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The extended osteoderm shield in *Paleosuchus* sp.: a dwarf crocodylian adaptation to the equatorial forest ecosystem?

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ABSTRACT

The crocodylian dwarf species (i.e., *Osteolaemus* sp. and *Paleosuchus* sp.) that live in the equatorial forests all share the peculiarity to present an osteoderm shield which extends beyond the dorsal area that lies between the skull and the caudal crest symphysis. Here we study both the morphology and the microanatomy of the osteoderms in *Paleosuchus palpebrosus* (Cuvier, 1807), in order to both assess the distribution of bone ornamentation over the osteoderm shield, and to compare the porosity between the dorsal osteoderms with the non-dorsal osteoderms. Since both the ornamental pit excavation and the bone porosity are relevant proxies to the osteoderm blood vessel content, we mapped the distribution of the vascular network within the osteoderm shield in *P. palpebrosus*. Our results show that both the bone ornamentation and the bone porosity are significantly more pronounced within the dorsal shield osteoderms. Our results suggest that the dorsal osteoderms may be involved in heat transfer via the superficial blood vessels that are located in the ornamental pits if they are artificially exposed to a basking lamp in captive conditions; it is however unlikely to be the case under the canopy of the equatorial forest since the sun exposure is poor. We therefore hypothesize that the dwarf crocodylian extended osteoderm shield mostly consists of a labile calcium resource that would allow to buffer the diet variations which are related to the various equatorial forest niches (i.e., streams, excavated pools, jungle floors, caves).

KEY WORDS
Crocodylia,
dwarfism,
heat transfer,
diet,
niche.

RÉSUMÉ

Le bouclier étendu d'ostéodermes chez Paleosuchus *sp. : une adaptation à l'écosystème des forêts équatoriales chez les crocodiliens nains ?*

Les crocodiliens nains (i.e., *Osteolaemus* sp. et *Paleosuchus* sp.) ont tous la particularité de vivre dans les forêts équatoriales et de présenter un bouclier d'ostéodermes qui s'étend au-delà de la zone dorsale (qui est comprise entre le crâne et la symphyse des crêtes caudales). Notre étude compare la répartition de l'ornementation osseuse et la porosité entre les ostéodermes dorsaux et les ostéodermes non-dorsaux au sein du bouclier d'ostéodermes d'un caïman nain de Cuvier (*Paleosuchus palpebrosus* (Cuvier, 1807)). Sachant que ces deux critères constituent des indicateurs du degré de vascularisation du bouclier dermique, nous avons alors estimé la répartition du réseau vasculaire au sein du bouclier d'ostéodermes de *P. palpebrosus*. Nos résultats montrent que l'ornementation et la porosité sont nettement plus prononcées au niveau des ostéodermes qui composent la partie dorsale du bouclier. Nos résultats suggèrent que les ostéodermes dorsaux peuvent être impliqués dans les transferts de chaleur via les vaisseaux sanguins superficiels quand ils sont artificiellement exposés à une lampe chauffante dans des conditions de captivité ; il est cependant peu probable que ce phénomène se produise sous la canopée de la forêt équatoriale, où l'exposition au soleil est peu accessible. Nous supposons donc que les ostéodermes des crocodiliens nains auraient principalement pour rôle de constituer une source de calcium labile qui permettrait d'amortir les variations de régime alimentaire liées aux différents habitats de la forêt équatoriale (i.e., les ruisseaux, les mares, les sols humides, les cavernes).

INTRODUCTION

The crocodylian osteoderms are bony plates that grow within the post-cranial dermis during the post-hatching development (Vickaryous & Hall 2008). These bones are formed through direct osseous metaplasia (Dubansky & Dubansky 2018) and are further remodelled by the combination of cyclic osteoclastic bone resorption and osteoblastic growth (de Buffrénil 1982; Klein *et al.* 2009). Both the primary growth (Dubansky & Dubansky 2018) and the secondary remodelling (de Buffrénil *et al.* 2015) rely on a local network of blood vessels that interconnect within both the bone internal cavities and the ornamental pits (Clarac *et al.* 2018). The crocodylian osteoderms thus gather the skin blood vessels and therefore shelter the dermal blood flow within a skin that is elsewhere poorly vascularized (Clarac *et al.* 2018). It has been hypothesized that these cutaneous vessels drive the heat exchanges between the skin and the external environment when basking (Seidel 1979; Farlow *et al.* 2010) via the control of both the vasodilation (Grigg & Alchin 1976) and of the heart beat rate (Seebacher & Franklin 2004, 2007). A recent experimental study on *Crocodylus niloticus* (Laurenti, 1768) (Crocodylidae (Cuvier, 1807)) and *Alligator sinensis* (Fauvel, 1879) (Alligatoridae (Gray, 1844)) sub-adult specimens (Clarac & Quilhac 2019) has indeed proved that the dorsal shield shows higher thermal variations than the flanks that are deprived of osteoderms (Trutnau & Sommerlad 2006; Kiladze & Chernova 2019). Nevertheless, other authors repeated this experimental protocol on *Paleosuchus palpebrosus* (Cuvier, 1807) (Alligatoridae; Veenstra & Broeckhoven 2022) and showed similar results although this species has the particularity to present osteoderms along the flanks, the limbs, the sides of the tail and the belly within both sub-adult and adult specimens (Magnusson 1992). However, both experiments relied on infrared images that only record the superficial skin temperature. This type of data may indeed be highly influenced by the temperature variation that is relative to the close dermis blood vessels that are housed by the osteoderm ornamental pits (Clarac *et al.* 2018). Therefore, in order to discuss the role of the osteoderms in heat transfers via the gathering of the skin vasculature, here we have sampled and compared a full set of osteoderms that come from a *Paleosuchus palpebrosus* adult specimen. We have localized and quantified the relative expression of bone ornamentation on both the dorsal keeled osteoderms and the lateral osteoderms that are present on the flanks, the tail sides, the limbs and the ventral side. We further calculated the bone porosity on a representative sub-sample in order to compute a proxy to the global osteoderm vascularization both with and without bone ornamentation (Clarac *et al.* 2018). Beside the full-body extension of the osteoderm shield, *Paleosuchus palpebrosus* also shares the peculiarity both to be a dwarf species that lives in an equatorial forest (Amazon basin; Trutnau & Sommerlad 2006; Campos *et al.* 2022) and to possess a lower body temperature (20-26°C; Campos & Magnusson 2013) than the crocodylians that live in open environments (e.g. 23-36°C in *Caiman crocodilus* (Linnaeus, 1758) [Diefenbach 1975]; 29-33°C in *Crocodylus johnstoni* Krefft, 1873 [Seebacher & Grigg 1997]; 25-35°C in *Crocodylus porosus* (Schneider, 1801) [Seebacher *et al.* 1999]). Here we discuss if the *P. palpebrosus* osteoderm microanatomy might consist of a good proxy to understand the peculiarity of the equatorial dwarf species thermoregulation process (i.e., *Paleosuchus palpebrosus*, *Paleosuchus trigonatus* (Schneider, 1801), *Osteolaemus tetraspis* (Cope, 1861)) in comparison with larger genera that occupy open environments such as *Crocodylus* (Crocodylus, 1768)*, Alligator* (Daudin, 1809)*, Caiman* (Spix, 1825) (Trutnau & Sommerlad 2006). Indeed, the equatorial forest dwarf species live under the canopy and may have a minor use of the
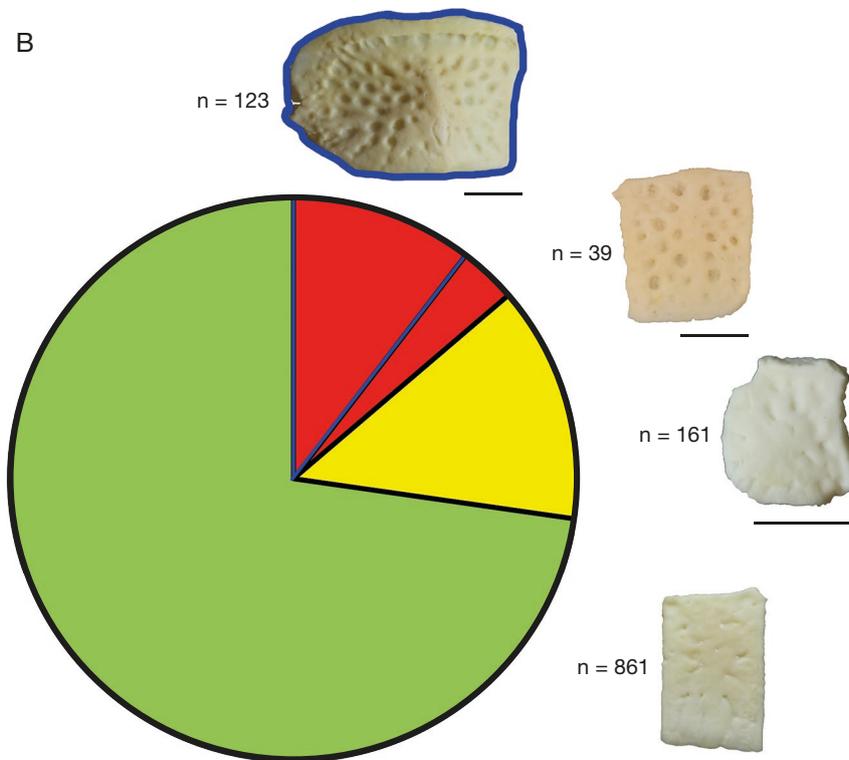
Fig. 1. — **A**, Specimen of interest (*Paleosuchus palpebrosus* (Cuvier, 1807)) in its vivarium at the Parc zoologique de Paris; **B**, diagram of the ornamental pit distribution on the osteoderm shield of *P. palpebrosus*: **red**, the deeply pitted osteoderms; **yellow**, the shallow pitted osteoderms; **green**, the non-ornamented osteoderms; **blue circle**, a deeply pitted dorsal osteoderm. Scale bars: 1 cm. Credits: photo by François-Gilles Grandin. Scale bars: 1 cm.

Paleosuchus palpebrosus (MNHN-RA-2022.0064)	Ornamentation			
	Deep	Shallow	Absent	Total
Dorsal osteoderms	123	0	0	123
Non-dorsal osteoderms	39	161	861	1061

osteoderm in heat transfer as they both possess a low body temperature (Campos & Magnusson 2013) and live in a rather thermally stable ecosystem that leaves poor exposure opportunities. Besides, previous studies have revealed that the equatorial dwarf genera (i.e., *Osteolamus* (Cope, 1861) and *Paleosuchus* (Gray, 1862)) have populations that show a cryptic behavior by living in caves (Shirley *et al.* 2017; Lemaire *et al.* 2018), streams (Magnusson & Lima 1991), digging pools (Riley & Huchzermeyer 1999, 2000) or dwelling under fallen trunks (Lemaire *et al.* 2018). These scenarios involve a poor sun exposure and therefore no significant basking behavior (Medem 1958; Magnusson & Lima 1991) which could potentially involve heat transfer via the osteoderm shield (Seidel 1979; Farlow *et al.* 2010). In this case, osteoderms might instead be involved as a calcium reservoir which would play a role in: 1) male-male contests and reproductive needs in females (Hutton 1986; Dacke *et al.* 2015; Broeckhoven & du Plessis 2022); and 2) transferring the calcium to both the axial skeleton and the teeth to further preserve the most vital functions when exposed to deficiencies that are due to the diet variations (Klein *et al.* 2009) which relate to the various habitat food resources (e.g. cave, jungle floor, streams; Magnusson *et al.* 1987). Within this function, both the number of osteoderms and their degree of mineralization are relevant parameters; nevertheless, the osteoderm relative location on the body has no significant importance unlike when involved in heat transfer during basking periods.

MATERIAL AND METHODS

We have studied a full dry skeleton of a *Paleosuchus palpebrosus* adult male specimen that is present in the comparative anatomy collections of the Muséum national d'Histoire naturelle (MNHN-RA-2022.0064). This animal used to live in captivity at the Parc zoologique de Paris within a vivarium that included both a 26°C water with a controlled quality and a beach that allowed access to both heat and UVb for an optimal vitamin D3 production. The specimen was weekly fed with dead fishes or rodents and died at the age of 23 years old in 2022. We have assessed that its full set of osteoderms is composed of 1184 units which we divided in two samples: 1) the large osteoderms that come from the dorsal area between the skull and the caudal crest symphysis, which all possess a high keel, a concave shape and an imbrication surface (n = 123; Table 1); and 2) the osteoderms that come from the other parts of the body (flank, belly, limbs, tail), which never possess the combination of all these above criteria (n = 1061;

Table 1). Within both samples we assessed the expression of bone ornamentation which we ranked according to three states of character (smooth, shallow, deep). We then sub-sampled a set of six osteoderms within each sample in order to perform one mid-line transversal cross-section per osteoderm. We further calculated the bone porosity as a proxy to the osteoderm vascularization since the relative size of both the internal cavities and of the ornamental pits is proportional to their content in blood vessels (Clarac *et al.* 2018). To do so, we took a picture of each cross section and rendered them binary in black and white with Photo Affinity 1.10.5 (Serif Europe Ltd. The Software Centre Wilford Industrial Estate Nottingham NG11 7EP) so that the bone matrix appears in black and the empty cavities appear in white. We included the open space that is consequent to the ornamental pit excavation into the white area by artificially connecting the top of the crests with a virtual black line (as in Clarac *et al.* 2020; using Affinity Designer 1.10.5; Serif Europe Ltd. The Software Centre Wilford Industrial Estate Nottingham NG11 7EP). We then measured the relative area that is occupied by the pits and cavities over the full cross-section envelope using Image J (version 1.53t, Wayne Rasband and Contributors National Institutes of Health, United States). Once we obtained the raw data, we proceeded to comparisons via non-parametric statistical tests (Mann-Whitney).

ABBREVIATION
MNHN   Muséum national d'Histoire naturelle, Paris.

RESULTS

THE DIFFERENTIAL EXPRESSION OF BONE ORNAMENTATION ON THE OSTEODERM SHIELD
The crocodylian osteoderm ornamentation is composed of a pattern of repetitive excavated pits that are separated by ridges (de Buffrénil 1982; Clarac 2021). Here we can observe that these pits are systematically deep on the dorsal part of both the trunk and the neck (Fig. 1; Table 1). Among the osteoderms which come from the flanks, the tail, the belly and the limbs; only 3.7% (n = 39) are deeply pitted, 15.1% (n = 161) show shallow pits and 81.1 % (n = 861) are deprived of ornamentation (Fig. 1; Table 1).

MICROANATOMICAL COMPARATIVE ANALYSES
Within our cross-section subsample that is composed of 12 osteoderms, the osteoderm porosity varies between 0.04 and 0.16 with a mean value of 0.071 and a median value of 0.06 (Table 2; Figs 2; 3). Within the dorsal osteoderms, which compose half of the cross-section subsample (Cat. 1; n = 6), the porosity varies between 0.06 and 0.16 with a mean value of 0.09 and a median value of 0.085 (Table 2; Figs 2A; 3A). Within the non-dorsal osteoderms, which compose the second half of the cross-section subsample (Cat. 2; n = 6), the porosity varies between 0.08 and 0.054 with a mean value of 0.053 and a median value of 0.05 (Table 2; Figs 2B; 3A). The Mann-Whitney test shows a significant
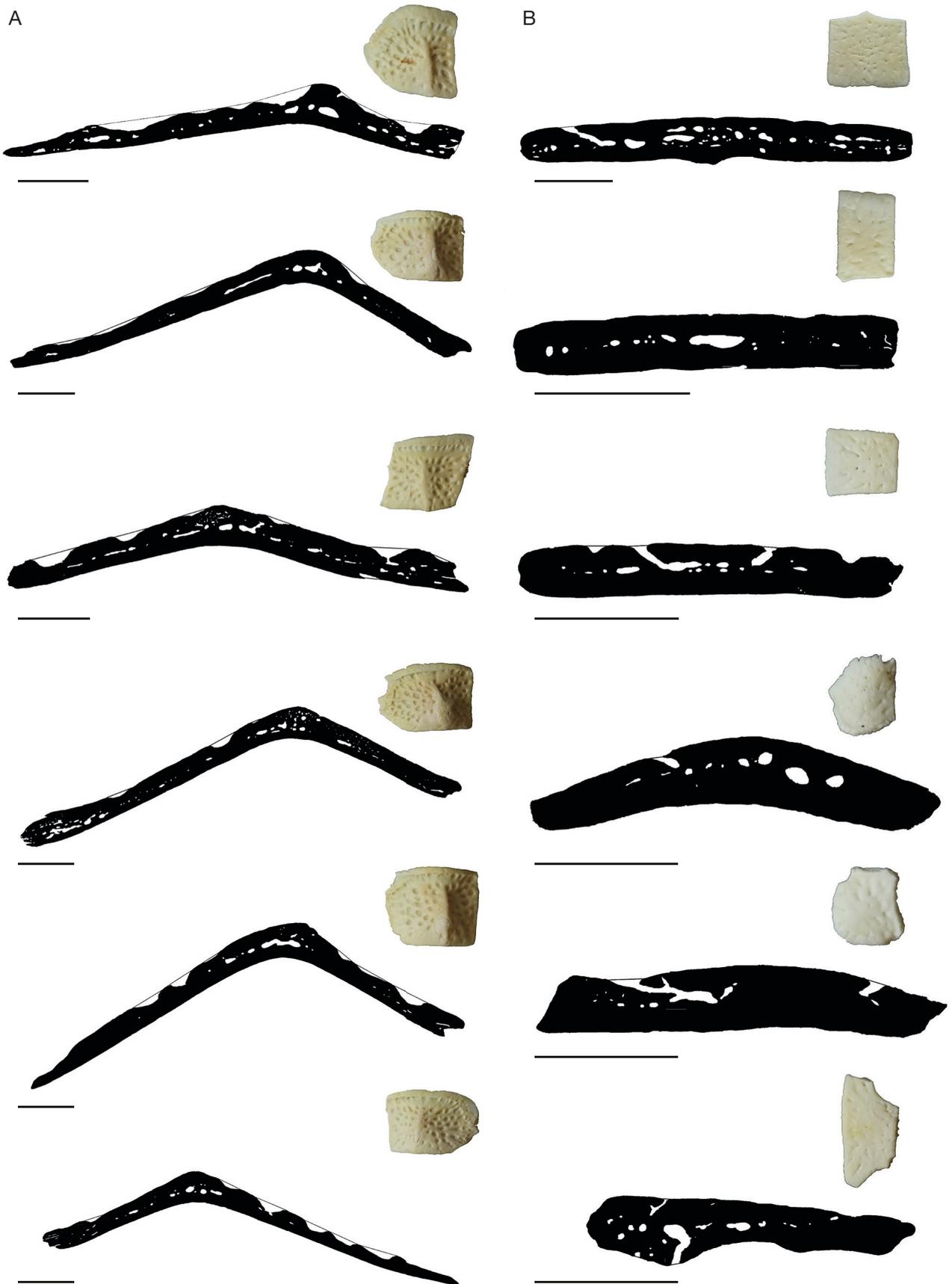
Fig. 2. — Osteoderm transversal cross-sections: **A**, dorsal osteoderms (Cat. 1; n = 6); **B**, non-dorsal osteoderms (Cat 2; n = 6). A dorsal view of each osteoderm is presented next to each cross section. Scale bars: 50 mm.

TABLE 2. — Variation of the osteoderm porosity in *Paleosuchus palpebrosus* (Cuvier, 1807) (MNHN-RA-2022.0064). Abbreviations: **Cat.**, category; **Max**, maximum value; **Min**, minimum value.

	Bone Porosity					
Sample	n_1	n_2	n_3	n_4	n_5	n_6
Dorsal osteoderms (Cat. 1; n = 6)	0.16	0.058	0.094	0.056	0.076	0.090
Non-dorsal osteoderms (Cat. 2; n = 6)	0.08	0.041	0.060	0.039	0.054	0.054
Statistic summary	**Min**	**25 percentile**	**Mean**	**Median**	**75 percentile**	**Max**
Dorsal osteoderms (Cat. 1)	0.06	0.06	0.09	0.085	0.1075	0.16
Non-dorsal osteoderms (Cat. 2)	0.04	0.04	0.053	0.05	0.065	0.08
Total sample (Cat. 1 and 2; n = 12)	0.04	0.05	0.071	0.06	0.0875	0.16

TABLE 3. — Statistical non-parametric test (Mann-Whitney): intraspecimen comparison between the porosity of the dorsal osteoderms (Cat. 1) with the non-dorsal osteoderms (Cat. 2). Abbreviation: **Cat.**, category.

Mann-Whitney test	*Paleosuchus palpebrosus* (MNHN-RA-2022.0064) Cat. 2; n = 6
Paleosuchus palpebrosus (MNHN-RA-2022.0064) Cat. 1; n = 6	Significant (P_{value} = 0.023)

TABLE 4. — Statistical non-parametric test (Mann-Whitney): interspecific comparison between the porosity of the *Paleosuchus palpebrosus* (Cuvier, 1807) osteoderms with a set of both terrestrial and semi-aquatic pseudosuchian osteoderms (see Clarac *et al.* 2020 for details). Abbreviation: **Cat.**, category.

Mann-Whitney test	Terrestrial pseudosuchians (n = 11; after Clarac *et al.* 2020)	Semi-aquatic pseudosuchians (n = 20; after Clarac *et al.* 2020)
Paleosuchus palpebrosus (MNHN-RA-2022.0064) Total sample (Cat. 1 and 2; n = 12)	Non-Significant (P_{value} = 0.90)	Significant (P_{value} = 2.77. 10^{-5})

difference between the median porosity of the dorsal osteoderms (Cat. 1) and the median porosity of the non-dorsal osteoderms (Cat. 2; Table 3) which plots a lower median value (median Cat. 2 = 0.05 < median Cat. 1 = 0.085).

We have compared the full dataset (Cat. 1 and 2; n = 12) with a previous dataset that is composed of an interspecific sample which includes both extant and extinct pseudosuchian species that lived during the Triassic and later periods (Clarac *et al.* 2020). Within this previous study, the sample was split in two sub-samples: 1) the terrestrial taxa which lived during the Mesozoic; and 2) the semi-aquatic taxa that appeared at the lower-Jurassic and who present some descendants that are still present in the extant nature (i.e., Crocodylia; Benton & Clark 1988). Here we have added a new dataset as a third sub-sample (Table 2; n = 12) in order to perform statistical comparisons via two-sampled non-parametric tests (i.e., Mann-Whitney). This test revealed that the median porosity is significantly different between *P. palpebrosus* and the other semi-aquatic forms whereas it is not with the terrestrial forms (Table 4; Fig. 3B). The test also revealed a significant difference of the median porosity between the semi-aquatic and the terrestrial forms (Table 4; Fig. 3B). The median value is indeed lower in both the terrestrial forms (Median = 0.05) and in *P. palpebrosus*

(Median = 0.06) than in the semi-aquatic interspecific sample (Med = 0.175). The second and the third percentile show a narrower range in *P. palpebrosus* than either in the terrestrial forms or in the semi-aquatic interspecific group (Fig. 3B).

DISCUSSION

THE ROLE OF BONE ORNAMENTATION IN THE CROCODYLIAN HEAT TRANSFERS

Previous works led to assess that the expression of bone ornamentation consists of a good proxy to infer a terrestrial or a semi-aquatic lifestyle among extinct crocodylomorphs, allowing to discuss habitat preferences during their evolution (Clarac *et al.* 2017; Pochat-Cottilloux *et al.* 2023). These two independent studies indeed revealed that the pits which compose the bone ornamentation are more deeply excavated on both the cranial dermal bones and the osteoderms within the semi-aquatic forms. The assessment of this morphological pattern led to argue that the expression of bone ornamentation relates to an adaptation to the semi-aquatic ambush predator lifestyle through two essential functions: 1) bone acidosis buffering during long term apnea (Jackson *et al.* 2003; Janis

A

B
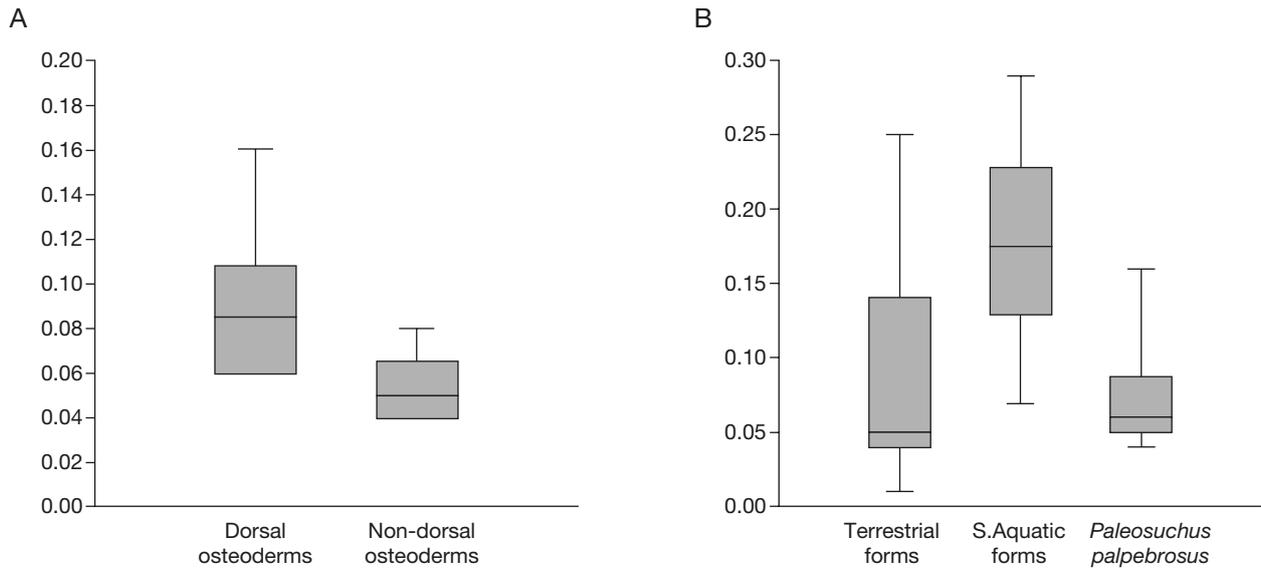
Fig. 3. — Boxplots of the osteoderm porosity summarizing the mean, the quartiles, the minimum and the maximum values: **A**, intraspecimen sample (*Paleosuchus palpebrosus* (Cuvier, 1807)); **B**, interspecific comparison. Abbreviation: **S.aquatic**, semi-aquatic ("Terrestrial forms" and "S.aquatic forms" both represent taxa that lived during the Jurassic and later periods, the data were previously published in Clarac *et al.* 2020).

et al. 2020); and 2) heat transfer when basking (Seidel 1979; Farlow *et al.* 2010; Clarac & Quilhac 2019). Both functions rely on the fact that the ornamental pits house cutaneous blood vessels, which can either be involved in heat transfer during both emerged and floating periods or in binding blood lactate to dermal bone calcium in order to reduce plasma acidity during long-term apnea (Jackson 2004). Although the functional relation between bone ornamentation and the bone acidosis buffering is still conjectural, the relation between heat transfer and osteoderm ornamentation has been indirectly revealed through the acquisition of infrared data in parallel with locating the skin blood vessel clusters on an albino *Alligator mississippiensis* (Daudin, 1802) sub-adult specimen (Clarac & Quilhac 2019). Nevertheless, this previous founding does not mean that this role is exclusive but may rather be instead an exaptation in extant species that commonly bask in open environments. Here we show that the pits which compose the bone ornamentation in *Paleosuchus palpebrosus* are deeply excavated on the dorsal part of both the trunk and the neck in comparison to the other body parts where the pits are either shallow or absent (i.e., the flanks, tail, belly and limbs; Fig. 1; Table 1). According to this new result, the distribution of bone ornamentation in the adult *Paleosuchus palpebrosus* shows a significant match with the surface temperature gradient when basking (Veenstra & Broeckhoven 2022). This correlation may be explained by the fact that the superficial skin vessels are housed in the ornamental pits and therefore influence the superficial temperature that has been measured with infrared cameras in previous studies (Farlow *et al.* 2010; Clarac & Quilhac 2019; Veenstra & Broeckhoven 2022). In this regard, our results also reveal that the resulting porosity is higher on the dorsal ornamented osteoderm than on the non-dorsal osteoderms (Fig. 3A; Table 3), which means that bone ornamentation increases

the osteoderm global vascularization over the dorsal shield. The studies that were proposed by Clarac & Quilhac (2019) and Veenstra & Broeckhoven (2022) were both conducted under experimental conditions and are likely to have indirectly revealed the functionality of the crocodylian osteoderm ornamentation in heat transfer. Nevertheless, this statement does not mean that bone ornamentation is systematically involved in such an adaptive function within all species and in all ecosystems (as discussed further below). Regarding the potential influence of the relative thickness variation of the superficial beta-keratin layer over the body (as raised by Veenstra & Broeckhoven 2022), further investigations need to be proceeded in order to draw any conclusion. Nonetheless, it might not be the most relevant parameter that explains the surface temperature display since the expression of scale keratin has proved to have no significant influence on heat transfers in snakes (Licht & Bennett 1972).

The peculiarity of the equatorial forest dwarf species
Even though *Paleosuchus palpebrosus* shows a well-ornamented dorsal shield, which has been evidenced to perform heat transfer in experimental forced conditions (Veenstra & Broeckhoven 2022), it is nevertheless possible that this anatomical feature has a poor implication in heat transfer within the natural environment because the internal body temperature of *Paleosuchus palpebrosus* ranges only between 20°C and 25°C (Campos & Magnusson 2013) whereas the optimal body temperature of the crocodylians that live in open environments do all show higher values (e.g. 23-36°C in *Caiman crocodilus* Diefenbach 1975, 29-33°C in *Crocodylus johnstoni* Seebacher & Grigg 1997, 25-35°C in *Crocodylus porosus* Seebacher *et al.* 1999). These data suggest that *Paleosuchus palpebrosus* may not naturally show any basking behavior because it does not need to increase its inner temperature, which scores within

Fig. 4. — **A**, **B**, Natural environment of *Paleosuchus trigonatus* (Schneider, 1801) in French Guiana; **C**, *Paleosuchus palpebrosus* (Cuvier, 1807) specimens in captivity at the Parc zoologique de Paris. Credits: A, B, photo by Jérémy Lemaire; C, photo by François-Gilles Grandin.

the air temperature variation range of the equatorial forest (e.g. 22-28°C in Guyana Gregory *et al.* 1986; 20-30°C in Congo Likoko *et al.* 2019). Even if some data are still missing regarding *Paleosuchus trigonatus*, it would be rather expected that they share similar characteristics in term of thermal behavior regarding its extreme close morphological and ecological resemblance with *Paleosuchus palpebrosus* (Trutnau & Sommerlad 2006). Even though, the expression of a deeply excavated ornamentation is almost exclusive to the dorsal shield in *Paleosuchus palpebrosus*, it is nevertheless to be noted that these osteoderms possess a global porosity that remains quite low in comparison with other semi-aquatic species; they would be instead definitely comparable to extinct forms that used to occupy a variety of terrestrial habitats (e.g. early crocodylomorphs Irmis *et al.* 2013, notosuchians Hill 2010; Martin 2014; Fig. 3B). Even though the results that were obtained by Veenstra & Broeckhoven (2022) on *P. palpebrosus* would rather lead to refute the role of the non-dorsal osteoderms in heat transfer, it is nonetheless possible that these bony plates might still play a role in other physiological functions such as bone acidosis buffering during long term apnea (Jackson *et al.* 2003) and in phosphorous-calcic regulations (Hutton 1986; Klein *et al.* 2009; Dacke *et al.* 2015; Broeckhoven & du Plessis 2022). Indeed, this last function might be especially relevant

to both *Paleosuchus* sp. and *Osteolaemus* sp. because these two taxa share a similar cluster of forest habitats within one same ecosystem (i.e., streams; Magnusson & Lima 1991), pools (Riley & Huchzermeyer 1999, 2000), jungle floor (Lemaire *et al.* 2018), caves (Shirley *et al.* 2017; Lemaire *et al.* 2018; Fig. 4). This cluster may include diet variations between niches and therefore imply deficiencies that are tributary to a narrow specific set of preys (e.g. the low calcium content in some invertebrates). The dwarf crocodylian extensive osteoderm shield would therefore consist of a labile resource of calcium that would allow the accommodation to a set of various niches. We hypothesize that the extensive nature of the osteoderm shield could come together with dwarfism in crocodylians since a small size facilitates access to equatorial forest narrow habitats (i.e., streams, excavated pools, jungle floors, caves) that may content a specific set of preys (Magnusson *et al.* 1987). Despite their small size, the extant dwarf crocodylian species are still apex predators so it seems unlikely that the osteoderm shield has a protective role against predators (Trutnau & Sommerlad 2006). This assumption is reinforced by the fact that the juveniles have not grown any osteoderm yet (Veenstra & Broeckhoven 2022) although they make easy prey for a diversity of predators (Somaweera *et al.* 2013). Regarding bone ornamentation, a previous biomechanical study has

shown that the excavation of the ornamental pits would be rather detrimental to the osteoderm resistance (Clarac *et al.* 2019), it is therefore also unlikely that bone ornamentation has a functional implication in protection against external threats (whether they come from predator attacks or intra-specific competition).

CONCLUSION

We assume that the extensive osteoderm shield in the extant dwarf crocodylian species would result from a "trade-off" between the body growth and the synthesis of a resorbable calcium storage which allows to buffer the calcium deficiency that depends on the food resources that are available among the various niches which compose the equatorial ecosystem (i.e., streams, excavated pools, jungle floors, caves). However, before drawing any global relation which we could apply to the study of extinct species (e.g. *Simosuchus clarki* Buckley Buckley, Brochu, Krause & Pol 2000) [Hill 2010]; *Diplocynodon* sp. [Massone & Böhme 2022]), we believe that this hypothesis shall at least be confronted to a similar analysis which would integrate both the intraspecific and interspecific variability among *Paleosuchus* sp. and *Osteolaemus* sp.

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