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SHORT COMMUNICATION

Physiological implications of the abnormal absence of the parietal foramen in a late Permian cynodont (Therapsida)

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Abstract The third eye (pineal eye), an organ responsible for regulating exposure to sunlight in extant ectotherms, is located in an opening on the dorsal surface of the skull, the parietal foramen. The parietal foramen is absent in extant mammals but often observed in basal therapsids, the stem-group to true mammals. Here, we report the absence of the parietal foramen in a specimen of *Cynosaurus suppostus*, a Late Permian cynodont from South Africa (SA). Comparison with *Procynosuchus delaharpeae*, a contemporaneous non-mammalian cynodont from SA, demonstrates that the absence of this foramen is an abnormal condition for such a basal species. Because seasonality was marked during the Late Permian in SA, it is proposed that the third eye was functionally redundant in *Cynosaurus*, possibly due to the acquisition of better thermoregulation or the evolution of specialized cells in the lateral eyes to compensate for the role of the third eye.

Keywords Cynodontia · Therapsida · Parietal foramen · Pineal · Thermoregulation · Paleoneurology

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Introduction

In extant reptiles, the pineal complex is a region of the brain devoted to the regulation of body temperature, reproductive synchrony, and circadian rhythms (Eakin 1973; Ralph et al. 1979; Quay 1979). This complex consists of the pineal gland (or epiphysis), the parapineal organ, and the third eye, the last of which is housed in the parietal foramen (Eakins 1973; Quay 1979). Non-mammalian cynodonts (NMC) comprise a large number of genera that are particularly well-represented in the Karoo Supergroup of South Africa (SA) (Abdala and Ribeiro 2010). This lineage represents the non-mammalian Therapsida (NMT) which is the stem-group to mammals (Hopson and Kitching 2001; Ruta et al. 2014). With the exception of representatives of Probainognathia, which is the only cynodont group to consistently display no parietal foramen, most NMT are distinguished from mammals by the presence of a parietal foramen for the third eye (Hopson 1979; Quay 1979). Given the important physiological role of the pineal complex in extant species, computer X-ray tomography (CT scan) studies on the brain cavity of NMT could provide insight into the biology and physiology of these mammal ancestors. Investigation of the brain cavity of specimens of the Late Permian basal cynodonts *Cynosaurus suppostus* and *Procynosuchus delaharpeae* reveals abnormal closure of the parietal foramen in a large specimen of *Cynosaurus*, confirmed by CT scan. The possible biological implications for this early NMC are discussed.

Material and methods

See Online Resource 1.

Collections abbreviations: AM, Albany Museum (Grahamstown, SA); BP/1, Evolutionary Studies

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Institute (Johannesburg, SA); SAM-PK, Iziko Museum (Cape Town, SA).

Description

BP/1/3926 is a relatively large and well-preserved *Cynosaurus* skull, which has a sharp sagittal crest which is flattened at the location of the parietal foramen. Brink (1965) considered that the oval and slightly concave morphology of this flattened area, which is visible in dorsal view (Fig. 1), indicated the presence of a parietal foramen. However, CT scanning of the specimen reveals no evidence of a parietal tube (Fig. 1a). Instead, below this flattened area, the endocranial cavity is vaulted in a manner similar to that observed a few millimetres anterior to the parietal foramen in *Cynosaurus* specimen BP/1/1563 (Fig. 1b) as well as other specimens.

In BP/1/1563, the parietal foramen and the underlying tube for the pineal nerve are clearly visible on CT images (Fig. 1b). Given the lack of distortion of the sagittal crest in BP/1/3926, the absence of the parietal foramen is not a taphonomic artefact. Therefore, either no parietal foramen was present in BP/1/3926 or it closed secondarily. Posterior to the flattened area, a shallow fossa is observed in the cranial vault of this specimen. The bone above this fossa was crushed, but the strong contrast between the bone and sediment infill indicates that no opening was present on the dorsal side of this fossa (Fig. 1a). This fossa may have accommodated the parapineal organ and the epiphysis, as in sea turtles and some lizards (Quay 1979). In *Procynosuchus*, a cynodont which lived at the same time as *Cynosaurus* (Ruta et al. 2014), a parietal foramen is present in all 17 specimens studied and its diameter increases in tandem with that of the foramen magnum, here used as a proxy for body size (R^2=0.7334) (Fig. 2).

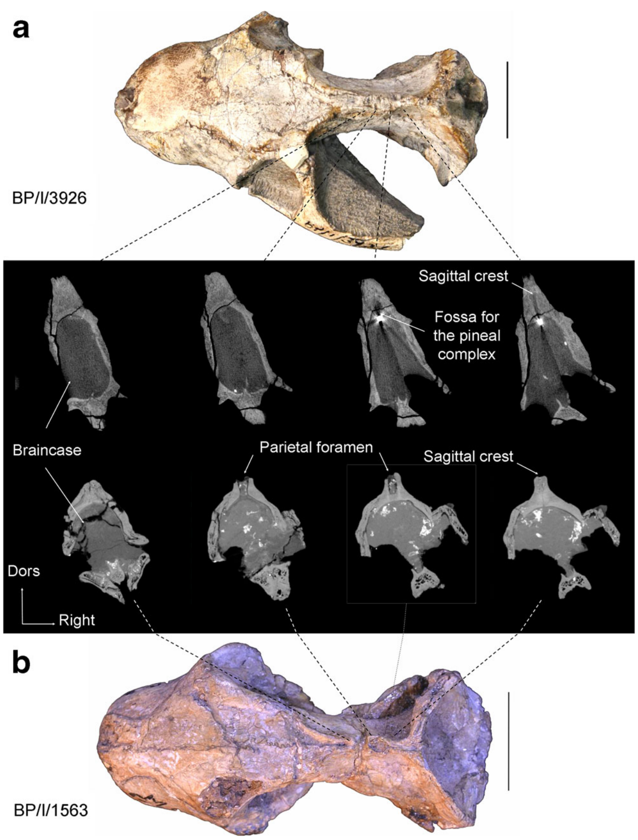

Fig. 1 Four CT slices and dorsal view of the parietal foramen in *Cynosaurus*. **a** BP/1/3926, *scale bar*=2 cm. The *white spot* inside the braincase is an artefact due to a metallic nodule. **b** BP/1/1563, *scale bar*=1 cm. See also Online Resources 3 and 4

Discussion

Brink (1965) considered the extremely small size of the parietal foramen in BP/1/3926 to be diagnostic of *Cynosaurus whaitsi*, now an invalid species (Hopson and Kitching 1972). However, CT scan data of this specimen presented here demonstrates the absence of a parietal foramen. In his description of the holotype of *C. whaitsi* (SAM-PK-4333), Haughton (1918) considered the parietal foramen as being small. In contrast, our examination reveals that a distinct and quite large parietal tube (4 to 5 mm in diameter) is present in SAM-PK4333, despite the sagittal crest being eroded and distorted.

As BP/1/3926 is amongst the largest specimens of *Cynosaurus* examined (Online Resource 2), the absence of the parietal foramen could be due to an ontogenetic change, as is the case in the traversodontid cynodont *Massetognathus* in which the parietal foramen closes in adults (Abdala and Giannini 2000). Roth et al. (1986) reported a similar situation in some extant lizards such as *Anolis carolinensis*, in which the size of the pineal opening decreases (but does not disappear) relative to body size during ontogeny. However, SAM-P-K4333 (skull length of 120–125 mm) is larger than BP/1/3926 and displays clear evidence of a well-marked parietal tube. This suggests that the absence of the parietal foramen in BP/1/3926 is not the result of ontogeny but instead results from intraspecific variability. Contrary to the condition of this trait in *Anolis carolinensis*, the size of the parietal foramen in these two basal cynodonts (Fig. 2) seems to increase with body size (Online Resource 2). In *Procynosuchus* (Fig. 2) and the Early Triassic stem epicynodonts *Thrinaxodon* and *Galesaurus*, the parietal foramen persists throughout ontogeny (Jasinoski et al. 2015; F. Abdala, personal data).

The presence of this structure in basal cynodonts suggests that the most likely adult condition of *Cynosaurus* was the presence of a parietal foramen, which clearly sets specimen BP/1/3926 apart from other South African contemporaneous species. Nevertheless amongst cynodonts, the absence of a parietal foramen has also been reported in the specimen AM461 of *Trirachodon* (Abdala et al. 2006), a gomphodont

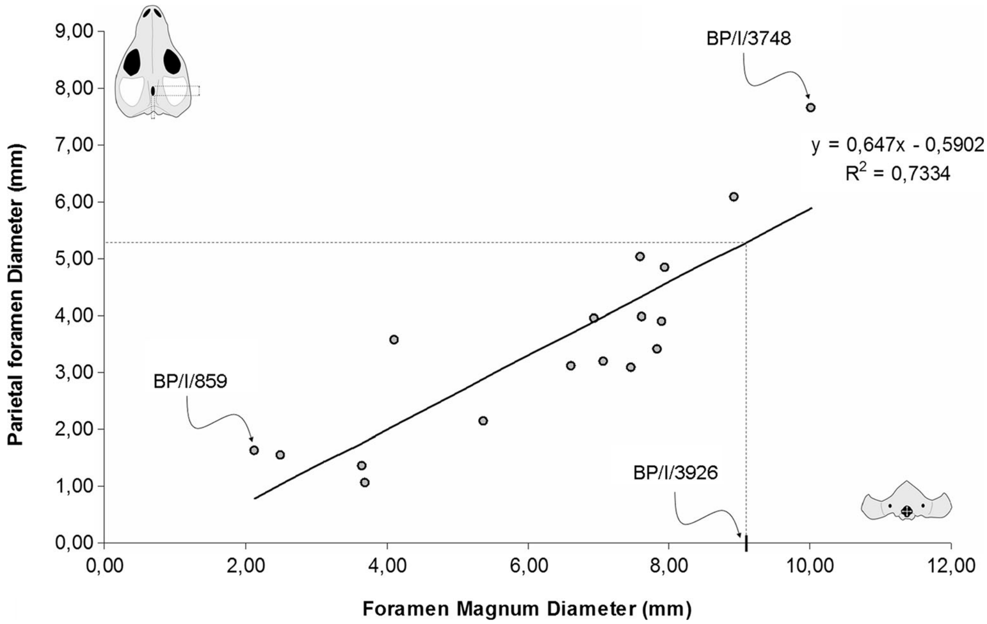

Fig. 2 Regression of the diameter of the parietal foramen over the diameter of the foramen magnum in *Procynosuchus*. The position of BP/1/3926 is indicated with *dotted lines*. Source data in Online Resource 2

eucynodont, but this has yet to be confirmed by CT scanning. As BP/1/3926 is clearly an adult based on its large size (Online Resource 2), the absence of a parietal foramen seems to not have severely affected its survival.

In some extant lizards such as *Sceloporus*, *Gerrhonotus*, *Iguana*, *Anolis*, and *Cyclura* (Quay 1979; Roth et al. 1986), the parietal foramen also disappears in some adults (Quay 1979). Histological studies of *Sceloporus* and *Gerrhonotus* show that the fronto-parietal fontanel is fully ossified but that the third eye is still present below the skull roof because it failed to split from the epiphysis (Quay 1979). In individuals of *Sceloporus* and *Gerrhonotus*, in which the parietal foramen is secondarily closed, no physiological or behavioural deficiency was recorded (Quay 1979).

It has been shown that extant ectotherms that live in equatorial environments tend to display a pineal opening less frequently as the stability of the temperature makes the third eye functionally redundant (Gundy et al. 1975; Ralph 1975). In *Dvinia*, a basal cynodont from the Late Permian of Russia, the pineal opening is absent (Ivakhnenko 2013), which is consistent with the equatorial latitude of the Russian deposits of that time (Zharkov and Chumakov 2001). In contrast, South Africa was closer to the polar region, and the Late Permian Karoo geological and palaeogeographical evidence suggests marked temperature and seasonal fluctuations (Retallack et al. 2003). This would have put strong selective pressure against the loss of the parietal foramen in South African NMC, except if the corresponding third eye was no longer functional. As a consequence, it might be hypothesized that the function of the third eye became dispensable in *Cynosaurus*.

This relaxation of functional constraints on the third eye could have been achieved by two different means. The first may have been by the evolution of a higher metabolic rate (a condition approaching endothermy in modern mammals) because animals with better body temperature control are less dependent on external heat sources, which makes the role of the third eye less critical (Camp and Welles 1956; Roth et al. 1986). The important role of the third eye in behavioural thermoregulation has been emphasized by numerous authors (see Ralph et al. 1979 and Eakin 1973 for reviews). The alternative hypothesis would be that the evolution, in NMC, of photosensitive melanopsin-containing retinal ganglion cells (MGCs) in the lateral eyes and the accompanying retinohypothalamic tract (Berson et al. 2002) began to replace and compensate for the role of the third eye. However, the spectral sensitivity of melanopsin overlaps that of cone type pigments, suggesting that MGCs evolved during the 'nocturnal bottleneck' correlating with the loss of colour vision in early Mammaliaforms, as they adapted to increasingly nocturnal ecological niches in the Late Triassic (Davies et al. 2010; Gerkema et al. 2013).

Admittedly, the timing of the evolution of MGCs still needs further research, but at the current state of knowledge the hypothesis involving endothermy seems the best supported. Nevertheless, it still remains unclear whether variability predates the definitive loss of the parietal foramen across the phylogeny of NMCs because, as stated above, *Thrinaxodon* and *Galesaurus*, which are more derived than *Cynosaurus*, always display a parietal foramen (Jasinoski et al. 2015; F. Abdala, personal data). Unfortunately, intraspecific and intrageneric variability of this trait is poorly known for most NMTs, although the reduction or loss of the parietal foramen has been documented in some therocephalians, dicynodonts, and cynodonts from different geological horizons (Hopson 1979; Quay 1979; Roth and Roth 1980).

Conclusion

The evolution and variation of the parietal foramen in NMT is a fascinating but yet poorly understood topic. The occasional absence of the parietal foramen in some NMT species has raised much interest in the past (Quay 1979; Roth and Roth 1980; Roth et al. 1986), but our study provides, for the first time, robust CT scan data and quantitative evidence for intra-specific variability of the parietal foramen in a therapsid species. Given the key roles played by the pineal eye in a variety of important physiological processes in extant reptiles (such as endothermy), the functional significance of such variability in a stem NMC such as *Cynosaurus* provides a glimpse into the physiology and biology of mammalian ancestors. In the future, this trait could provide more information relevant to variations of reproductive cycles, migratory behaviours, or even paleoenvironment.

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Compliance with Ethical Standards

Conflict of interest The authors declare no conflict of interest.

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