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Supplementary information

Exceptional brain and ecological diversity in the earliest snakes

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Exceptional brain and ecological diversity in the earliest snakes

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Description

General morphology

The holotype (MPM 420) of *Tametara mirim* gen. et sp. nov. includes an articulated cranium and postcranium exposed in dorsal view with its ventral side embedded in sandstone matrix (Figure 1a). The posterior half of the skull is almost perfectly preserved, including parts of the dermatocranium (postfrontal, frontal, parietal, supratemporals), splanchnocranium (right pterygoid and both quadrates) and chondrocranium (supraoccipital, otoccipitals, prootics, basioccipital and parabasisphenoid). The postcranium preserves at least the anterior half of the vertebral column (except atlas and axis) represented by ca. 103 precloacals. There are no traces of forelimbs (presumably absent in the species) or hindlimbs (if present, would not have been preserved as the sacral/cloacal region is not present).

Cranium

Postfrontal. The right postfrontal is preserved immediately lateral to the frontoparietal suture, as in most squamates, includingsnakes (Figure 1b,c; Figure 2b-e). It has a distinct frontal (anterior) process and a single distal process, as in other stem snakes, such as *Dinilysia* and *Najash* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher et al. 2009; Zaher and Scanferla 2012; Palci et al. 2013; Garberoglio et al. 2019a). Unlike the two latter, however, the postfrontal does not bear a distinct parietal (posterior) process. There are no articular facets on the distal process for articulation with a jugal or postorbital, suggesting the latter were not present, but which cannot be confirmed based on this specimen alone.

Pterygoid. An incomplete, posterior half of the right pterygoid is preserved, in articulation with the quadrate via the complete quadrate ramus (Figure 2b-e). The quadrate ramus of the pterygoid is toothless, elongated, thin and blade-shaped, having a medial side that is moderately concave. The anterior end of the preserved portion of the pterygoid is tilted medially and might represent the remnants of the transverse process, but taphonomic distortion may have impacted the shape of the latter.

Supratemporal

Both supratemporals are preserved and are robust elements, bearing a well-developed and ventrally projected posterior end with a large articular facet for the quadrate laterally (Figure 1b,c; 2a-e; Extended Data Figure 1a-c), as also seen in other stem snakes, including *Dinilysia* and *Najash* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher et al. 2009; Zaher and Scanferla 2012; Palci et al. 2013; Garberoglio et al. 2019a). Each supratemporal contacts the paroccipital processes of the otoccipitals ventrally,the supratemporal process of the parietal anteromedially, and the prootic ventromedially. The supratemporals extend anteriorly close to the level of the anterior margin of the fenestra ovalis. The supratemporals of *Tametara* are elongated longitudinally and do not have the free ending posterior process of most crown snakes. Moreover, the supratemporal does not possess a mid-shaft lateral bulge as observed in *Dinilysia* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher and Scanferla 2012).

Frontal. Part of the right frontal is preserved in articulation with the parietal posteriorly and the postfrontal posterolaterally (Figure 1b,c; 2a-b,d-e). It has a large articular facet for the frontal process of the postorbital, but no facet for a possible prefrontal (but we note that the anterior end of the frontal is mostly missing). The medial border of the right frontal is relatively straight and bears no indication of a midventral pillar. The lateral border bears the base of the subolfactory process projecting ventrally. As preserved, the subolfactory process is short dorsoventrally, but due to its incompleteness we cannot determine how far ventromedially it could have extended. Although the anterior frontal is incomplete, the preserved margins do not indicate that the observed morphology is solely a preservational artefact. The medial border of the frontal is smooth, indicating it articulated with its contralateral pair and that they were not fused.

Parietal. The parietal is unpaired and contacts the right postfrontal and the posterior edge of the frontal anteriorly, and the supratemporal and most braincase elements posteriorly (Figure 1b,c,h; 2a-e; Extended Data Figure 1b,f). In dorsal view, the parietal has a subtriangular shape expanding posteriorly. The right side of the parietal is entirely preserved, bearing a large facet for the postfrontal anterolaterally, and a short anteromedial process that would have inserted in between the two frontals, which is absent in absent in *Najash*, but arguably present in *Dinilysia* where the parietal contacts the frontals in a W-shaped interdigitating suture(Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher and Scanferla 2012)—but definitely occurring in *Wonambi* (Scanlon and Lee 2000). There is no indication of anterolateral processes, as seen in *Najash* and *Dinilysia* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher and

Scanferla 2012) *Sanajeh* (Wilson et al. 2010; Zaher et al. 2023), *Wonambi* and *Yurlunggur* (Scanlon and Lee 2000; Scanlon 2006), and most extant snakes.

A well-developed sagittal crest extends longitudinally along the dorsal surface of parietal, extending further posteriorly over the supraoccipital. The descending flange (= descensus parietalis) of the parietal is only preserved on the right side, and it contacts the dorsal surface of the prootic in a wedge-shaped suture. In lateral view, the descending flange overlaps the medial wall of the prootic crest, and has no 'medial parietal pillar' *sensu* Zaher and Scanferla (2012), which contributes to the separation between the telencephalon and mesencephalon in snake brains; similar to the condition in *Dinilysia*, *Najash,* and in scolecophidians (Zaher and Scanferla 2012).

The posterior margin of the parietal forms the supratemporal processes (= postparietal process) posterolaterally, which is also observed in some other stem snakes—e.g., *Najash*, *Dinilysia, Sanajeh* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Wilson et al. 2010; Zaher and Scanferla 2012; Zaher et al. 2023)—but absent in most crown snakes. However, differently from all other early deriving snakes with the posterior parietal margin well-preserved (e.g., *Najash*, *Dinilysia, Yurlunggur*, *Wonambi,* and *Haasiophis*), *Tametara* has a well-developed posteromedial process that slots into the anteromedial margin of the supraoccipital.

Quadrate. The quadrate of *Tametara* is strongly posteriorly emarginated, bears a shallow quadrate conch, and a well-developed suprastapedial process (Figure 1b,c,h; 2a-e; Extended Data Figure 1a), different from the straight quadrate with no conch or suprastapedial process of the vast majority of snakes, including some early fossil forms such as *Pachyrhachis* and *Haasiophis* (Caldwell and Lee 1997; Lee and Caldwell 1998; Tchernov et al. 2000; Rieppel et al. 2003). The cephalic condyle is anteroposteriorly longer than dorsoventrally tall, with a concave medial surface. There is a well-developed tympanic crest on the quadrate, similar to *Dinilysia* (not preserved or partially broken in all specimens of *Najash*). Ventromedially, the quadrate shaft bears a small quadrate lappet (a much shorter version of the pterygoid or medial process of other reptiles), which articulates with the quadrate ramus of the pterygoid. There are no signs of a stapedial pit or a quadrate foramen.

Supraoccipital. The supraoccipital contacts the parietal anteriorly, whereas ventrolaterally it contacts the prootic and otoccipitals (Figure 1b,c; 2a-e; Extended Data Figure 1a-c,f). As in most snakes, the supraoccipital lacks an anteromedially ascending process of the tectum

synoctum, which is expected given the absence of a parietal fossa on the ventral side of the parietal. However, it has well-developed anterolateral processes contacting the parietal posterolaterally, a condition similar to *Yurlunggur* (Scanlon 2006), but different from most other snakes, including other early fossil snakes—e.g., *Najash*, *Dinilysia,* and *Haasiophis* (Tchernov et al. 2000; Caldwell and Albino 2003; Rieppel et al. 2003; Caldwell and Calvo 2008; Zaher and Scanferla 2012) (Supplementary Table S1). Along with the anterolateral processes, these have a substantial overlap with the ventral side of the parietal. Although such overlap is observed in other snakes, including the braincase of early snakes such as *Dinilysia* (Caldwell and Calvo 2008; Zaher and Scanferla 2012) and *Najash* (Garberoglio et al. 2019a), the extent of this overlap with the prootics and parietals is greater than in any other taxon known to us. For instance, the supraoccipital of *Tametara* represents ca. 25% of the preserved dorsal surface of the skull roof. Adult specimens of *Dinilysia* have a supraoccipital that is strongly overlapped by the parietal, but it represents only between 8-11% of the total dorsal surface of the skull roof (e.g., MACN-Pv RN1013 and MLP 26-410, respectively).

The supraoccipital in *Tametara* also has a well-developed descending process that wedges between the medial walls of the prootics and otoccipitals, forming the dorsomedial corner of the otic capsule, including the common crus. However, in contrast with non-ophidian squamates, but confirming to other fossil snakes (Garberoglio et al. 2019a), the supraoccipital contributes substantially to the roof of the otic capsule, forming the dorsal part of the utricular recess (Extended Data Figure 1b). On the ventral side, the supraoccipital is perforated by the anterior and posterior semicircular canals. The supraoccipital also contributes to the posterior margin endolymphatic foramen, an uncommon feature for squamates. In most squamates, including at least some scolecophidian snakes, the foramen is usually housed only by the supraoccipital (Oelrich 1956; Cundall and Irish 2008). Among stem-snakes, *Dinilysia* (Zaher and Scanferla 2012) conforms to the pattern of most squamates, whereas the condition in *Najash* appears to be similar to *Tametara mirim* (Garberoglio et al. 2019a) . The endolymphatic foramen is also enlarged and slightly elongate in the latter two when compared to *Dinilysia* (Zaher and Scanferla 2012).

Dorsally, the supraoccipital bears a short sagittal crest, as in most other snakes, with the exception of scolecophidians and a few alethinophidians (e.g., *Xenopeltis* and *Loxocemus*). Further, it has laterally projecting nuchal crests, as in *Dinilysia* and most alethinophidians (with the exception of booids and pythonoids), differing from other fossil snakes such as *Najash* (Garberoglio et al. 2019a), *Yurlunggur* (Scanlon 2006), and *Haasiophis* (Tchernov et al. 2000; Rieppel et al. 2003).

Otoccipital. The otoccipital (fusion between exoccipital and opisthotic) forms most of the posterior/occipital portion of the braincase, with each otoccipital contributing to the occipital condyle and to the dorsolateral margins of the foramen magnum (Figure 1b,c; 2a,c-e; Extended Data Figure 1a-e). The otoccipitals of *Tametara* are mostly flat dorsally, similar to the otoccipital of the *Dinilysia*, and different from the bulbous otoccipitals of *Najash* (Garberoglio et al. 2019a). Paired nuchal crests occur in *Tametara mirim*, but they are weakly developed when compared to *Najash* (Garberoglio et al. 2019a) and many extant alethinophidians, such as *Anilius scytale* and *Cylindrophis ruffus*.

The otoccipitals of *Tametara* do not meet each other at the midline of the cranial roof, being separated by the posteromedial process of the supraoccipital (Figure 2c,d). Dorsolaterally, each otoccipital has a small area of contact with the prootic and the paroccipital process meets the medial part of the supratemporal. The paroccipital processes have their posteriormost end almost at the same level of the posterior end of the supraoccipital, similarly to *Najash* (Garberoglio et al. 2019a). *Dinilysia*, on the other hand (Zaher and Scanferla 2012), has paroccipital processes comparatively longer posteriorly, going beyond the level of the occipital condyle. On their anterolateral corner, each otoccipital is pierced by a small vascular foramen—more easily discernible on the right side (Figure 2d).

The lateral corner of the occipital condyle is not preserved and the left otoccipital is better preserved than the right one, which is represented only by dorsal portion. The otoccipitals of *Tametara* do not preserve the descending ventrolateral walls. Nevertheless, the medial wall of the left otoccipital is complete, and the entrance foramina for CN X (vagus) and CN XII (hypoglossal) could be located posterodorsally to CN X and thus closer to the border of the foramen magnum (Figure 1d; Extended Data Figure 1f). It is difficult to determine, however, whether the exact number of openings for CN XII. Among other stem snakes, three CN XII foramina have been identified in *Dinilysia patagonica* (Zaher and Scanferla 2012). In *Najash rionegrina* (G.S. pers. obs.) the CN XII appears to have only one foramen, which opens laterally in a common fossa housing the exits of CN X dorsally and anteriorly and another foramen below this, which may be for CN IX considering its anterior, instead of posterior direction within the otoccipital. In *Tametara mirim*, however, no common fossa for both nerves could be identified. The CN XII runs almost straight laterally, but its external foramen could not be located, whereas the CN X runs anteromedial to posterolateral and opens on the lateral wall of the otoccipital just posterior to the anterior border of the crista tuberalis (Figure 2c;

Extended Data Figure 1b,d). Part of the course of the CN X can be seen on the eroded posterior wall of the recessus scalae tympani (Extended Data Figure 1e).

The posterior wall of the left otoccipital of *T. mirim* is concave and houses the posterior portion of the otic capsule. The foramina indicating the course of the posterior and lateral semicircular canals could only be partially identified, and the location of the posterior ampulla can be seen partially eroded on the posterior wall of the otic capsule (Extended Data Figure 1g). The otoccipital forms the crista interfenestralis, but a crista circumfenestralis *sensu* Palci & Caldwell (2014) is absent, as the basioccipital contributes to the floor of the recessus scalae tympani, including the ventral border of the apertura lateralis—a condition shared with several early fossil snakes in which this can be determined (e.g., *Najash* MPCA 500, *Dinilysia*, and *Sanajeh*; TRS pers. obs, and Palci and Caldwell (2014). A deep and narrow excavation on the floor of the otoccipital, medial to the fenestra ovalis, indicates the position of the posterior portion of the lagenar recess (Extended Data Figure 1e). The perilymphatic foramen is large but incomplete on the postero-ventral wall of the otic capsule (Extended Data Figure 1e).

Basioccipital. The basioccipital of *Tametara* is almost complete and has a trapezoidal shape, forming the posteroventral portion of the braincase, and contacting the parabasisphenoid anteriorly, the prootic dorsolaterally, and finally the otoccipital posterodorsally (Figure 2c,e; Extended Data Figure 1a-d). In ventral view, the suture between the basioccipital and the parabasisphenoid is slightly convex anteriorly, with the basioccipital forming a reduced anteromedial process. This conforms to *Dinilysia* (Zaher and Scanferla 2012), but differs from *Najash* (Garberoglio et al. 2019a), where the suture is mediolaterally straight. There is no ventral concavity for attachment of the axial musculature. Sphenoid tubercles are also not discernible, thus differing from the well-developed sphenoid tubercles found in *Dinilysia* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Zaher and Scanferla 2012). The basioccpital contributes to the floor of the recessus scalae tympani and to the ventral border of its apertura lateralis.

Parabasisphenoid. The parabasisphenoid of *Tametara* is incompletely preserved in the region corresponding to the basisphenoid body (Figure 2a,c,e; Extended Data Figure 1a-d). The lateral and anterior margins of the main body of the parabasisphenoid contact the ventral process of the prootic, whereas the posterior part contacts the basioccipital. The bases of the basipterygoid processes are preserved ventrolaterally, and the dorsum sella is well-developed relative to most snakes, and visible in anterior view (Extended Data Figure 1c). Foramina for CN VI (abducens)

could not be detected. The dorsum sella shows no retractor bulbi pits for the corresponding ocular muscles. These patterns conform to the condition of most snakes, as the retractor bulbi muscles are absent in all extant snakes (Zaher and Scanferla 2012). The crista trabecularis of *Tametara* is moderately developed and posterolateraly elongated as in *Najash* (Garberoglio et al. 2019a), but not protruding as in *Dinilysia* (Zaher and Scanferla 2012).

There is no midsagittal crest on the ventral surface of the basisphenoid for the insertion of the protector pterygoid muscles, as also observed in the most complete specimens of *Najash* (e.g., MPCA 500) and *Dinilysia* (Zaher and Scanferla 2012; Garberoglio et al. 2019a), and differently from *Sanajeh* (Wilson et al. 2010; Zaher et al. 2023) and *Wonambi* and *Yurlunggur* (Scanlon and Lee 2000; Scanlon 2006). The anterior opening of the Vidian canal is observed ventrolaterally on either side of the basisphenoid (Extended Data Figure 1a).

Prootic. The prootics are almost completely preserved, being longitudinally short and contacting many cranial bones: (i) they meet the parietal anterior- and dorsomedially; (ii) the basisphenoid anterior- and medioventrally; (iii) the basioccipital porsterior- and medioventrally; (iv) the supratemporal posterior- and dorsolaterally; (v), and finally, a broad posterior contact with the otoccipital (Figure 1b,c,h; 2a-e; Extended Data Figure 1a-d). It has a well-developed alar crest anterodorsally that contacts the descending flanges of the parietal through a wide dorsoventrally sloped suture, forming the dorsal margin of the trigeminal notch. The prootic anterior inferior process extends further anteriorly forming the ventral margin of the trigeminal notch. As in other early fossil snakes in which this can be determined—e.g., *Najash*, *Dinilysia, Yurlunggur*, *Wonambi,* and *Sanajeh*—and scolecophidians, there is no ossification of the pila antotica (laterosphenoid), which encloses the trigeminal notch anteriorly in alethinophidians. The single facial nerve is visible on the lateral wall of the prootic (Figure 2a,b; Extended Data Figure 1a,d).

The prootic crest (= crista prootica) is present but poorly developed. A small portion of the dorsomedial part of the prootic is compressed posteriorly by the parietal, medially by the supraoccipital, laterally by the supratemporal, and by the otoccipital posteriorly. Moreover, this dorsally exposed contact between the prootic and the supraoccipital is a condition also found in *Dinilysia* and *Najash* (Estes et al. 1970; Zaher and Scanferla 2012; Garberoglio et al. 2019a) and basal alethinophidians—e.g., *Cylindrophis ruffus* and *Anilius scytale* (TRS pers. obs,).The posterodorsal process of the prootic is elongated and overlaps the dorsal margin of the fenestra ovalis. In dorsolateral view, it is possible to note a notch on the dorsal surface of the otoccipital process of the prootic at half level of the fenestra ovalis. Such notch, has a marked sharp ventral

margin on the lateral surface of the posterodorsal process of the prootic. The ventral surface of the prootic is excavated by the anterior portion of the lagenar recess, which is separated from the saccular region immediately above by an incomplete shelf (Figure 2c; Extended Data Figure 1b). Dorsomedially to the saccular recess, the prootic bears the wide and round utricular recess (Figure 2c; Extended Data Figure 1b). The medial wall of the prootic (Extended Data Figure 1d) is perforated by the internal foramen of the facial nerve (CN VII) and by the anterior branch of the acoustic nerve (CN VIII). In addition, the medial wall of the prootic forms the anterior border of the endolymphatic foramen.

Stapes. A small portion of the stapes is preserved on the left side of the skull (Figure 2c,d and Extended Data Figure 1b), represented by a short and robust stapedial shaft, similar to the stapedial shaft in *Dinilysia* (Zaher and Scanferla 2012), and more robust than that in *Najash* (Garberoglio et al. 2019a). The stapedial footplate is not preserved, but considering the large size of the oval window, it is expected to have been expanded, as in all known snakes.

Mandibles. Only the two posterior portions of the compound bones are preserved from the mandibular set, with the right compound bone better preserved than the left one (Figure 1b,c,h-j; 2a-e; Extended Data Figure 1h). The compound bones are elongated longitudinally and almost cylindrical in cross-section. The compound bone has a long and deep mandibular fossa facing dorsolaterally, as in most snakes, bearing a couple of nutrient foramina located on the lateral wall of the fossa. Furthermore, a posterior surangular foramen is present, as in many early fossil snakes in which this can be determined—e.g., *Najash*, *Dinilysia,* and *Sanajeh* (Caldwell and Albino 2003; Caldwell and Calvo 2008; Wilson et al. 2010; Zaher and Scanferla 2012; Garberoglio et al. 2019a; Zaher et al. 2023)—but different from most extant snakes. The glenoid articulation between the quadrate and articular portion of the compound bone bears a small foramen for the chorda tympani (Extended Data Figure 1h). The articular facet of the compound bone of *Tametara* has saddle-shaped with a well-developed anterior border. Such condition is also shared by *Dinilysia* (Zaher and Scanferla 2012) and common among extant snakes. The retroarticular process is absent in *Tametara*, as in *Dinilysia* (TRS pers. obs., but see alternative interpretation by (Caldwell and Calvo 2008; Zaher and Scanferla 2012)), whereas *Najash* exhibits a small one (Garberoglio et al. 2019a). We note that in all these taxa the area beyond the glenoid articulatory facet is quite small and thus of difficult interpretation, but we consider it present in *Najash*, unlike the two other taxa, as in the latter has a small but dorsally projecting RAP, clearly beyond the confines of the glenoid border.

A small fragment of the coronoid is preserved, represented by a small dorsal process, located just anterior to the mandibular fossa (Extended Data Figure 1h). The anterior part of the compound bone, coronoid, and whole of the dentary bones are not preserved.

Brain endocast

Endocast–brain correspondence in squamates varies across species and neuroanatomical regions, but, especially in snakes, it is generally very close in the forebrain, particularly the cerebral hemispheres and olfactory bulbs (Scanferla 2022; Allemand et al. 2023). This correspondence enables meaningful comparisons among extant snakes (Allemand et al. 2017; Segall et al. 2021). It has also been used both for qualitative assessments of fossil endocasts relative to extant taxa to inform interpretations of brain ecomorphology (Scanferla 2022), and for quantitative comparisons of fossil squamates within a phylogenetic context (Allemand et al. 2017; Segall et al. 2021; Allemand et al. 2024). Given the preservation of the anterior cranial region, careful examination of the frontal and associated endocast morphology was necessary to assess whether the structure interpreted as the olfactory bulb could instead reflect preservational artefact. Although parts of the anterior frontal region are incomplete, the preserved morphology remains consistent with our interpretation of the frontal/endocast relationship. We nevertheless treat this region cautiously and base our comparisons only on preserved structures that can be confidently delimited.

The brain endocast of *Tametara* mirim is anteroposteriorly elongated and defined anteriorly by short olfactory bulbs (Figure 2j; Extended Data Figure 1i-k). It is followed immediately posteriorly by mildly enlarged cerebral hemispheres in the telencephalon followed by a slightly narrower mesencephalon (i.e., optic lobes not well-developed). This diverges from the condition observed in most squamates, including other snakes, which display well-expanded cerebral hemispheres that strongly contrast with the mesencephalon and rhombencephalon (= mid- and hind-brain, respectively)(Allemand et al. 2017; Segall et al. 2021; Allemand et al. 2023). The telencephalon condition of *Tametara mirim* closely resembles that of species with high degrees of fossoriality, where the distinction in relative width between the cerebral hemispheres and the midbrain components immediately posterior to them are more subtle, including fossorial snakes such as scolecophidians (e.g., Liotyphlops), and *Uropeltis* (Olori 2010; Allemand et al. 2017), as well as other fossorial, limb reduced non-ophidian squamates, such as the amphisbaenian *Blanus,* and the skink *Melanoseps* (Allemand et al. 2023). However, the midbrain of *Tametara mirim* differs from most of the previous examples with regards to the optic tectum (=lobe), as this structure is

poorly defined and unusually elongated relative to other squamates. Among extant snakes, the most similar condition to *Tametara mirim* is seen in *Cylindrophis ruffus* (Olori 2010; Allemand et al. 2017). Squamate species with higher degrees of fossoriality, nocturnal habits, or aquatic murky environments, also tend to have poor development of the optic tectum, which contributes to the reduced resolution of the midbrain component in endocasts (Allemand et al. 2017; Segall et al. 2021; Allemand et al. 2023).

Posterior to the midbrain region, the endocast of *Tametara* is characterized in dorsal view by a strongly laterally constrained region, which is hourglass-shaped (Extended Data Figure 1i). The anterior half of the hourglass is elevated relative to the optic tectum anterior to it, and its dorsal surface is positioned obliquely anteroventral to posterodorsal. A similar structure is found in *Anilius scytale* and *Dinilysia*, but not identified, although it lies in the area corresponding to the choroid plexus of the fourth ventricle (Scanferla 2022). The choroid plexus is a branching network of cells that secretes most of the cerebrospinal fluid. However, this region of the endocasts in *Anilius* and *Dynilisia* are distinctly bilobed (Scanferla 2022), whereas in *Tametara* the only indications of paired structures is a faint sulcus running anteroposteriorly along the midline, following a corresponding low crest on the ventral surface of the parietal (Extended Data Figure 1i).

The remaining hindbrain region of *Tametara* is separated from the more anterior region by the approximating contralateral common crura (Figure 2j; Extended Data Figure 1i). The dorsal surface lies ventral to the collicular and cerebellar regions and the mostly flat rhombencephalon indicates the medulla oblongata is not as expanded as in most extant snakes (Scanferla 2022; Allemand et al. 2023). In dorsal view (Extended Data Figure 1i), the medulla is narrower than the cerebral hemispheres, but it has a similar width to the optic tetum. The pontine flexure is very gentle in *Tametara* (Extended Data Figure 1). The medulla oblongata of *Tametara* shows a rather close correspondence with the basioccipital, whereby the ventral surface of the endocast bears a faint medial ridge running anteroposteriorly along the midline, corresponding to a shallow trough on the dorsal surface of the basioccpital.

Although the anterior portion of the pituitary region of *Tametara* is missing, the posterior projection is notably long (following measurement #14 of Allemand et al. 2017), tilting strongly ventrally towards the hypophyseal fossa. Among extant snakes, fossorial species do not tend to show a markedly long pituitary, while marine and terrestrial taxa tend to have a more ventrally developed gland (Allemand et al. 2017; Segall et al. 2021; Allemand et al. 2023). Compared to extant snakes, *Tametara* and *Dinilysia*, have remarkably long pituitary glands, although the length of these structures might only correspond to the elongate

parietal of these species, bearing no significant ecological or hormonal effect, as pointed in previous studies (Allemand et al. 2017; Segall et al. 2021; Allemand et al. 2023).

Inner Ear

The vestibular region of the otic capsule in *Tametara* is much enlarged, occupying most of the prootic and otoccipital bones (Figure 2c; Extended Data Figure 1b). The separation between saccular and utricular recesses are visible on the posterior surface of the prootic (Figure 2c; Extended Data Figure 1b). Both are wide and round, separated from each other by a subtle constriction. Ventral to the saccular recess, the lagenar recess is separated by the former by an incomplete shelf, both on the prootic anteriorly (better visible on the right side; Figure 2c; Extended Data Figure 1b) and on the ottoccpital posteriorly (better visible on the left side). The lagenar recess appears wider anteriorly than posteriorly, but it is unclear if the recess was actually asymmetrical or whether this is due to damage to the otoccipital in this region. The anterior ampullary recess is small, but in contrast to *Dinilysia* (Palci *et al.* 2020, Yi & Norell 2015), the anterior and lateral ampullae are indistinguishable. The posterior ampullary recess is unremarkable. Likewise, the common crus is almost non-existent: the junction between anterior and posterior semicircular canals occurs dorsomedially very close to the utricular area, being almost undistinguishable from the remainder of the vestibular endocast. The endolymphatic foramen is positioned just anteroventral to the common crus. The perilymphatic foramen is large and located posteroventral on the otic capsule, opening into the recessus scalae tympani (Extended Data Figure 1e). The recessus scale tympani is relatively large, excavating the laterodorsal part of the dorsal surface of the basioccpital. The medial aperture of the recessus scale tympani is represented by a narrow and slit-like opening at the articulation between otoccipital and basioccipital (Extended Data Figure 1d), as in *Dinylisa* (Zaher & Scanferla 2012). The lateral opening of the scale tympani (LARST) is expanded, and formed mostly by the otoccipital, but with a basiccopital contribution ventrally.

Postcranium

The preserved vertebral column of *Temetara* includes 103 precloacal vertebrae (Figure 1a). However, it is not possible to determine the total vertebral count.

Vertebral anatomy. The vertebral elements exhibit a typical morphology of snake vertebrae, as well as patterns in intracolumnar variation. Subdivisions of the presacral/precloacal elements

411 in reptiles are difficult to determine in snakes and other limbless squamates as these are
412 typically defined based on vertebra bearing ribs contacting the sternal plate to discern between
413 cervicals and dorsals (Hoffstetter and Gasc 1969). However, here we follow previous studies
414 in characterizing the anteriormost precloacal bearing hypotheses as cervicals, and the
415 remaining precloacals as dorsals (Holman 2000; Caldwell 2019; Garberoglio et al. 2019c).
416 In block 1, which displays the preserved skull, there are 39 vertebrae starting from the
417 highly fragmented third anterior vertebra. Block 2 preserves an additional 32 vertebrae;
418 however, the posterior portion of the block is heavily fragmented, preventing the visualization
419 of additional elements. Block 3 also contains 32 vertebrae, but the most anterior portion is
420 severely damaged, making it impossible to analyze the vertebrae in that region. The total
421 number of preserved vertebral elements is estimated to be 103 precloacal (Figure 1a).
422 All vertebrae (Figure 1d-g; 2f-i; Extended Data Figure 2) have a depressed neural arch,
423 except for the anteriormost cervicals, in which they are relatively taller. Neural spines are low,
424 blade-like, and longitudinally elongate, starting immediately posterior to the zygosphene dorsal
425 margin. They all exhibit well-developed zygosphenes and zygantra. All vertebrae also display
426 a margo ventralis (Hoffstetter and Gasc 1969) (= ventrolateral crest (Auffenberg 1963);
427 posterior centrosynapophyseal lamina crest (Tschopp 2016)) connecting the paradiapophysis
428 to the vertebral condyle. They also all bear a margo lateralis (Hoffstetter & Gasc 1969) (=
429 interzygapophyseal ridge sensu (Auffenberg 1963)) joining the pre- and postzygapophyses.
430 However, we note that the expression of both the margo ventralis and margo lateralis can vary
431 along the precloacal column and may also vary among individuals/specimens within species.
432 These structures are therefore most reliably interpreted in a comparative framework that
433 accounts for intracolumnar and intraspecific variation, particularly when they are weakly
434 developed. Both margo ventralis and lateralis are more subtle anteriorly but strongly developed
435 towards the posterior precloacals (Figure 2h,i; Extended Data Figure 2). The prezygapophyses
436 are elongated, mainly directed anteriorly in dorsal view, and show a dorsal inclination in
437 anterior view. The postzygapophyses are elongated and slightly inclined dorsolaterally.
438 The vertebral centra are all subtriangular in ventral view, being wider anteriorly, and
439 each one bearing a well-defined midventral ridge (= haemal keel). The midventral ridge is
440 smooth and weakly developed anteriorly, becoming more pronounced further posteriorly
441 (Figure 2g; Extended Data Figure 2c). Along with the margo ventralis, the midventral ridge
442 contributes to form subcentral grooves ventrolaterally, which are relatively shallow and extend
443 from the ventral margin of the cotyle to the middle portion of the centrum. Subcentral grooves
444 taper posteriorly contributing to a moderate precondylar constriction along the mid-dorsals,

while remaining relatively broad as they approach the precondylar constriction in the posteriormost preserved vertebrae.

Vertebral condyles are circular and characterized by a weak precondylar constriction (Figure 2; Extended Data Figure 2). Each cotyle is rounded in posterior view across anterior and middle vertebrae, but oval among posterior ones. The paradiapophyses are prominent and positioned ventrolaterally, separated from the prezygapophyseal articular surfaces. The diapophyseal and parapophyseal surfaces are distinctly separated as in most snakes; the diapophyses are convex, whereas the parapophyses are concave (Figure 2h and i; Extended Data Figure 2a-c).

Subcentral foramina located on either side of the midventral ridge occur intermittently throughout the anteriormost vertebrae (mostly cervicals),but occur in nearly all observed dorsals (Figure 2g; Extended Data Figure 2b,c), as in *Dinilysia* (Scanferla and Canale 2007), but differently from *Najash*, where these are absent (Zaher et al. 2009) (Supplementary Table S1). Most vertebrae have paracotylar foramina on each side of the cotyle, which become more frequently observed further posteriorly along the column (Extended Data Figure 2d), as in *Dinilysia* (Scanferla and Canale 2007), and in *Najash* (Garberoglio et al. 2019b) (Supplementary Table S1). Finally, small parazygantral pits enclosing parazygantral foramina are present on either side of each zygantrum on most vertebrae (Extended Data Figure 2a-d), as in *Najash*, but differently from *Dinilysia* (Apesteguía and Zaher 2006; Scanferla and Canale 2007; Zaher et al. 2009) (Supplementary Table S1).

Cervical variations. The first (atlas) and the second (axis) cervicals are not preserved. The preserved cervical vertebrae are composed of seven anterior vertebrae, thus reaching a total of nine cervicals. This number is smaller compared to most extant snakes, with some reaching up more than 30 cervicals (e.g., *Eunectes murinus*) [ASH, pers. obs.].

Cervicals have their neural spines located mostly posteriorly and slightly increasing in height towards the posterior cervicals (Extended Data Figure 2a,b). Their zygosphenes are moderately developed, with nearly the same size as the cotyle. There is no discernable precondylar constriction in this region. The prezygapophyses are shorter and more anteriorly oriented than the anterior and mid-dorsal vertebrae.

There is a pair of subcentral foramina on either side of the hypapophysis (Extended Data Figure 2a,b). The base of the hypapophysis is longitudinally elongated, covering most of the ventral surface of the centrum and forming a prominent ventral projection. Cervical 4 has a hypapophysis with an open articulatory facet (Extended Data Figure 2a), remarkably similar

to the condition observed in *Dinilysia* and *Najash,* in which these are the articulatory facets for the cervical intercentra (Garberoglio et al. 2019c). Accordingly, we interpret the ventral projection on all subsequent cervicals as representing the fusion of the hypapophysis and cervical intercentrum in each element (Figure 2h; Extended Data Figure 2a,b).

Dorsal variations. Similarly to the condition in other squamates, and reptiles in general, vertebral accessory processes become more pronounced further posteriorly along the dorsal component of the precloacal/presacral region. This includes more pronounced zygosphenes, margo ventralis and lateralis, and midventral crests (Figure 2i; Extended Data Figure 2c). Nevertheless, because the degree of development of the margo ventralis and margo lateralis can be subtle and variable, we do not treat these features alone as definitive diagnostic evidence for *Tametara*. The neural spine also becomes more pronounced further posteriorly, but in general it remains constantly low developed in height about the vertebral column. Moreover, the prezygapophyses are more laterally directed and well-developed compared to cervicals.

The dorsal margin of the zygosphene shows a subtle crenate format—sensu (Auffenberg 1963), and a weak precondylar constriction occurs. Notably, a distinct foramen is present in the posterior portion of the neural arch of the posterior vertebra, perforating both postzygapophyseal facets (Extended Data Figure 2c). It is unlikely to be an artifact, given that the same foramina occur in both the preceding and following vertebrae. Apparently, there are no arqual ridges (sensu Scanferla & Canale 2007) on the neural arch in any of the vertebrae examined.

In summary, the margo lateralis and margo ventralis are present in the preserved dorsal series of *Tametara*, but their development is variable along the column and comparable structures may be expressed to different degrees in other snakes. We therefore regard these characters as informative but potentially variable features, rather than as unambiguous standalone diagnostic traits.

Synapomorphies list

Here we provide the list of unambiguous and accelerated transformation (ACCTRAN) synapomorphies for early snake branches recovered from maximum parsimony ancestral state reconstructions of the node + tip dates relaxed clock Bayesian inference analysis (Figure 2a, Extended Data Figure 5b and 6). For node numbers and full list of synapomorphies, see Supplementary Data 1.

node_319 --> node_318 (Serpentes Total Group)

```
  6 (Premaxillae, dentition)        0.400  0 --> 1
  11 (Premaxillae, vomerine medial flange)
0.182  0 --> 2
  17 (Septomaxillae, lateral flange)      0.067  0 --> 1
  37 (Maxilla, ventral side, palatine process)
0.167  0 ==> 1
  46 (Lacrimals)                    0.059  0 --> 1
  63 (Postorbitals)                 0.111  0 ==> 1
  69 (Squamosals)                   0.167  0 ==> 1
  79 (Postfrontals, medial forking)       0.111  1 --> 0
  86 (Frontals, fusion to each other)     0.059  1 --> 0
  91 (Frontals, subolfactory process, ventral lamina)
0.500  0 ==> 1
  98 (Pineal foramen)               0.050  0 ==> 1
  110 (Parietals, parietal table, shape)  0.059  1 ==> 0
  118 (Vomers, ventral surface, midline crest)
0.067  0 --> 1
  148 (Ectopterygoid, anteriormost end, contact with maxilla suborbital
process)   0.250  0 ==> 1
  150 (Epipterygoid)                0.200  0 ==> 1
  158 (Quadrates, quadrate conch)   0.071  1 ==> 0
  231 (Surangular, lateral adductor crest)
0.056  1 --> 0
  236 (Articular, fusion)           0.238  1 ==> 2
  238 (Articular, retroarticular process) 0.067  1 --> 0
  240 (Articular, retroarticular process, dorsal fossa)
0.053  1 ==> 0
  245 (Prearticular, mandibular fossa, orientation)
0.286  0 ==> 1
  248 (Coronoid, anterolateral process)   0.083  1 ==> 0
  250 (Coronoid, posterodorsomedial process)
0.043  0 --> 1
  288 (Presacral pleurocentra, midventral crest, dorsal vertebrae)
0.034  0 --> 1
  293 (Posterior presacral pleurocentra, dorsal verterae, margo
ventralis)   0.053  0 ==> 1
  295 (Sacral vertebrae, number)    0.400  2 ==> 1
  303 (Chevron bones, articulation)       0.125  1 --> 2
  310 (Neural arches and pleurocentrum, diapophysis, dorsal vertebrae,
fusion to parapophysis)                         0.200  1 ==> 0
  312 (Neural arches, margo lateralis, posterior presacral vertebrae)
0.083  0 ==> 1
  322 (Presacral ribs, posterodorsal process at rib head (=
pseudotuberculum))     0.200  0 ==> 1
```

329 (Sternum, mineralized) 0.100 1 ==> 0
340 (Epicoracoid) 0.111 1 ==> 0
382 (Calcaneum, lateral flange (or process) of the calcaneum)
0.333 0 --> 1
394 (Scleral ossicles) 0.333 0 --> 1

node_318 --> node_317 (Tametara + Najash)
58 (Jugals, posteroventral process) 0.045 0 --> 1
112 (Parietals, dorsal surface, anteromedial process)
0.111 0 --> 1
141 (Pterygoids, transverse processes, flange)
0.042 1 --> 0
156 (Quadrates, pterygoid process) 0.111 1 ==> 0
283 (Axis, intercentrum, fusion to axial pleurocentrum)
0.071 1 --> 0
324 (Posteriormost presacral vertebra, ribs articulation)
0.143 0 --> 1
376 (Femora, internal trochanter) 0.143 1 --> 0

node_317 --> Tametara mirim
78 (Postfrontals, parietal process) 0.091 1 ==> 0
106 (Parietals, posteromedial (=postparietal) process)
0.067 0 ==> 1
168 (Supraoccipital, lateral ascending processes)
0.037 0 ==> 1
171 (Supraoccipital, lateral nuchal crest)
0.063 0 ==> 1
288 (Presacral pleurocentra, midventral crest, dorsal vertebrae)
0.034 1 --> 0
node_317 --> Najash rionegrina
167 (Supraoccipital, medial ascending process)
0.042 0 ==> 1

node_318 --> node_316 (Serpentes -Tametara+Najash)
121 (Vomers, shape in cross-section) 0.095 1 ==> 0
126 (Palatines, teeth) 0.100 0 ==> 1
135 (Palatines, ventral side, anterior (=vomerine) process, anterior
end, location, relative to vomer posteri) 0.375 0 ==> 1
136 (Pterygoids, teeth) 0.042 0 ==> 1
147 (Ectopterygoids, lateral process) 0.059 1 ==> 0
181 (Basisphenoid, dorsum sellae) 0.143 1 --> 0
183 (Basisphenoid, ventral side, midsagittal crest)
0.100 0 --> 1
198 (Exoccipitals (or otoccipitals), contact to each other medially)
1.000 0 ==> 1
230 (Surangular (or fused compound bone), coronoid process)
0.125 0 --> 1
379 (Fibulae, articulation with femur, location)
0.500 1 --> 0

node_316 --> node_286 (Dinilysia + Sanajeh)
119 (Vomers, ventral surface, lateral crests:)
0.077 0 --> 1
140 (Pterygoids, transverse processe) 0.125 1 --> 0
153 (Quadrate foramen) 0.042 1 --> 0
171 (Supraoccipital, lateral nuchal crest)
0.063 0 --> 1

node_314 --> node_288 (Simoliophiidae)

99 (Parietals, supratemporal process) 0.100 0 --> 1
272 (Posterior dentition, lingual and labial carinae) 0.167 0 --> 1
290 (Presacral pleurocentra, pachyostosis) 0.333 0 ==> 1
321 (Presacral ribs, anteroventral process at rib head (= pseudotuberculum)) 0.083 0 --> 1

node_314 --> node_313 (Serpentes crown)

23 (Maxillae, contact, with premaxilla) 0.333 1 ==> 2
30 (Maxillae, premaxillary process) 0.143 0 ==> 1
57 (Jugals) 0.167 0 ==> 1
87 (Frontal, anterolateral corner, shape) 0.176 0 --> 3
149 (Ectopterygoid, anteriormost end, division) 0.143 0 --> 1
180 (Basisphenoid, basispterygoid process) 0.250 0 ==> 1
237 (Articular, foramen chorda tympani) 0.063 1 --> 0
277 (Atlas, neural arches, contact) 0.100 0 --> 1
293 (Posterior presacral pleurocentra, dorsal verterae, margo ventralis) 0.053 1 ==> 0
295 (Sacral vertebrae, number) 0.400 1 ==> 0
297 (Intercentra, on cervical vertebrae) 1.000 1 ==> 0
302 (Chevron bones) 1.000 0 ==> 1
307 (Neural arches, prezygapophyses, presacral vertebrae, anterolateral processes of zygapophyses) 0.500 0 ==> 1
312 (Neural arches, margo lateralis, posterior presacral vertebrae) 0.083 1 ==> 0

node_290 --> node_289 (Scolecophidia)

21 (Septomaxilla, midventral pillar) 0.333 0 --> 1
80 (Supratemporals) 0.100 1 ==> 0
118 (Vomers, ventral surface, midline crest) 0.067 1 ==> 0
146 (Ectopterygoids) 1.000 1 ==> 0
166 (Supraoccipitals, fusion to each other) 0.500 0 ==> 1
253 (Dentary tooth row, orientation) 1.000 0 --> 1
277 (Atlas, neural arches, contact) 0.100 1 --> 0
288 (Presacral pleurocentra, midventral crest, dorsal vertebrae) 0.034 1 ==> 0
310 (Neural arches and pleurocentrum, diapophysis, dorsal vertebrae, fusion to parapophysis) 0.200 0 ==> 1
321 (Presacral ribs, anteroventral process at rib head (= pseudotuberculum)) 0.083 0 --> 1

node_313 --> node_312 (Alethinophidia)

52 (Prefrontal, lateral foot process) 0.250 0 --> 1
120 (Vomers, ventral foramina, in each vomer element) 0.077 0 --> 1
171 (Supraoccipital, lateral nuchal crest) 0.063 0 --> 1
203 (Laterosphenoids) 0.500 0 ==> 1

230 (Surangular (or fused compound bone), coronoid process)
0.125 0 --> 1
238 (Articular, retroarticular process) 0.067 1 --> 0
247 (Coronoid, dorsal process) 0.143 1 ==> 0

node_310 --> node_298 (Constrictores)
20 (Septomaxillae, lateral flange, posterior process)
0.111 0 ==> 1
87 (Frontal, anterolateral corner, shape)
0.176 3 --> 0
128 (Palatines, ascending process) 0.125 0 --> 1
149 (Ectopterygoid, anteriormost end, division)
0.143 1 --> 0
163 (Quadrates, medial margin, midshaft stapedial process)
0.167 0 --> 1
171 (Supraoccipital, lateral nuchal crest)
0.063 1 --> 0

node_310 --> node_309 (Caenophidia)
3 (Premaxillae, nasal process, ventral septum)
0.200 0 --> 1
35 (Maxilla, suborbital process, posteromedial margin, ectopterygoid process) 0.333 0 ==> 1
110 (Parietals, parietal table, shape) 0.059 0 --> 1
117 (Vomers, lateral expansion) 0.063 0 --> 1
137 (Pterygoid, tooth row, location) 0.333 0 ==> 1
140 (Pterygoids, transverse processe) 0.125 1 --> 0
238 (Articular, retroarticular process) 0.067 0 --> 1
245 (Prearticular, mandibular fossa, orientation)
0.286 1 ==> 2
246 (Coronoids) 0.500 0 ==> 1
272 (Posterior dentition, lingual and labial carinae)
0.167 0 --> 1
279 (Atlas, neural arches, postzygapophyses)
0.038 1 --> 0
291 (Anterior pleurocentra, prezygodiapophyseal lamina)
0.200 1 --> 0
294 (Posterior presacral pleurocentra, hypapophyses)
0.333 0 ==> 1
375 (Femora) 0.083 0 ==> 1

node_308 --> node_307 (Colubriformes)
16 (Septomaxillae, posterodorsal process, contact, with frontals)
0.333 0 --> 1
18 (Septomaxillae, lateral flange, orientation)
0.111 2 --> 1
117 (Vomers, lateral expansion) 0.063 1 --> 0
124 (Vomers, middorsal septum, foramen) 0.333 0 ==> 1
145 (Pterygoids, quadrate rami, posterolateral excavation)
0.111 0 ==> 1
154 (Quadrates, posterior shaft, upper quadrate foramen)
0.167 0 ==> 1
178 (Basioccipital, midventral tuberosity)
0.333 0 ==> 1
187 (Prootics, prootic crest, shape) 0.071 1 --> 0
194 (Parasphenoid, cultriform process, lateral wings)
0.333 0 --> 1

```
  279 (Atlas, neural arches, postzygapophyses)
0.038  0 --> 1
  291 (Anterior pleurocentra, prezygodiapophyseal lamina)
0.200  0 --> 1
  321 (Presacral ribs, anteroventral process at rib head (=
pseudotuberculum))     0.083  0 ==> 1
```

Supplementary Tables

Supplementary Table 1: Differential taxonomic diagnosis with *Najash rionegrina* and *Dinilysia patagonica.*

Character	*Tametara*	*Najash*	*Dinilysia*	*Reference*	*Personal observation*
Postfrontals, parietal process, present	A	P	P	Garberoglio *et al.* 2019a	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Parietals, posteromedial (=postparietal) process)	P	A	A	Garberoglio *et al.* 2019a; Caldwell and Calvo, 2008; Zaher & Scanferla, 2012	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Supraoccipital, lateral ascending processes	P	A	A	Garberoglio *et al.* 2019a; Caldwell and Calvo, 2008; Zaher & Scanferla, 2012	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Supraoccipital, lateral nuchal crest	P	A	A	Garberoglio *et al.* 2019a; Caldwell and Calvo, 2008; Zaher & Scanferla, 2012	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Otoccipitals, meet each other at midline	A	A	P	Garberoglio *et al.* 2019a; Caldwell and Calvo, 2008; Zaher & Scanferla, 2012	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Quadrate conch	P	A	P	Garberoglio *et al.* 2019a; Zaher & Scanferla, 2012	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013, 1014)
Compound bone, retroarticular process	A	P	A	undescribed (Najsh, Dinilysia)	Najsh (MPCA-PV-500); Dinilysia (MLP 26-410 [holotype], MACN-RN 27, 1013).
Midventral ridge (= haemal keel), occurs throughout precloacals	P	P	A	Apesteguía & Zaher 2006; Scanferla & Canale 2007; Zaher *et al.* 2009	Najsh (MPCA-PV-386, 391, 395, 397, 400); Dinilysia (MLP 79-11-27-2, MLP 79-11-27-8, MACN-RN 25, 115, 976)
Subcentral foramina	P	A	P	undescribed (Najsh, Dinilysia)	Najsh (MPCA-PV-386, 391, 395, 397, 400); Dinilysia (MLP 79-11-27-2, MLP 79-11-27-8, MACN-RN 25, 115, 976)
Parazygantral foramina	P	P	A	Apesteguía & Zaher 2006; Scanferla & Canale 2007; Zaher *et al.* 2009; Garberoglio et al., 2019b	Najsh (MPCA-PV-386)

Abbreviations: A, absent; P, present.

Supplementary Table 2: Phylogenetic analysis of variance (pANOVA) for telencephalon shape.

Partition	Effect	df*	SS†	MS‡	Rsq	F	Z	*p*-value§
Telencephalon	Habitat	3	0.0036	0.0012	0.1255	2.584	2.321	**0.00949**
	Residuals	54	0.025	0.00046				
	Total	57	0.0287					

*df, degree of freedom; †SS, sum of squares; ‡MS, mean squares; §Significant values (*p*-values < 0.05) from permutation tests (10,000 permutation rounds) are bolded.

Supplementary Table 3: Pairwise habitat differences from phylogenetic ANOVA of telencephalon shape

Habitat*	d†	UCL (95%)‡	Z	Pr > d§
Aq *Vs* Ar	0.07629384	0.11597680	0.4682568	0.324
Aq *Vs* Fos	0.11048815	0.10843779	1.7422553	**0.042**
Aq *Vs* Ter	0.04852122	0.10802456	-0.5002425	0.687
Ar *Vs* Fos	0.17315794	0.11818454	2.8909222	**0.001**
Ar *Vs* Ter	0.05118034	0.10439963	-0.2782407	0.606
Fos *Vs* Ter	0.12781033	0.09331382	2.6054538	**0.002**

*Habitat: Aquatic (Aq); Arboreal (Ar); Fossorial (Fos); Terrestrial (Ter); † Distance between LS means; ‡ Upper confidence limits from the distributions of pairwise distances; § Significant *P* values between pairwise means (< 0.05) from permutation tests (10,000 permutation rounds) are shown in bold.

Supplementary Table 4: Results of linear discriminant analysis on habitat predictions for fossil specimens based on telencephalon shape

Observation	Predicted habitat group	Telencephalon* (5 PCs) Accuracy = 0.65; Kappa = 0.5
Tametara mirim	Terrestrial	0.0019
	Arboreal	0.0001
	Aquatic	0.0056
	Fossorial	**0.9923**
Dinilysia patagonica	Terrestrial	**0.5698**
	Arboreal	0.0570
	Aquatic	0.1158
	Fossorial	0.2572

* The habitat with the highest predicted probability is shown in bold.

Supplementary Table 5: Results of habitat typicality probability analyses for fossil specimens based on telencephalon morphology

Species	Predicted habitat group	Typicality probability (5PCs)
Tametara mirim	Terrestrial	0.0079
	Arboreal	0.00095
	Aquatic	0.0244
	Fossorial	**0.5744**
Dinilysia patagonica	Terrestrial	**0.0854**
	Arboreal	0.0180
	Aquatic	0.0318
	Fossorial	0.0358

* The habitat with the highest typicality probability is shown in bold.

Supplementary Table 6: Summary statistics for bone microstructure analysis by habitat category. Values represent group means and standard deviation (sd).

	comp [%]	comp_sd	thick [%]	thic_sd	ovl [%]	ovl_sd	rfp	rfp_ sd	elon	elon_sd	diam [mm]	diam_s d
non-fossorial	89.29	9.99	1.41	0.29	19.57	11.40	0. 95	0.26	1.95	0.44	12.29	6.54
semi-fossorial	97.59	3.24	1.65	0.40	26.44	7.99	0. 75	0.26	2.23	0.36	8.50	8.25
fully fossorial	98.95	1.31	1.95	0.75	29.92	12.35	0. 71	0.29	2.29	0.29	5.65	3.80
Dinilysia & Tametara	99.49	0.17	3.39	0.53	22.25	3.87	0. 65	0.11	2.79	0.03	25.17	18.97

Abbreviations: comp, skull roof compactness; diam, head diameter; elon, cranial elongation; ovl, roofing bone anteroposterior overlap; rfp, anteroposterior length ratio of frontal and parietal bones; thick, skull roof thickness.

Supplementary Table 7: Phylogenetic analyses of variance (pANOVA) for bone microstructure. Different approaches were used, testing with three lifestyle categories (non-fossorial, semi-fossorial, and fully fossorial) or two categories, where semi-fossorial and fully fossorial are collapsed to a single "fossorial" category.

Variable	Three categories					Two categories				
	F	df1	df2	P_raw	P_holm	F	df1	df2	P_raw	P_holm
comp	10.4056	2	103	7.34E-05	2.94E-04	20.738	1	104	1.44E-05	5.74E-05
thick	9.543	2	103	1.58E-04	4.73E-04	16.384	1	104	9.97E-05	2.99E-04
elon	2.018	2	103	1.38E-01	1.38E-01	4.073	1	104	4.61E-02	4.61E-02
ovl	16.618	2	103	5.56E-07	3.33E-06	23.422	1	104	4.54E-06	2.27E-05
rfp	4.943	2	103	8.92E-03	1.78E-02	9.966	1	104	2.09E-03	4.17E-03
diam	12.405	2	103	1.49E-05	7.45E-05	24.202	1	104	3.26E-06	1.96E-05

Abbreviations: comp, skull roof compactness;df1, numerator degrees of freedom; df2, denominator (residual) degrees of freedom; diam, head diameter; elon, cranial elongation; F, the F-statistic (the ratio of among-group to within-group variance); ovl, roofing bone anteroposterior overlap; P_holm, Holm-adjusted p-values for the pairwise post-hoc comparisons between groups; P_raw, the p-value for the overall group effect; rfp, anteroposterior length ratio of frontal and parietal bones; thick, skull roof thickness.

Supplementary Table 8. Results of statistical tests for regional differences in skull roof thickness between lifestyle groups

	anterior	posterior
Shapiro	4.20153E-09	0.000294759
Levene	0.005826953	0.912228172
Kruskal	4.16784E-05	0.364630349
Anova	1.56955E-05	0.48379916
use test	Kruskal	Kruskal
difference	significant	non-significant

Supplementary Table 9: Principal component loadings for bone microstructure variables from principal components analysis.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
PoV	0.404677	0.199267	0.179018	0.092769	0.067718	0.056552
anova_p	1.15E-07	1.4E-06	0.474466	0.993125	0.474466	0.447631
comp	0.533682	0.119418	0.163502	0.286903	0.489281	0.593701
thick	0.30301	-0.16606	-0.74858	-0.36766	-0.2495	0.350463
elon	0.534821	0.050937	0.043831	-0.48031	0.376006	-0.58084
ovl	0.063611	-0.82823	-0.17821	0.419022	0.22427	-0.22883
rfp	-0.48192	-0.30306	0.132223	-0.55848	0.493483	0.320938
diam	-0.31787	0.421626	-0.60145	0.253653	0.512983	-0.17877

Abbreviations: anova_p, Holm-adjusted p-value from phylogenetic ANOVA across the six principal components; comp, skull roof compactness; diam, head diameter; elon, cranial elongation; ovl, roofing bone anteroposterior overlap; PC, principal component; PoV, proportion of variance explained by each principal component; rfp, anteroposterior length ratio of frontal and parietal bones; thick, skull roof thickness.

Supplementary Table 10: Phylogenetic signal for bone microstructure variables. Trait aggregation for fossoriality is comparatively low (with r-pls = 0.33 and ri = 0.38).

	Compactness	Thickness	Elongation	Overlap	rfp	Diameter
lambda	0.908415956	0.29312876	0.647597056	0.746958906	0.994180419	0.927291776
logL	-356.6420334	-95.35749621	-48.60770617	-390.5591124	24.26465692	-361.847393
logL0	-385.0561763	-97.28217068	-59.64476054	-418.871345	-16.66561069	-371.6586046
p_lambda	4.75576E-14	0.04976531	2.62324E-06	5.27514E-14	1.46036E-19	9.43553E-06
K	0.638875694	0.23017025	0.370113618	0.574505469	0.86112311	0.868345455
p_K	0.001	0.591	0.011	0.001	0.001	0.001

Abbreviations: K, Blomberg's K; Lambda, Pagel's λ (the maximum likelihood estimate); logL, log-likelihood of the model fitted with the estimated λ; logL0, log-likelihood of the constrained model (with λ = 0); p_lambda, p-value from the likelihood ratio test against the λ = 0 model; p_K, p-value for K from randomization; rfp, anteroposterior length ratio of frontal and parietal bones.

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