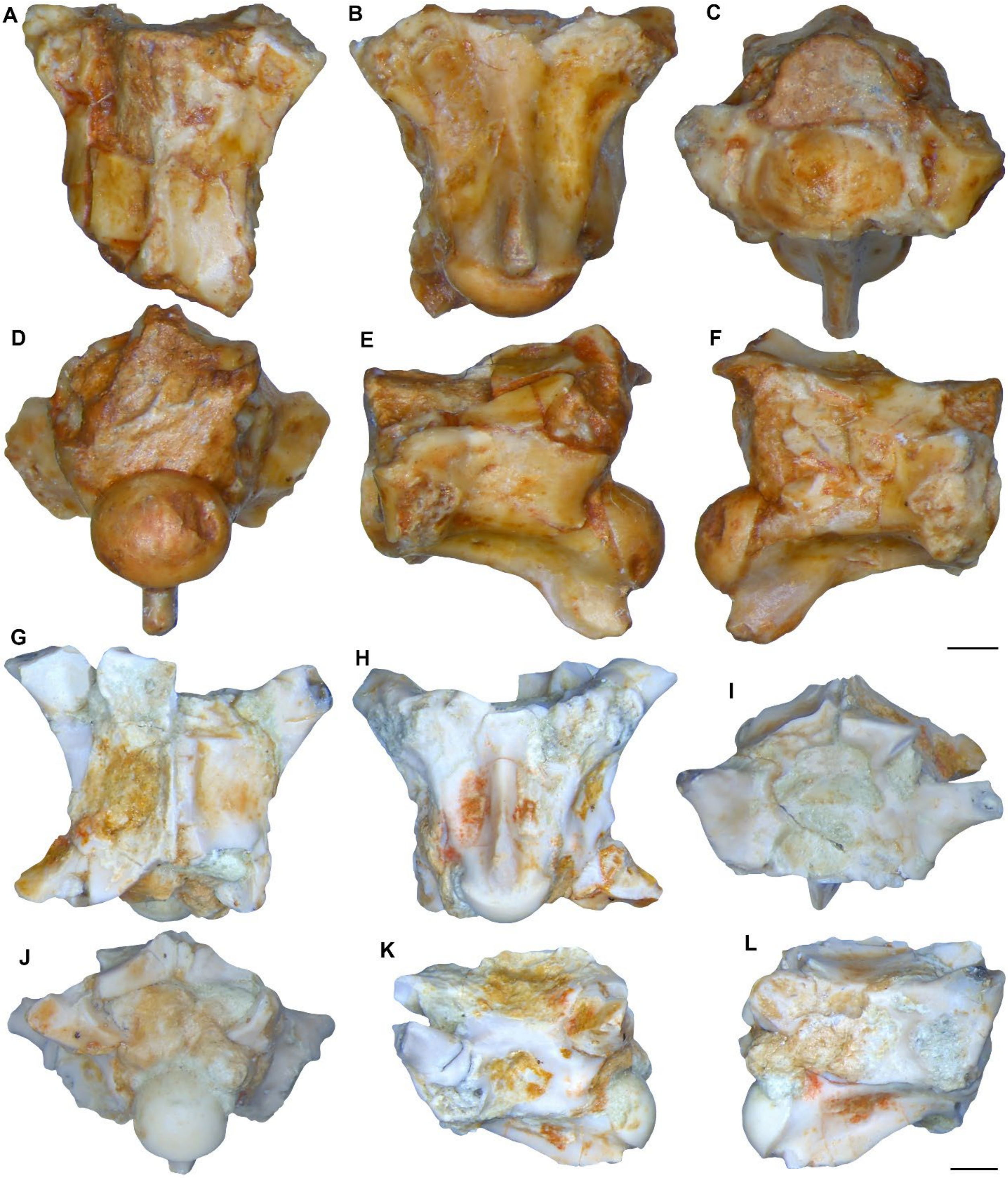

**Fig. 4.** *Naja* sp. from ACM/C5-C3: precloacal vertebra (IPS42393) in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS42472) in dorsal (G), ventral (H), anterior (I), posterior (J), left lateral (K) and right lateral (L) views. All scale bars represent 1 mm.

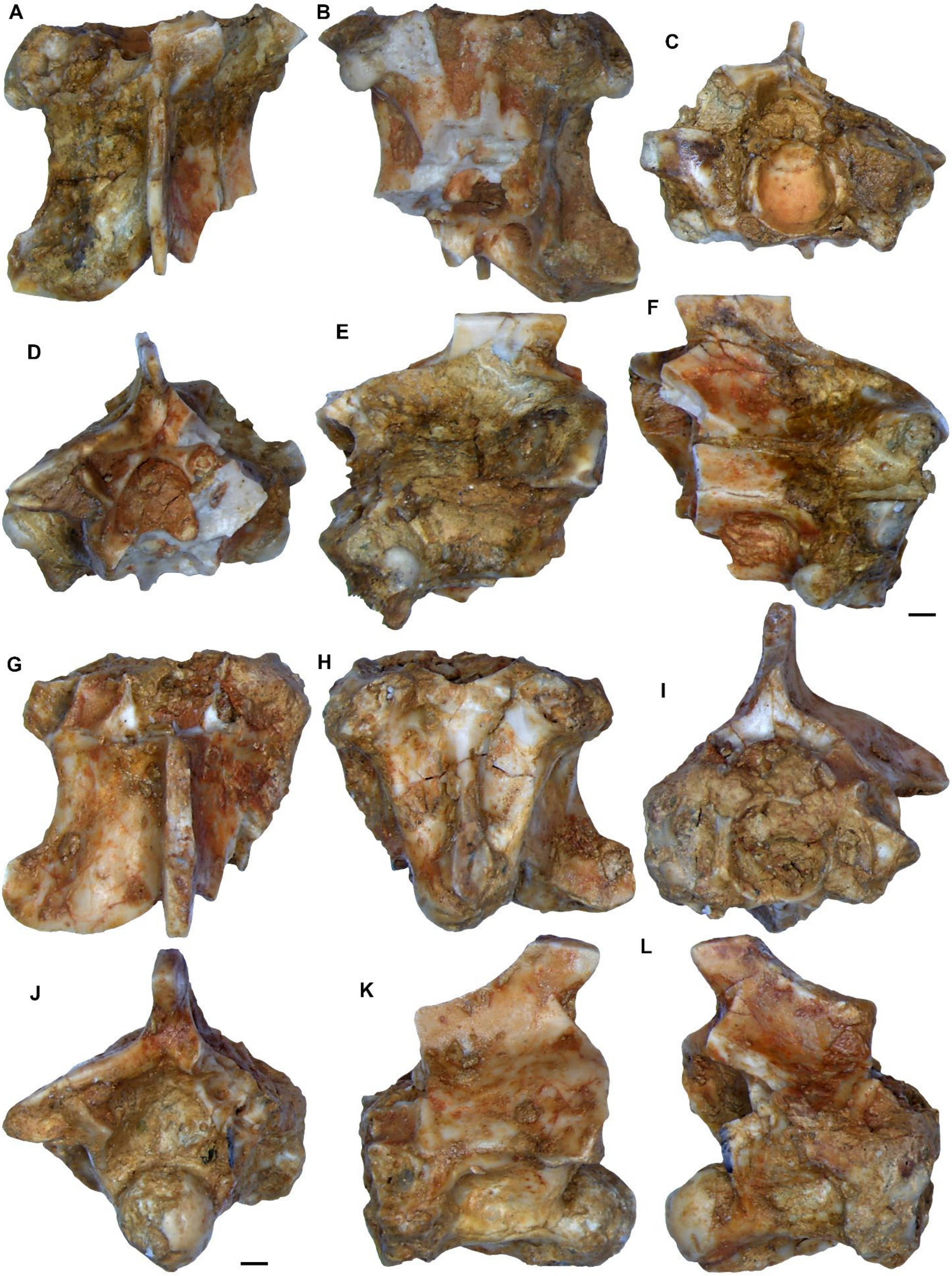
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**Fig. 5.** *Naja* sp. from ACM/C5-C3: precloacal vertebra (IPS42390) in anterior (A), posterior (B), dorsal (C), ventral (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS42218) in posterior (G), anterior (H), dorsal (I), ventral (J), left lateral (K) and right lateral (L) views. All scale bars represent 2 mm.

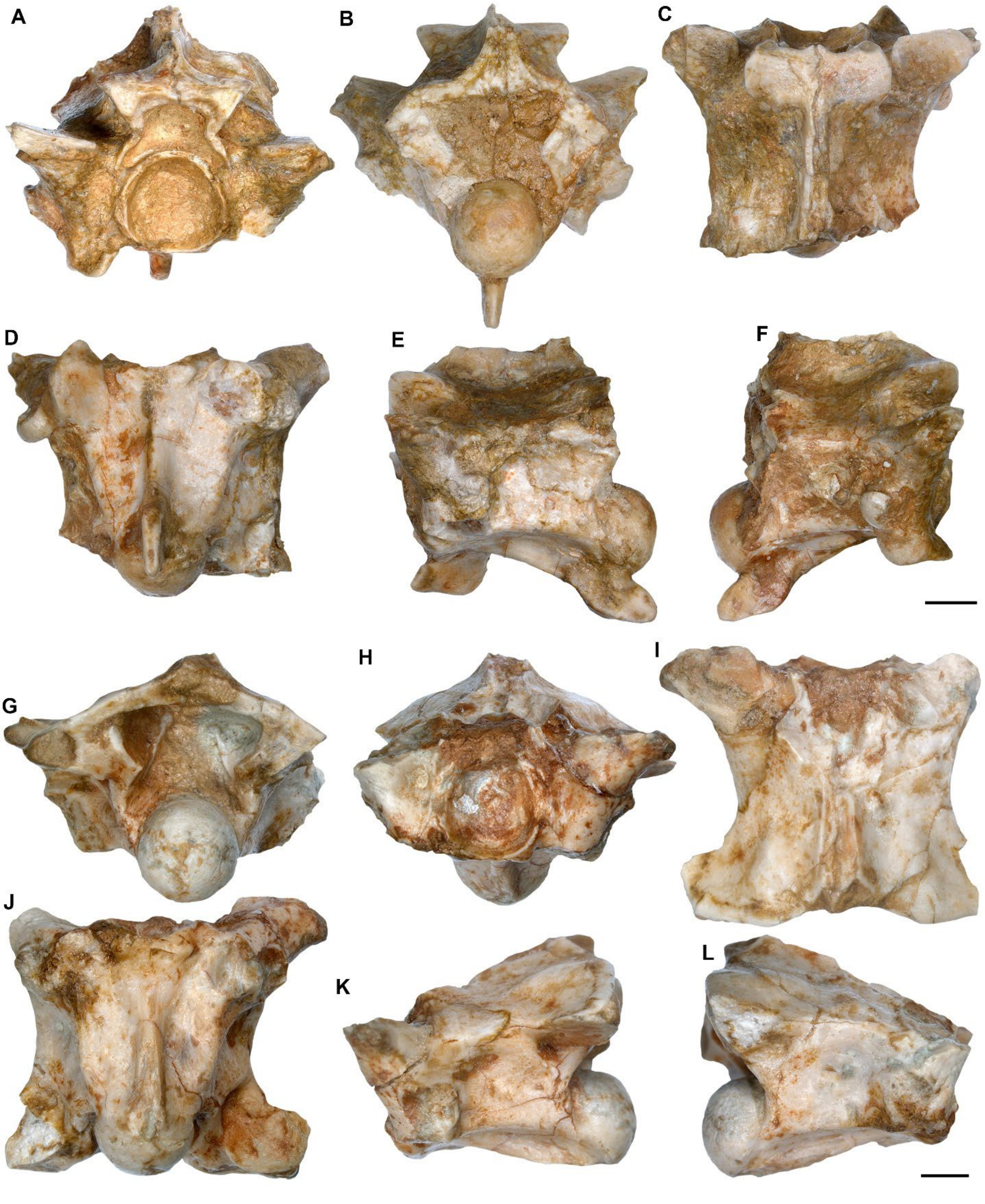

**Fig. 6.** *Naja* sp. from ACM/C5-C3: precloacal vertebra (IPS43553) in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS42445) in dorsal (G), ventral (H), anterior (I), posterior (J), left lateral (K) and right lateral (L) views. All scale bars represent 2 mm.

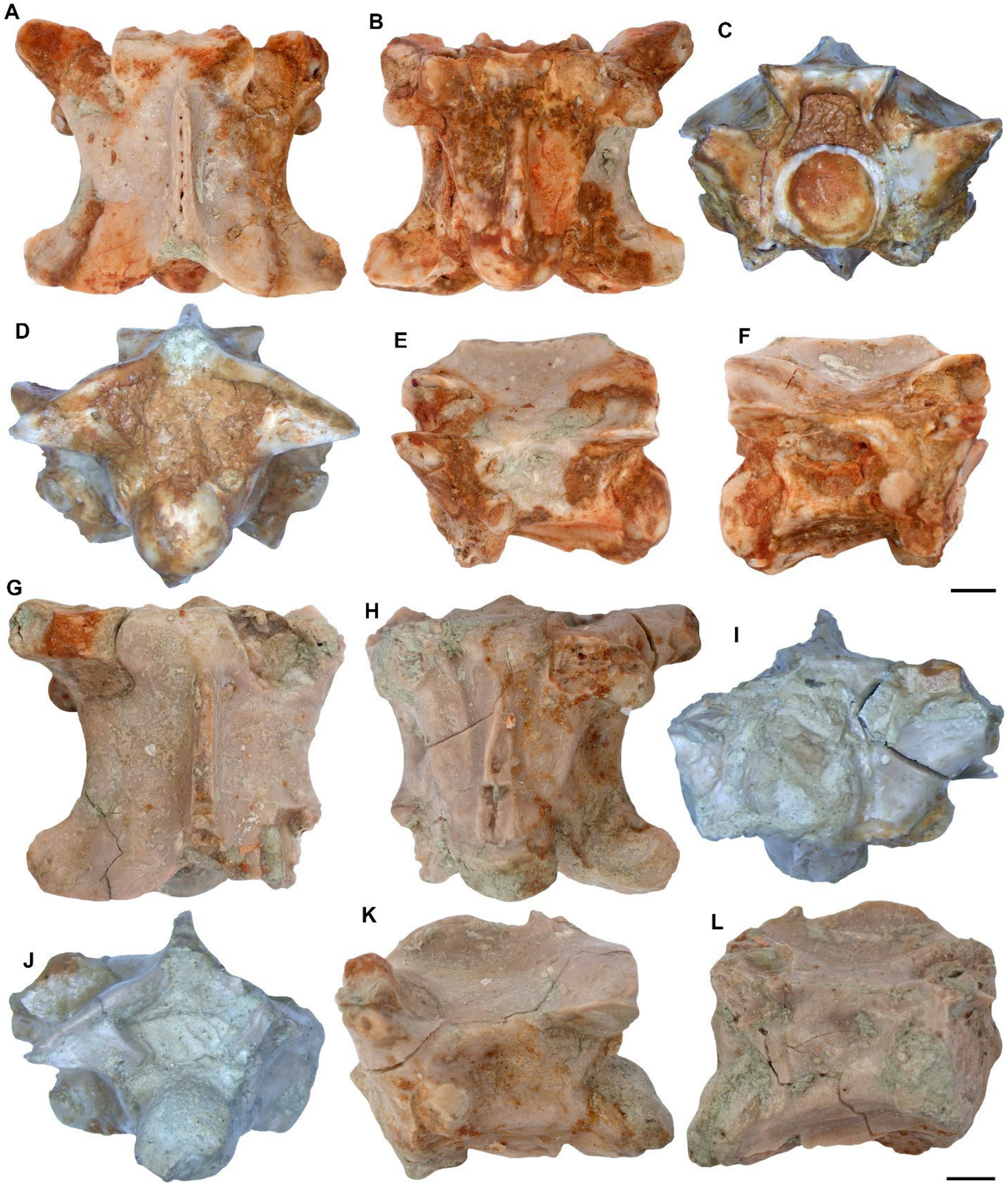

**Fig. 7.** Variation in the presence of the epizygapophyseal spine in *Naja* vertebrae from the VPB: A) Right lateral view of IPS43553 from ACM/C5-C3, bearing a small epizygapophyseal spine (white arrows). B) Left lateral view of IPS87398 from HP, devoid of the spine. Each vertebra is flanked by a detail of the postzygapophyseal area and the related interpretative drawing. All scale bars represent 2 mm.

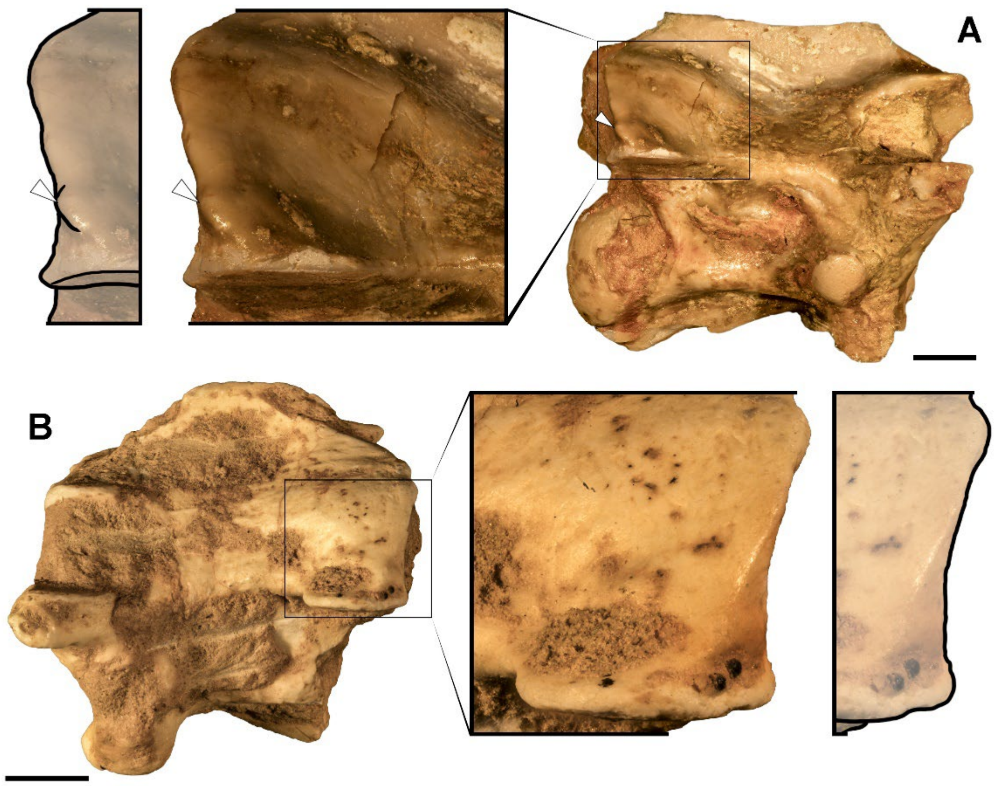

**Fig. 8.** *Naja* sp. from HP: precloacal vertebra (IPS127511) in anterior (A), posterior (B), dorsal (C), ventral (D), left lateral (E) and right lateral (F) views; precloacal vertebra (IPS127512) in anterior (G), posterior (H), dorsal (I), ventral (J), right lateral (K) and left lateral (L) views. Scale bars represent: 1 mm (A–F), 2 mm (G–L).

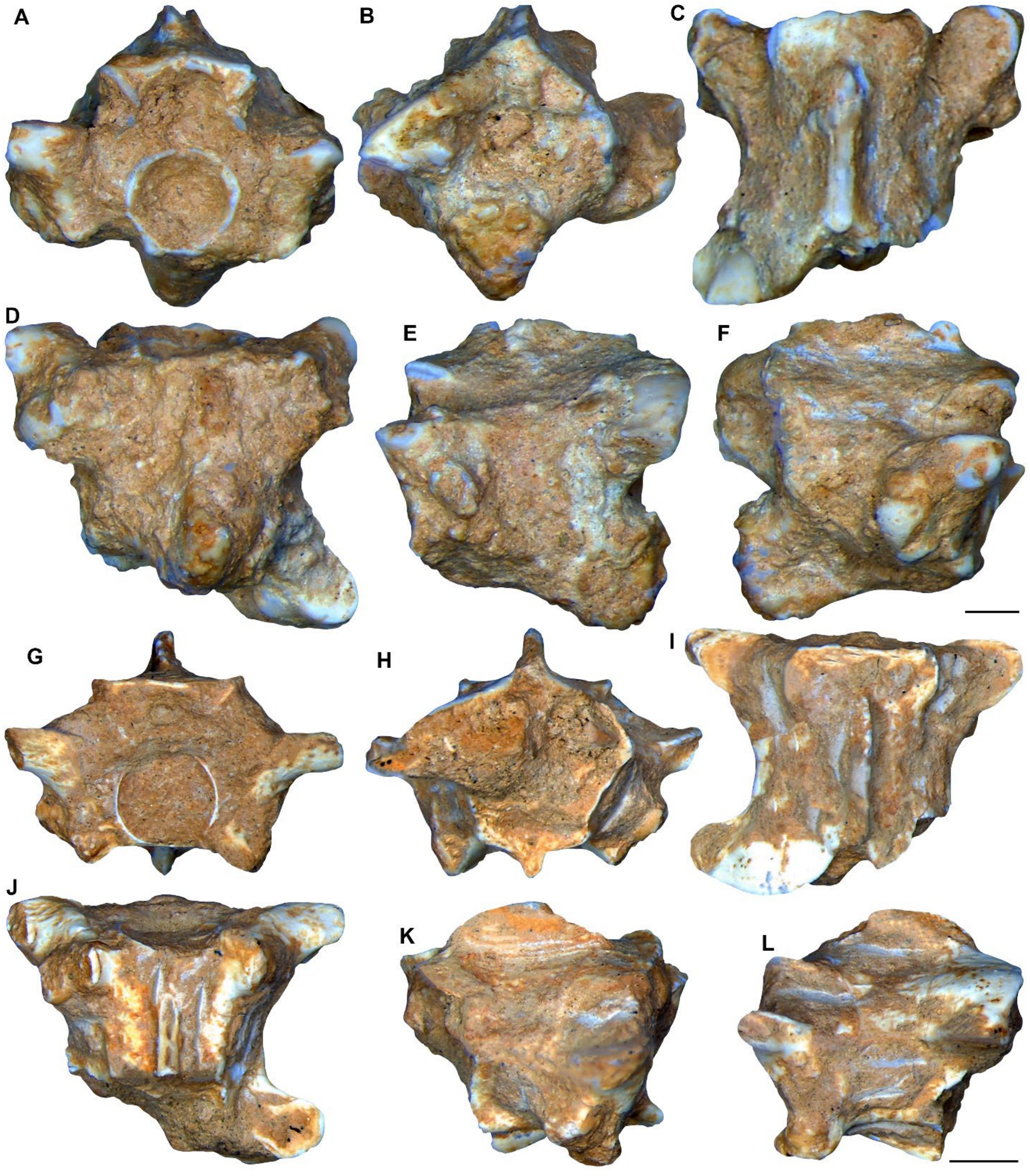

**Fig. 9.** *Naja* sp. from HPI: precloacal vertebra (IPS128030) in anterior (A), ventral (B), dorsal (C) and left lateral (D) views; precloacal vertebra (IPS128031) in anterior (E), posterior (F), ventral (G), dorsal (H), right lateral (I) and left lateral (J) views; precloacal vertebra (IPS128034) in ventral (K) and left lateral (L) views. All scale bars represent 2 mm.

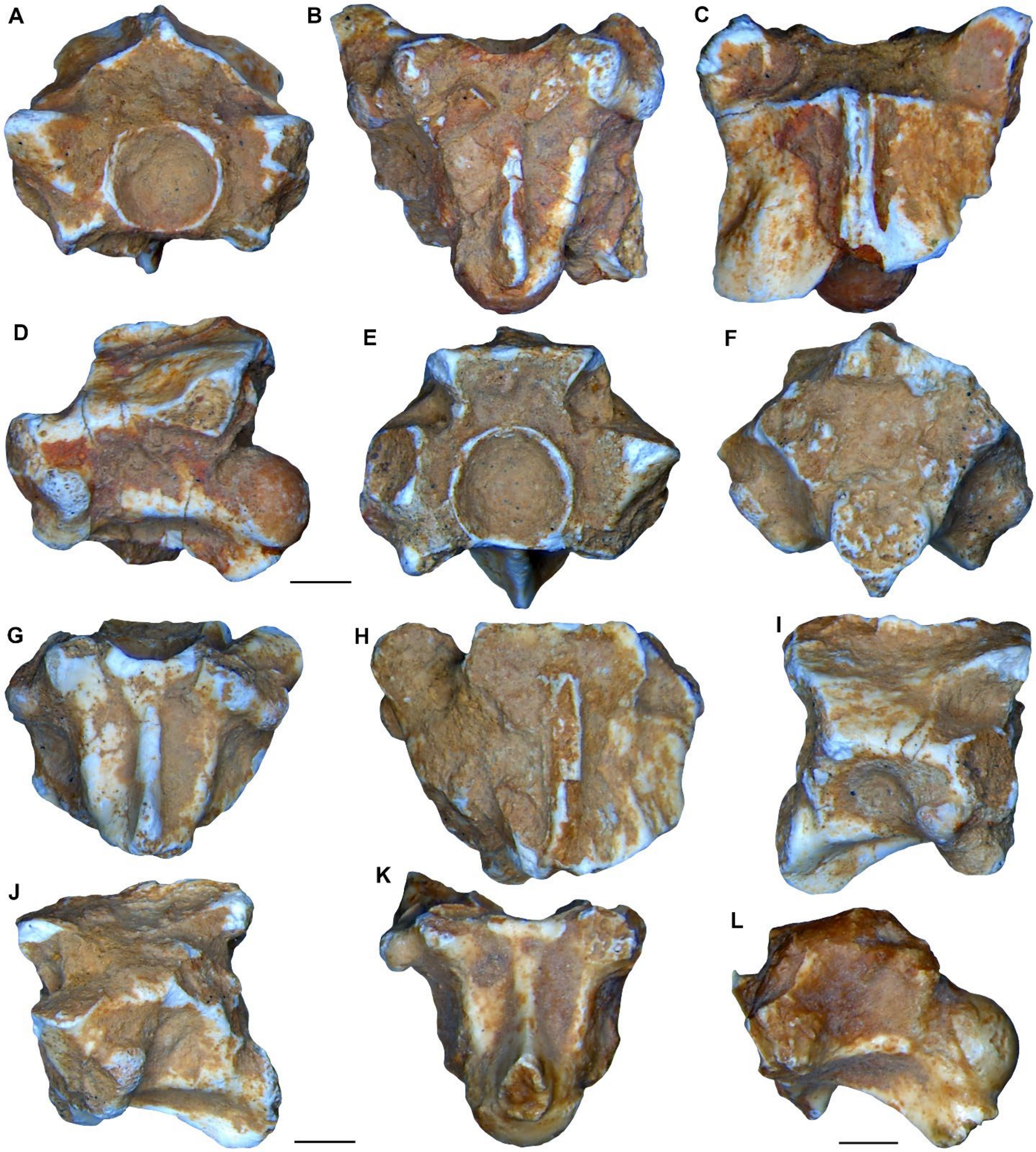

**Fig. 10.** *Naja* sp. from SG: precloacal vertebra (IPS128022) in dorsal (A), left lateral (B) and right lateral (C) views; precloacal vertebra (IPS128023) in anterior (D), ventral (E), dorsal (F) and left lateral (G) views; precloacal vertebra (IPS128024) in anterior (H), posterior (I), ventral (J), dorsal (K) and right lateral (L) views. All scale bars represent 2 mm.

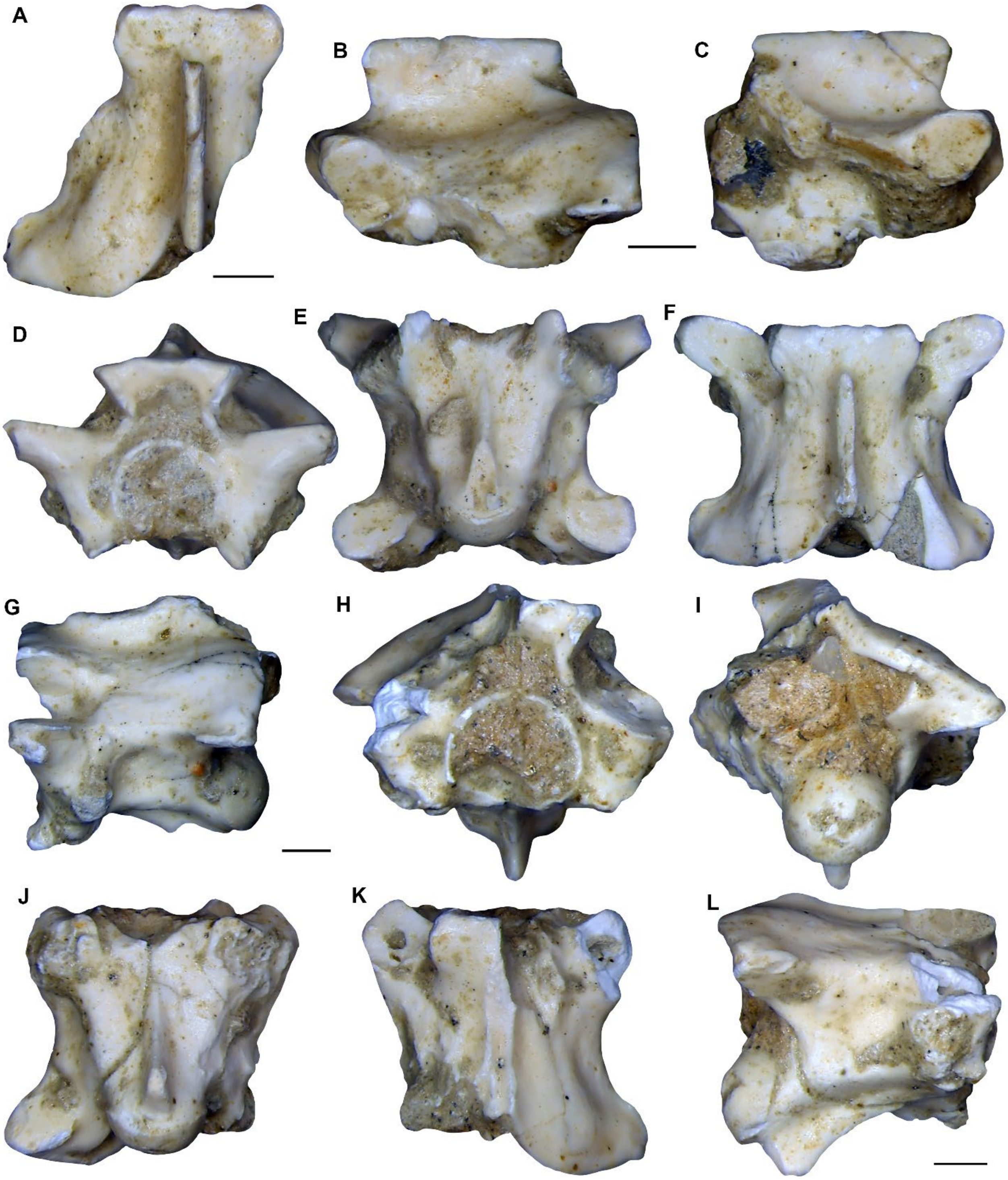

**Fig. 11.** Fossil record of *Naja* in the circum-Mediterranean area in general (A) and the Iberian Peninsula and southern France (B) in particular. Localities: 1, Beni Mellal, Morocco; 2, Guefaït-1, Morocco; 3, Serrat d'en Vaquer, France; 4, Algora, Spain; 9, Grund, Austria; 10, Kohfidisch, Austria; 11, La Grive-Saint-Alban, France; 12, Petersbuch 2, Germany; 13, Rudabánya, Hungary; 14, Solnechnodolsk, Russia; 15, Hrytsiv (= Gritsev), Ukraine; 16, Vieux-Collonges, France; 17, Echzell, Germany; 18, Ravin de la Pluie, Greece; 19, Fălciu-Prut 1, Romania; 20, Gratkorn, Austria; 21, Isle d'Abeau, France; 22, Sète, France; 23, Rothenstein 1/13, Germany; 24, Sandelzhausen, Germany; 25, Maramena 1, Greece; 26, Tourkobounia 1, Greece; 28, Irhoud Ocre, Morocco; 29, Altıntaş, Turkey; 30, Çalta, Turkey; 32, Abocador de Can Mata (ACM/C3-A7, ACM/C4-A1, ACM/C5-C3), Spain; 33, Córcoles, Spain; 34, Hostalets de Pierola and Hostalets de Pierola Inferior; 35, Layna, Spain; 36, Librilla, Spain; 37, Moreda, Spain; 38, Venta del Moro, Spain; 39, Sant Mamet, Spain; 40, Santiga, Spain; 42, Balaruc 2, France; 43, Hambach 6C. Primary references for the *Naja* occurrences from these localities can be found in Appendix S2.

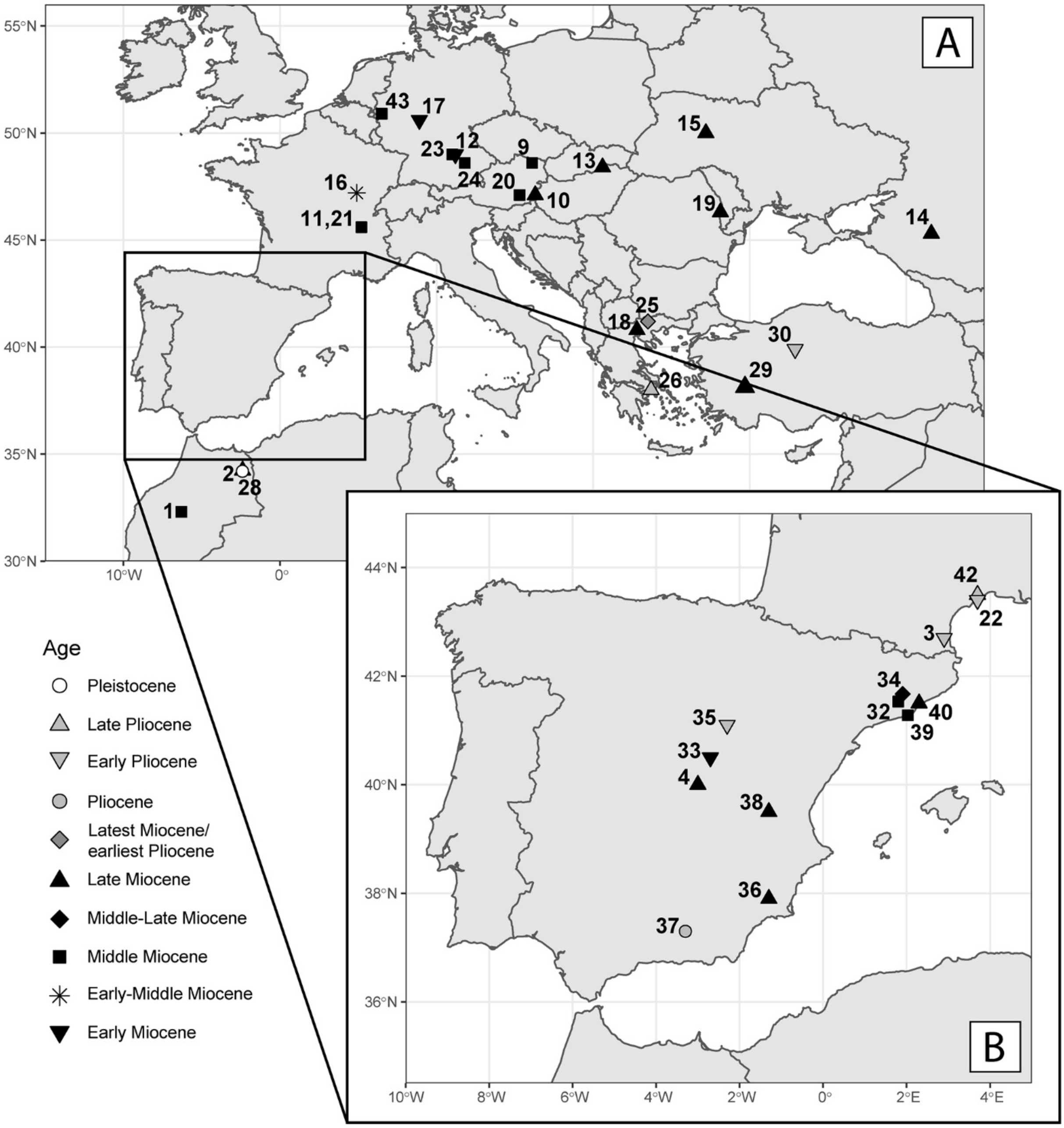
A
55°N
50°N
45°N
40°N
35°N
30°N
10°W
0°
43
17
23
12
9
15
13
24
20
10
16
11,21
19
14
25
18
30
26
29
2
28
1
Age
Pleistocene
Late Pliocene
Early Pliocene
Pliocene
Latest Miocene/ earliest Pliocene
Late Miocene
Middle-Late Miocene
Middle Miocene
Early-Middle Miocene
Early Miocene
B
44°N
42°N
40°N
38°N
36°N
10°W
8°W
6°W
4°W
2°W
0°
2°E
4°E
42
22
3
34
32
40
39
35
33
4
38
36
37

**Fig. 12.** Global fossil record of *Naja*. Localities: 5, Kurnool caves, India; 6, Taurung-tung, Philippines; 7, Olduvai Bed 1, Tanzania; 8, Loc. 10W, Upper Laetolil Beds, Tanzania; 27, Layer XIX, Qafzeh Cave, Israel: 31, Loc. 21, Al-Sarrar, Saudi Arabia; 41, DIK-1, Dikika, Ethiopia; 44, Arrisdrift, Namibia. Primary references for the *Naja* occurrences from these localities can be found in Appendix S2. For the circum-Mediterranean area check Fig. 11.

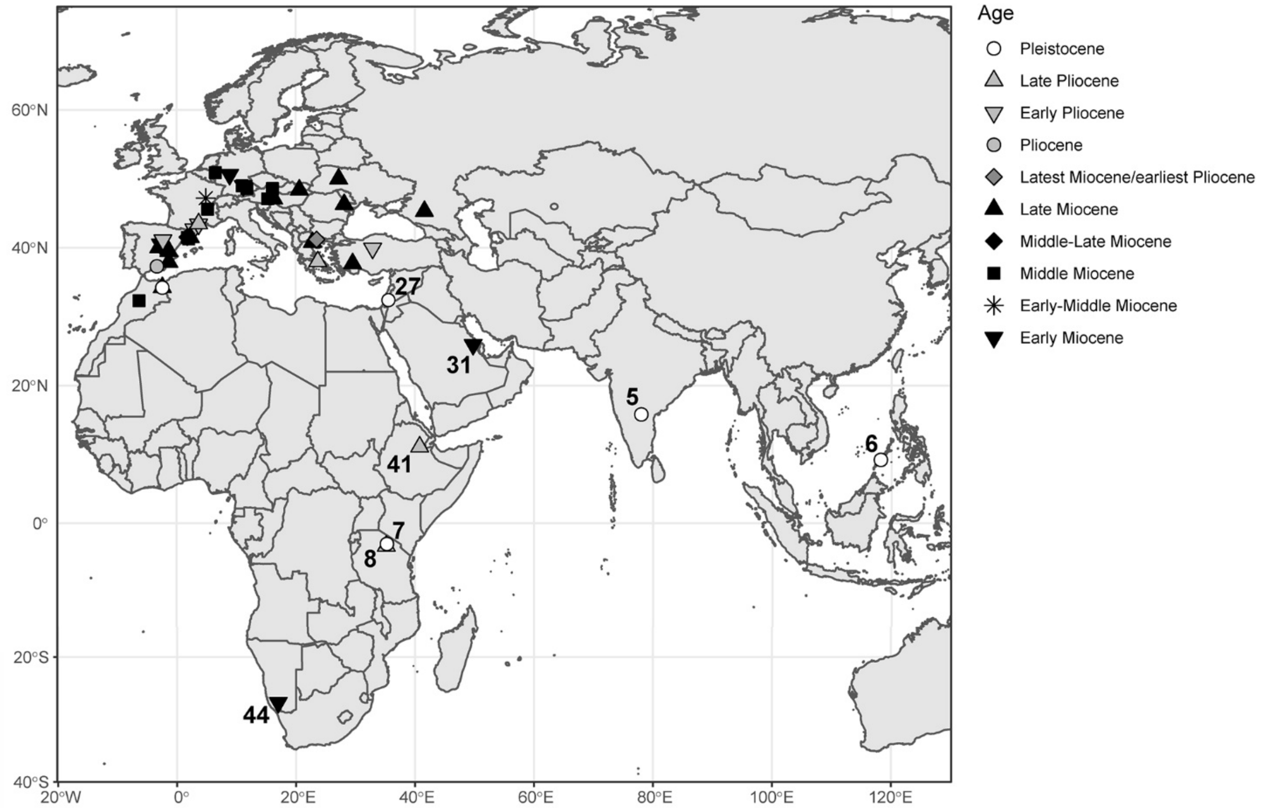

**Fig. 13.** Palaeobiogeography of *Naja*. A) Current and past distribution of the genus *Naja* in the circum-Mediterranean area, showing the progressive southward retraction. Current distribution after Pokrant *et al.* (2017). B) Potential dispersal routes of VPB *Naja* in the first half of the Miocene, showing the possible arrival either from an Eastern route through Central Europe (white arrow) or directly from Africa (black arrow). The precise origin of the Eastern lineage of European cobra is still uncertain. The cobra silhouette is made available by Chris Hay under a CC BY-NC 3.0 Deed license, through PhyloPic ([https://www.phylopic.org/](https://www.phylopic.org/)).