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Yohan Pochat-cottilloux, Jeremy E Martin, Romain Amiot, Jorge Cubo, Vivian de Buffrénil. A survey of osteoderm histology and ornamentation among Crocodylomorpha: A new proxy to infer lifestyle?. Journal of Morphology, 2022, 284, 10.1002/jmor.21542 . hal-03902565

HAL Id: hal-03902565

<https://hal.science/hal-03902565v1>

Submitted on 16 Dec 2022

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A survey of osteoderm histology and ornamentation among Crocodylomorpha: A new proxy to infer lifestyle?

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Funding information

Sorbonne Université; Agence Nationale de la Recherche

Abstract

Osteoderms of eight extant and extinct species of crocodylomorphs are studied histologically and morphologically. Most osteoderms display the typical “crocodylian” structure with a woven-fibered matrix surrounded by an upper and a lower parallel fibered matrix. The dorsal ornamentation of those specimens consists of a pit-and-ridge structure, with corresponding remodeling mechanisms. However, an osteoderm of *Iberosuchus*, studied here for the first time, differs in being nearly devoid of ornamentation; moreover, it shows strong bundles of straight Sharpey's fibers perpendicular to the surface in its lateral and dorsal walls, along with a rough plywood-like structure in its basal plate. This suggests that this osteoderm was more deeply anchored within the dermis than the other osteoderms studied hitherto. This peculiar structure might have been linked to a terrestrial ecology and a specific thermoregulation strategy. Some other notosuchians in our sample do not exhibit ornamentation on their osteoderms, as opposed to neosuchians. Considering current interpretations of osteoderm function(s) in crocodylians, our observations are discussed in reference to possible ecophysiological peculiarities of Notosuchia in general, and *Iberosuchus* in particular.

KEYWORDS

Notosuchia, ornamentation, osteoderm, paleohistology

1 | INTRODUCTION

Osteoderms are part of the dermal armor of numerous sauropsids (lizards, Williams et al., 2022; dinosaurs, Curry Rogers et al., 2011; phytosaurs, Scheyer et al., 2014; aetosaurs, Cerda et al., 2018; placodonts, Scheyer, 2007). In most of these taxa, the ornamentation consists of hollow pits or grooves, separated by protruding ridges. The ontogenetic process responsible for this morphology has long remained controversial. It was first studied by Buffrénil (1982), who concluded that in Crocodylomorpha Hay (1930) osteoderm ornamentation is mainly created by local bone resorption, with complex

remodeling processes resulting in the adaptation of the depth and size of the pits to the size of the osteoderm during the growth of the individual. However, this interpretation was rejected by Vickaryous and Hall (2008) because they found no sign of osteoclasts (cells responsible for bone erosion) in these bony structures, arguing in favor of the formation of crests rather than the resorption of pits (as in temnospondyls, Witzmann & Soler-Gijón, 2010). Finally, Buffrénil et al. (2015) showed through an experimental approach (in vivo labeling of skeletal growth) and observations conducted on a wide taxonomic sample, including fossil forms, that although there is still no definite evidence of osteoclasts close to osteoderm surfaces,

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resorption is evidenced by both bone labeling technics and the occurrence of reversion lines. The formation of pits is thus mainly due to superficial bone resorption, followed by partial reconstruction, and to a lesser extent to the formation of ridges. The presence of osteoderm ornamentation is hypothesized to have been selected in semiaquatic crocodylomorphs because this feature contributes to heat captation, through enhanced vascularization (Clarac et al., 2018).

This process is plesiomorphic to Crocodylomorpha (absent in rauisuchians, Scheyer & Desojo, 2011); indeed, most taxa in this group show the classical ornamentation of hollow pits and grooves and protruding ridges. However, some taxa belonging to Notosuchia Gasparini (1971) do not show this kind of ornamentation (baurusuchids, Cotts et al., 2017; *Malawisuchus mwakasyungutiensis*, Gomani, 1997; sebecids, Martin, 2014, 2016; *Simosuchus clarki*, Buckley et al., 2000; sphagesaurids, Martinelli et al., 2018). These taxa are also thought to have had more terrestrial habits than their neosuchian relatives (Klock et al., 2022; Pol et al., 2012). Given the apparent morphological differences in osteoderm ornamentation between putative terrestrial and semiaquatic crocodylomorphs, the hypothesis of osteoderm morphology reflecting lifestyle is addressed.

To test this hypothesis, we compare the macroscopic structure of osteoderms belonging to four extinct notosuchians including the sebecid *Iberosuchus* described here for the first time, as well as those of semiaquatic neosuchians and a teleosaurid. Furthermore, we also aim to expand the histological taxonomic sample of previous studies, as well as gain insights on the paleoecology of those taxa using both histological (with a focus on *Iberosuchus*) and external features.

2 | MATERIALS AND METHODS

The sample used for histology consists of eight osteoderms belonging to eight extant and extinct crocodylomorph taxa (three are not identified at the species level). They represent at least five different families and genera (Table 1). All osteoderms were embedded under vacuum in a polyester resin (bones from extant specimens were dehydrated and defatted in ethanol and acetone before being embedded) and each was processed into at least one thin section,

following the standard procedure for this kind of preparation (Lamm & Padian, 2013). The sections were then observed microscopically at low (x20) to medium (x40) power magnification, under natural or polarized transmitted light using three different devices: a Nikon Eclipse E600 POL photomicroscope, an Olympus CX-31P coupled with a Canon EOS6D, and a Zeiss Axioshop coupled with a Canon Power Shot A640. As the goal of this study is to include fossil taxa, soft tissue histology was not used. The terminology used to describe bone histology follows that of Francillon-Vieillot et al. (1990). Global compactness was measured and calculated manually.

The osteoderm belonging to *Iberosuchus* sp. Antunes (1975) (Université Claude Bernard Lyon 1 [UCBL]-FSL 530948-90080) was cut in four thin sections (see Supporting Information: Figure S1). This specimen comes from the middle Eocene (upper Bartonian) Robiac locality, mostly known for its mammalian fauna (Martin, 2016; Mathis, 1985; Remy, 2015; Sudre, 1969). Remains of *Iberosuchus* in this locality were mentioned by Antunes (1986) and Martin (2016).

3 | RESULTS

The osteoderm of *Crocodylus acutus* (Figure 1a) is triangular-shaped with a strongly differentiated dorsal keel. It is also highly cancellous: its global compactness (i.e., relative surface of the mineralized osseous tissue within the whole sectional surface) is quite low (83%). The thin section shows that inner remodeling was intense: there are almost no signs of primary bone left and secondary osteons are especially developed. A vascular canal outcrops at the top of the dorsal keel (Figure 2d). The typical crocodylian dorsal ornamentation pattern can be observed in this osteoderm, with two huge pits that have undergone intense remodeling. One of them is almost filled with secondary deposits of parallel fibers.

The osteoderm of *Mecistops* sp. (Figure 1b) is thin, elongate and almost rectangular-shaped in cross section. It has a medium level of global compactness (95%) and bone remodeling. The core part displays numerous secondary osteons developing centripetally and the superficial layers of parallel-fibered matrix are clearly visible. An interesting feature of this specimen is the presence of numerous vascular canals

TABLE 1 Specimens sampled in this study

Family	Genus	Species	Age	Reference
Uruguaysuchidae	<i>Araripesuchus</i>	<i>tsangatsangana</i>	Campanian-Maastrichtian	MNHN-Histos 1685
Uruguaysuchidae	<i>Araripesuchus</i>	<i>wegeneri</i>	Aptian	MNHN-GDF 660
Sebecidae	<i>Iberosuchus</i>	Indet.	Bartonian	UCBL-FSL 530948-90080
Indet.	<i>Simosuchus</i>	<i>clarki</i>	Maastrichtian	MNHN-Histos 1759
Crocodylidae	<i>Crocodylus</i>	<i>acutus</i>	Extant	MNHN-Histos 1713
Crocodylidae	<i>Mecistops</i>	Sp.	Extant	MNHN-Histos 1716
Teleosauridae	Indet.	Indet.	?	MNHN-Histos 1660
Dyrosauridae	Indet.	Indet.	?	MNHN-Histos 1724

Abbreviations: MNHN, Muséum National d'Histoire Naturelle; UCBL, Université Claude Bernard Lyon 1.

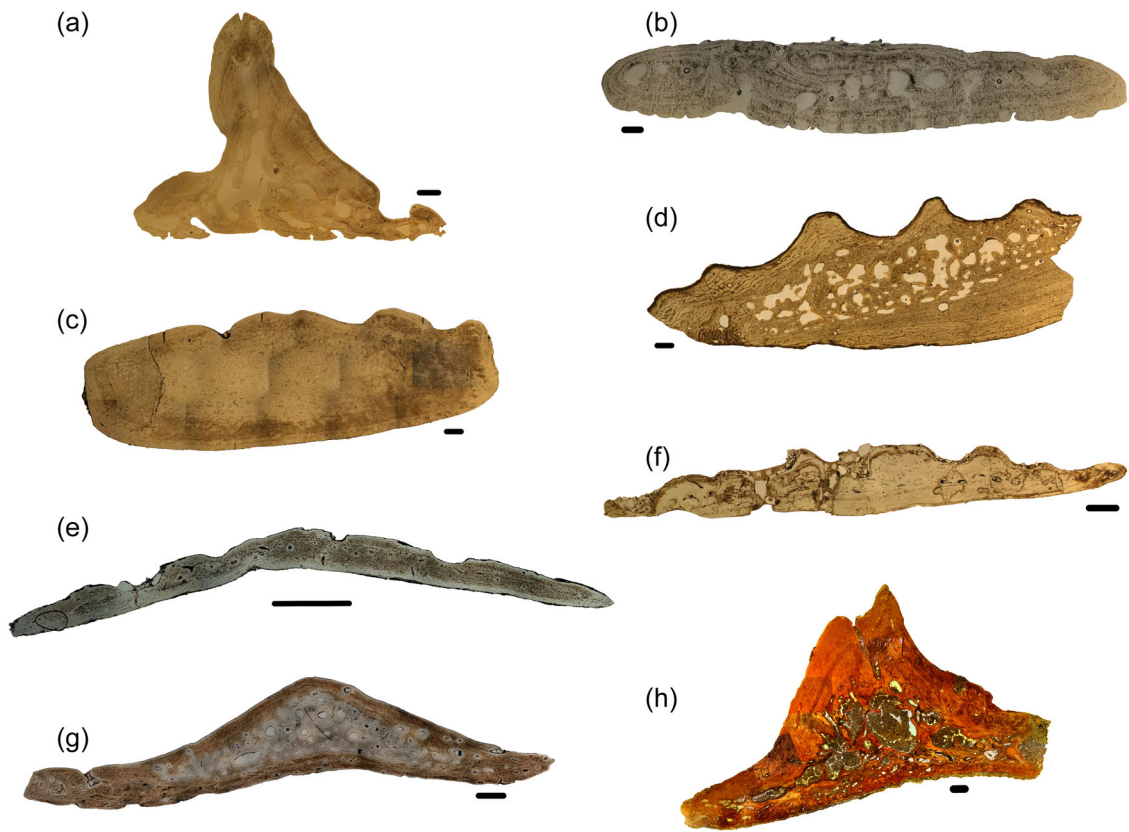


FIGURE 1 Thin sections of extant and extinct crocodylomorph osteoderms. (a) *Crocodylus acutus*; (b) *Mecistops* sp.; (c) Dyrosauridae indet.; (d) Teleosauridae indet.; (e) *Araripesuchus tsangatsangana*; (f) *Araripesuchus wegeneri*; (g) *Simosuchus clarki*; (h) *Iberosuchus*. Scales are 1 mm.

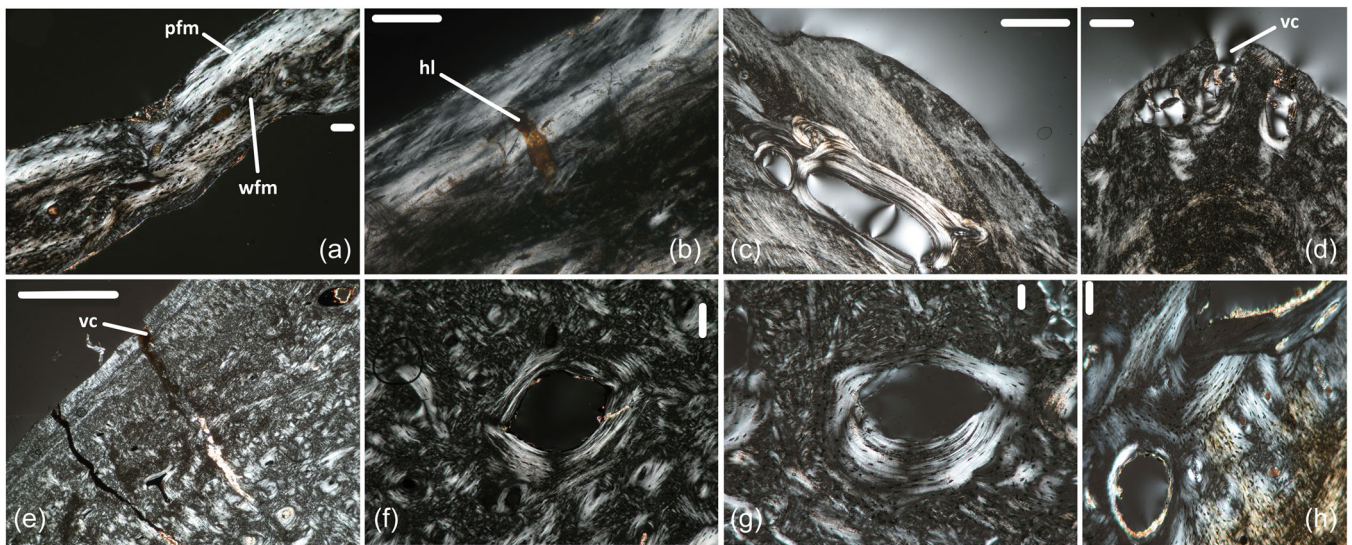


FIGURE 2 Histological structures of osteoderms. (a) Typical osteoderm layout, with woven-fibered matrix (wfm) in between parallel-fibered matrix (pfm). (b) Howship lacuna (hl). (c, f, g, & h) secondary osteon. (d & e) vascular canal (vc). (a & b) *Araripesuchus tsangatsangana*; (c & d) *Crocodylus acutus*; (e & f) Dyrosauridae indet.; (g) *Mecistops* sp.; (h) *Simosuchus clarki*. Scales are 0.1 mm for (a, b, f, g, & h) and 1 mm for (c, d, & e).

originating from the basal side. The dorsal ornamentation is reduced compared to other neosuchians specimens but is still present.

The osteoderm of the dyrosaurid (Figure 1c) is extremely thick, compact (global compactness > 99.9%), and almost devoid of

cancellous bone. This specimen shows no signs of secondary deposits: even its core part is compact and does not show any resorption trace. However, ornamentation on the dorsal side involved secondary centrifugal deposits of parallel fibered tissues (Figure 3d).

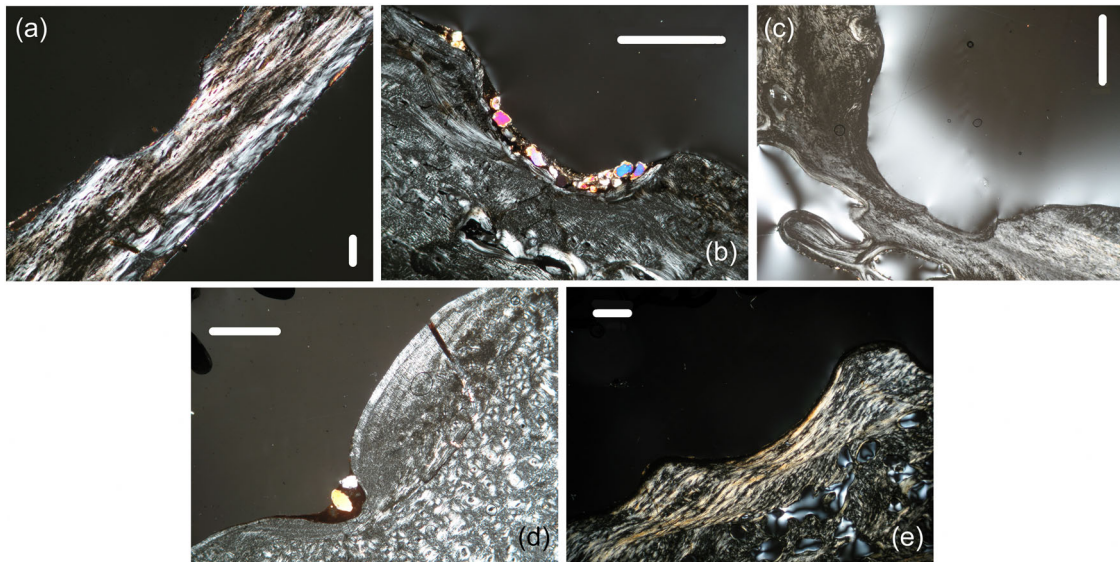


FIGURE 3 Pit-like structures on osteoderms of: (a) *Araripesuchus tsangatsangana*; (b) *Araripesuchus wegeneri*; (c) *Crocodylus acutus*; (d) Dyrosauridae indet.; (e) Teleosauridae indet. Scales are 0.1 mm for (a) and 1 mm for the rest.

This side also displays a few foramina through which inner vascular canals outcrop at the surface (Figure 2e).

The osteoderm of the teleosaurid (Figure 1d) is also quite thick, but less compact (global compactness = 91%): its core contains a formation of cancellous bone. The histological organization described above for the other osteoderms also occurs in this osteoderm: the core consisting of woven-fibered bone is framed by two layers of parallel-fibered tissue. Some secondary osteons can also be found but they are rather sparse. The dorsal ornamentation is clearly visible and especially developed. It has the typical histological structure of crocodylian pit-and-ridge ornamentation, with secondary ossification deposited at the bottom of the pits (Figure 3e).

The osteoderm of *Araripesuchus tsangatsangana* (Figure 1e) has an elongate and thin shape and a high global compactness (almost 100%). It has the typical histological structure of a crocodylomorph osteoderm (as described by Buffr enil et al., 2015): its core shows large globular osteocyte lacunae embedded within a woven-fibered matrix. This central formation is framed by two cortices made of parallel-fibered tissue (exhibiting thin annuli), forming the outer and inner walls. There are no secondary osteons, which would be clear signs of secondary ossification, however a howship's lacuna (bone resorption area; Francillon-Vieillot et al., 1990) can be seen in the parallel-fibered bone (Figure 2b). The relative thinness of the parallel-fibered deposits suggests that the osteoderm was still in an early stage of development at the time of death. It also displays the typical crocodylian dorsal ornamentation (pits-and-ridges), which is visible in thin section with local areas of bone resorption corresponding to pits. However, the osteoblastic reconstruction process that normally follows is not visible, which is possibly due to the early development stage of the individual.

The osteoderm of *Araripesuchus wegeneri* (Figure 1f) has the same thin and elongate shape than *A. tsangatsangana* but a lower

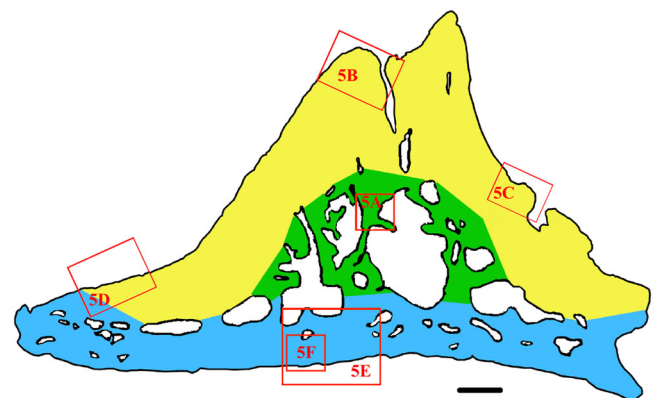


FIGURE 4 *Iberosuchus* osteoderm, schematic representation of the location of bone tissue types. Blue: incorporation and calcification of deep dermal fibers, green: remodeled woven-fibered bone, yellow: periosteal parallel-fibered tissue. The frames localize the pictures of Figure 5. Scale is 1 mm.

global compactness (98%). Secondary osteons are more visible in this specimen. The typical crocodylian dorsal ornamentation also occurs here, and, in relation with a more active remodeling, secondary centrifugal deposits can be seen in the bottom of the pits (Figure 3b). Those are clearly separable from the subjacent bone tissues by a reversion line and a discordant orientation.

The osteoderm of *Simosuchus clarki* (Figure 1g) is also elongate but bears a smooth dorsal keel, allowing its identification as a dorsal osteoderm (Hill, 2010). It has a medium global compactness (97%) with some cancellous bone in the core part. Together with numerous secondary osteons, those features reflect the remodeling activity that occurs in the central part of the osteoderm (but it is lesser than in the osteoderm studied by Hill [2010]). The main difference is the absence

of pit-and-ridge patterns in the dorsal ornamentation of this specimen. Hill (2010) reported perpendicularly oriented fibers in the dorsal part of the osteoderm, but those structures were not observed here.

Finally, the osteoderm of *Iberosuchus* (Figure 1h) has a triangular shape due to the strong differentiation of the keel. Global compactness (87%) is similar to that encountered in many neosuchians (see above). The sketch presented in Figure 4 shows the local variation in the tissue composition of the osteoderm. It also gives the location of the photographic fields presented in Figure 5. The core of the osteoderm is cancellous, with broad coalescent cavities separated by robust trabeculae (Figure 4, green, Figure 5a). The basal and lateral walls are thick, but their vascular supply is sparse. Some canals outcrop at the dorsal surface but the openings of the canals are not preferentially located in the middle of the pit floors. The core of the

osteoderm consists of a small formation of woven-fibered bone tissue. In the dorsal three quarters of the osteoderm, the compact cortex consists of parallel-fibered bone with cyclical growth marks in the form of thin annuli, poorly characterized and unevenly spaced (Figure 4, yellow, Figure 5b,c). The lower, basal quarter of the osteoderm cortex (Figure 4, blue) includes big interwoven fiber bundles with irregular orientations (Figure 5d), within the parallel-fibered tissue. Most of the volume of the basal plate is an assemblage of extremely big fiber bundles (some 600 μm in diameter) displaying a clear geometrical structuration (Figure 5e,f). They form a rough plywood-like structure where three bundle systems occur: two of them are horizontal (i.e., parallel to the surface of the basal cortex), but with diverging obliquities, to the right and to the left (this results in distinct refringence patterns of these bundles in polarized light).

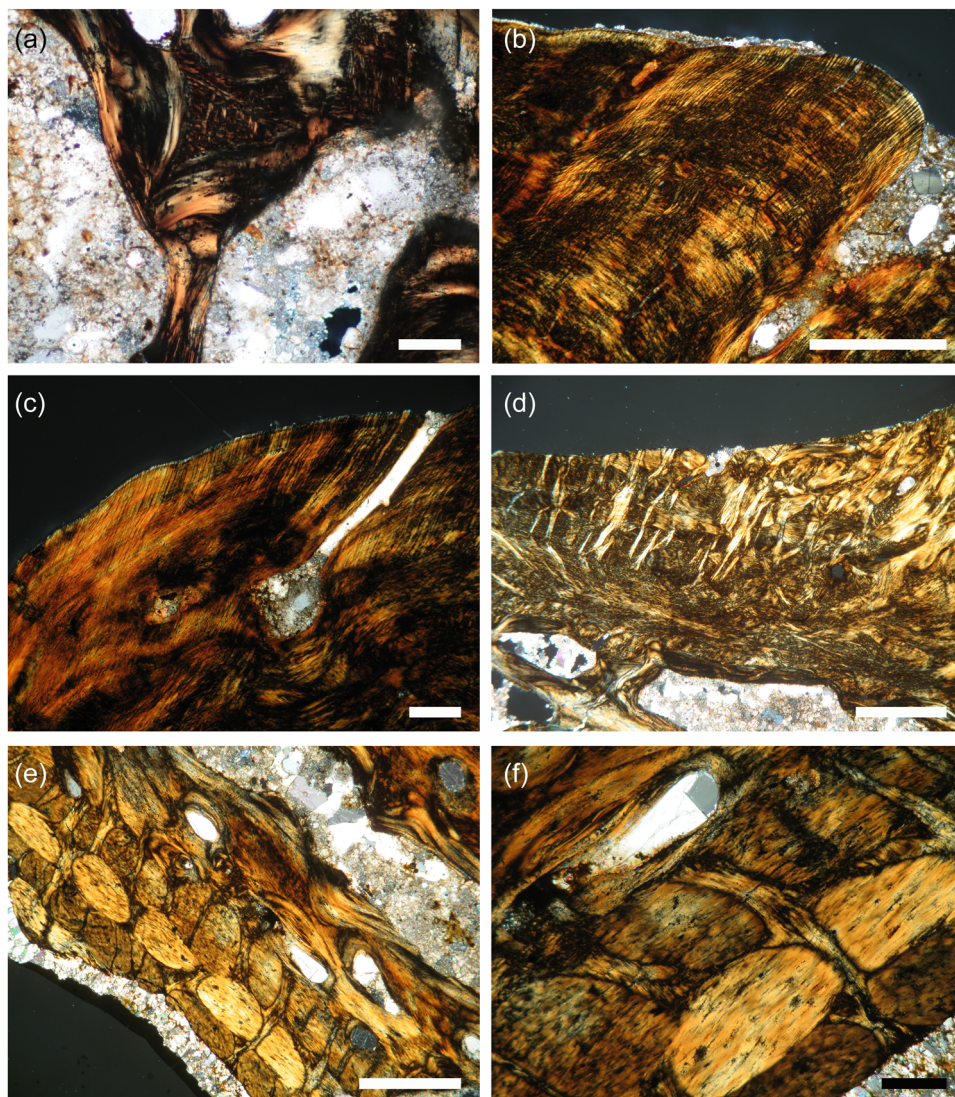


FIGURE 5 *Iberosuchus* osteoderm, histological tissue types forming the osteoderm (see also Figure 4). All pictures are seen in polarized light. (a) Remodeled woven-fibered bone in the core of the osteoderm. (b & c) Parallel-fibered bone on the apex and walls of the osteoderm. This tissue contains long and straight fiber bundles from the loose dermis (stratum superficiale). (d) Parallel-fibered tissue with extremely thick fiber bundles from the neighboring dermis. (e & f) Rough plywood-like formation representing the incorporation into the osteoderm and the calcification of a part of the dense dermis (stratum compactum). Scales are 0.2 mm for (a, c, and f) and 1 mm for (b, d, and e).

The third system consists of vertically oriented fiber bundles. The surface of the basal plate lacks a tissue histologically recognizable as bone: the basal plate looks entirely made of diverse assemblages of calcified fibrillar material devoid of the basic characteristics of bone.

Ornamentation on the dorsal surface of the osteoderm does not result from the succession of complete remodeling cycles, including osteoclastic resorption followed by osteoblastic reconstruction with lamellar secondary bone over the bottom of the pits. Some faint resorption traces can be observed on the floor of one pit only, but there is no evidence of a local reconstruction process. Moreover, the parallel-fibered tissue of the dorsal cortex, throughout its thickness and in every spot where it appears, is deeply penetrated by series of strong parallel bundles of fibers running perpendicularly or obliquely from the osteoderm surface (Figure 5b–d). These bundles are sparser, but their diameter is much bigger and their orientation less even toward the base of the osteoderm.

4 | DISCUSSION

4.1 | Peculiar characteristics of the osteoderm of *Iberosuchus*

The microanatomical characteristics of *Iberosuchus* osteoderm do not differ from those of most crocodylomorph osteoderms in terms of gross geometry and global compactness (Buffrénil et al., 2015; Burns et al., 2013; Vickaryous & Hall, 2008). However, the peculiar histological structure of this specimen shows two unique features: (1) there is no typical remodeling involved in the differentiation and growth of superficial ornamentation (Figure 5b,c) and (2) the occurrence of strong fiber bundles, either interwoven or forming a plywood-like structure within the lower cortex (Figure 5e,f) is unknown in other crocodylomorphs, at least in adults (the situation could occur during early ontogenetic stages: Vickaryous & Hall, 2008). These histological peculiarities, and especially the abundance and distribution of extrinsic, non-osseous fiber bundles, suggest a special mode of growth.

The osteoderms of *Iberosuchus* were strongly anchored into the dermis. In other crocodylians, however, the permanent superficial remodeling of ornamented surfaces prevents a strong and stable anchoring of the upper side of the osteoderms (as well as the thinness of the stratum superficiale, or superficial dermis; Burns et al., 2013; Clarac et al., 2018; Vickaryous & Hall, 2008). Most anchoring fibers are then limited to thin Sharpey's fibers in the parallel-fibered tissue of the basal plate, or in deep cortical strata elsewhere.

Histologically, *Iberosuchus* osteoderm may be compared with those of *S. clarki* described by Hill (2010), which also show perpendicularly oriented fibers relative to the external surface. However, those structures are not encountered in the specimen described here (Muséum National d'Histoire Naturelle [MNHN]-Histos 1759). It may also be compared with those recently described of *Marillasuchus amarali*, *Armadillosuchus arrudai*, *Itasuchus jesuinoi*, *Uberabasuchus terrificus*, *Aplestosuchus sordidus*, and baurusuchid

(Sena et al., 2022). Indeed, these also exhibit Sharpey's fibers on the external surface, indicating that the deep implantation of osteoderms could be a general feature of notosuchians. Furthermore, the carapace plates of some fully aquatic turtles, especially the Trionychidae, are covered with thick dermal tissue which, along with the cambial and cornified layers of the epidermis, constitutes a tough, though flexible, protection (Alibardi & Toni, 2006; Cherepanov, 1995; Scheyer & Cerda, 2021; Scheyer et al., 2007). The basal cortex of *Tryonxys triunguis* or *Tryonxys spiniferus* plates typically consists of an orthogonal plywood-like system with regularly arranged horizontal and vertical fiber bundles (a geometric pattern much more regular than in *Iberosuchus*). Moreover, the dorsal cortex shows the same kind of strong pattern consisting of parallel bundles of fibers penetrating the cortex vertically throughout its whole thickness as observed in *Iberosuchus* (Buffrénil et al., 2015).

The histological characteristics of the osteoderm of *Iberosuchus*, compared to those of its integument, suggest that its formation mode was different from that of most neosuchians (for a complete review, see Buffrénil et al., 2015; Vickaryous & Hall, 2008). The thick, roughly orthogonal plywood formation that exclusively composes the basal part of the osteoderm may have formed through a local incorporation and calcification of the fibrillar apparatus of the dense stratum compactum, in the depth of the dermis. The osteoderm cortex at this level, being essentially composed of extrinsic fibrillar material, did not result from osteoblastic osteogenesis, but from a process akin to metaplasia (at least for the extracellular matrix). Conversely, the cortex located in a more superficial position grew through the typical osteoblastic osteogenesis of parallel-fibered bone. Moreover, as in soft-shelled tortoises (Alibardi & Toni, 2006; Cherepanov, 1995; Scheyer & Cerda, 2021; Scheyer et al., 2007), a thick and relatively dense dermal layer, from which the strong perforating parallel fibers originated, covered the external side of the osteoderm. According to this interpretation, osteoderm formation and position within the skin were deeper in *Iberosuchus* than in other crocodylomorphs: by incorporating the fibers of the stratum compactum, the osteoderm tends to sink into the dense dermis, and their development is unlikely to have occurred mainly in the stratum superficiale, as it does in neosuchians. The distribution of extrinsic fibers within the osteoderm shows that it was firmly attached to both the superficial and deep dermal layers through its upper (ornamented) and basal surfaces, respectively.

The histological data presented here show that the peculiar morphology of osteoderm ornamentation in *Iberosuchus* was not due to a total filling of former ornamental pits (as it may occur, at least locally, in many crocodylomorphs; see Buffrénil et al., 2015); it was due to a disappearance (or dedifferentiation) of the basic morphogenetic mechanisms that create ornamental reliefs (iterative remodeling of the ornamental surface).

The functional meaning of the histological peculiarities of the *Iberosuchus* osteoderm remains enigmatic, as are more generally the lifestyle and ecological adaptations of this taxon. Its overall morphology suggests a terrestrial animal adapted to active predation and possibly relying on a high metabolic activity, as compared with other

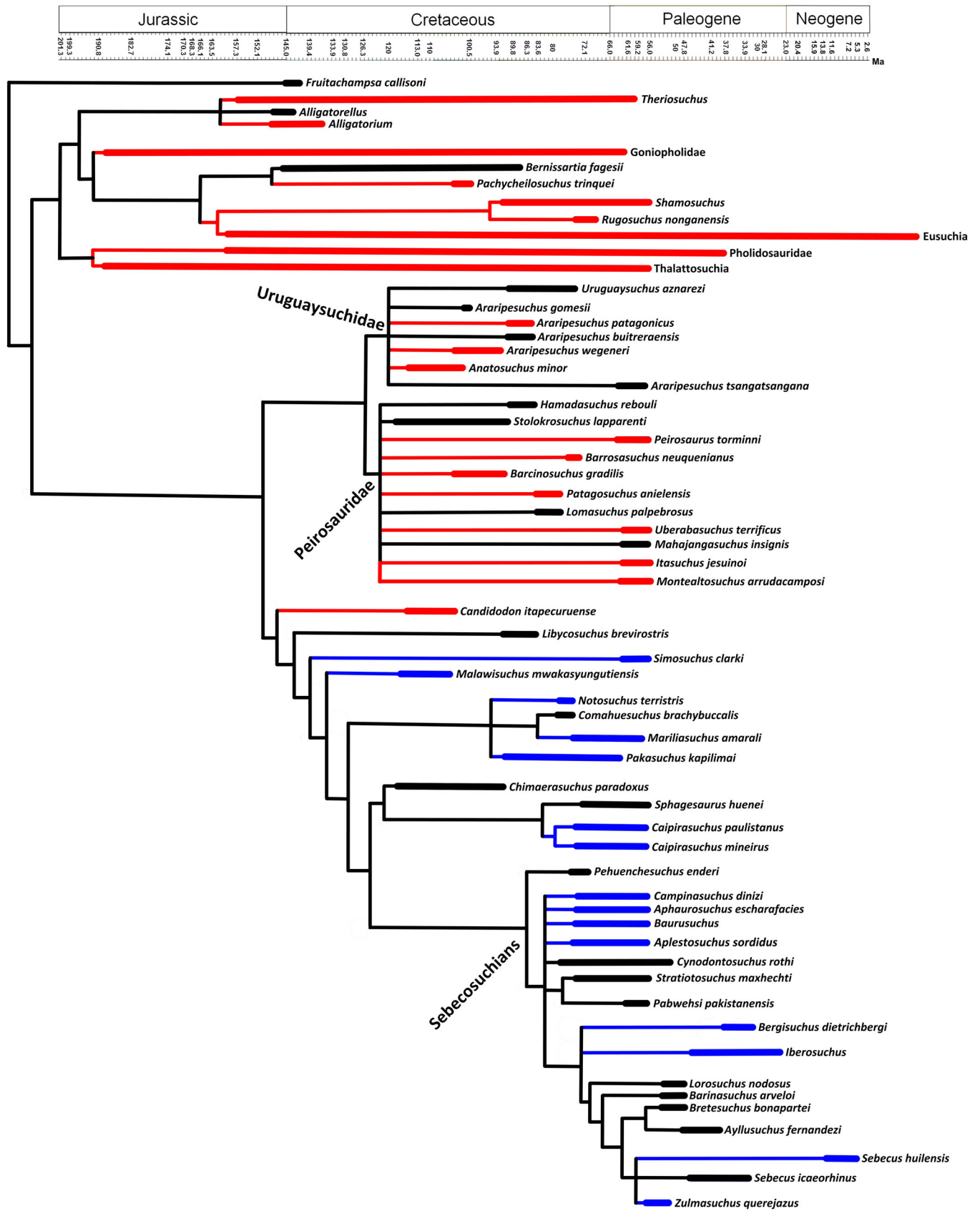


FIGURE 6 (See caption on next page)

close taxa (Pol et al., 2012). However, the histological characteristics of *Iberosuchus* limb bones (Cubo et al., 2017), and the basal metabolic rate inferred using these features (Cubo et al., 2020), are closer to those of bradymetabolic lizards than to those of dinosauromorphs or mammals (Buffrénil et al., 2021). The histological peculiarities of *Iberosuchus* osteoderm might be related to muscular insertion. Crocodylian osteoderms are indeed considered to improve the insertion of the epaxial muscles into the skin and increase their efficiency for thrust production during swimming (Schwarz-Wings et al., 2009; Seidel, 1979). In the context of the terrestrial and cursorial locomotion commonly attributed to sebecosuchians, a tougher integration of the osteoderms within the dermis would not have been involved in improving propulsion but might have been beneficial to the control of an erect posture in forms like *Iberosuchus*. This hypothesis, although also put forward recently in Sena et al. (2022), currently remains conjectural and calls for further substantiation.

A possible involvement of intradermal blood vessels in thermoregulation also remains a possibility. In extant forms, an important role is attributed to dermal vascularization in the regulation of thermal exchanges in crocodiles (Clarac et al., 2018; Seidel, 1979 but see Inacio Veenstra & Broeckhoven, 2022). Dermal thickening and superficial vascular proliferation might then have, in some taxa, restored a capacity to accelerate blood warming. However, no positive anatomical data about skin vascularization in extinct crocodiles is available in support of this conjecture. Moreover, this would constitute a hazardous solution, likely to produce important hemorrhage in the case of skin injuries.

4.2 | Osteoderm ornamentation as a paleoecological proxy?

More generally, osteoderm ornamentation is absent in most notosuchians (Figure 6) apart from uruguaysuchids, peirosaurids, and *Candidodon*. Those taxa are inferred to have been terrestrial (Fernández Dumont et al., 2021), however some bear pits on their osteoderms (Coria et al., 2019; Leardi & Pol, 2009; Lio et al., 2016; Ortega et al., 2000; Price, 1955; Sereno & Larsson, 2009; Tavares et al., 2015).

These observations could be linked to both the living environment and thermoregulation. The presence of osteoderm ornamentation may have been selected in semiaquatic crocodylomorphs because the presence of this feature contributes to heat capture, through enhanced vascularization (Clarac et al., 2018). Indeed, all the species studied here are inferred to be ectotherms (from histological

and geochemical proxies; Cubo et al., 2020; Faure-Brac et al., 2021). Because thermal conductivity, heat capacity, and density in water are higher than those in air, body heat loss is higher in water than in air and maintaining a high body temperature is more costly (Schmidt-Nielsen, 1997; Vogel, 2005). Selective pressure for osteoderm ornamentation may thus be lower in terrestrial taxa, so this feature could become vestigial or completely disappear. This could then support a terrestrial ecology but with semiaquatic affinities for uruguaysuchids, peirosaurids, and *Candidodon*, as seen today for example in extant dwarf crocodiles belonging to the genus *Osteolaemus* (Shirley et al., 2017). This idea has been put forward in a histological study of *Pepesuchus deiseae* (Peirosauridae), where Sena et al. (2018) observed osteosclerosis in metacarpals and fibro-lamellar tissue in advanced ontogeny, linking it with a more aquatic lifestyle. However, as for the impact of dermal vascularization, the debate on the ecological impact of osteoderm ornamentation remains open (Clarac et al., 2017; Clarac & Quilhac, 2019; Inacio Veenstra & Broeckhoven, 2022; Seidel, 1979).

Furthermore, as seen in Figure 6, the loss of osteoderm ornamentation is restricted to a group including *S. clarki* and sebecosuchians, becoming the derived condition in notosuchians. As a result, another possibility could be that notosuchians illustrate a case of phylogenetic time lag (Harvey & Pagel, 1991): the osteoderm ornamentation representing the ancestral condition in crocodylomorphs having been ultimately lost (derived condition) in derived notosuchians. Ornamentation is identified in some of them, such as uruguaysuchids, peirosaurids, and *Candidodon*, even though it would not have the hypothesized thermoregulative function because those taxa would not need it.

5 | CONCLUSION

For the first time, an osteoderm of *Iberosuchus* from France (Robiac) is described. Histologically, we notice some peculiar characteristics such as a dorsal surface penetrated by a series of strong parallel bundles of fibers running perpendicularly from the osteoderm surface, which does not bear any trace of bone remodeling. The organization of the basal part of the specimen is also different from what is known in other crocodylomorphs and suggests a deeper osteoderm implantation within the integument in this taxon. Up to now, the interpretation of this special and puzzling characteristic in functional terms remains uncertain and conjectural. Further data on notosuchian ecology, based on different lines of evidence than histology, remains obviously needed.

FIGURE 6 Phylogenetic relationships of some crocodylomorphs highlighting the morphology of osteoderms. Red branches represent the presence of ornamentation whereas the absence of ornamentation is in blue. Black is the unknown condition. Occurrences and phylogenetic relationships are from Cotts et al. (2017); Darlim et al. (2021); Godoy et al. (2014); Gomani (1997); Hill (2010); Iori et al. (2016); Leardi et al. (2015); Marchetti et al. (2022); Marinho et al. (2006); Martin (2016); Martinelli et al. (2018); Montefeltro (2019); Nascimento and Zaher (2010); Nobre and Carvalho (2013); O'Connor et al. (2010); Ortega et al. (2000); Pol (2005); Sena et al. (2022); Sereno and Larsson (2009); Tavares et al. (2015); as well as data from Fossil Work. *Iberosuchus* osteoderm is hypothetically placed at the base of Sebecidae.

More generally, we observe that the ornamentation of osteoderms is lost in derived notosuchians. As those taxa are inferred to be terrestrial, we hypothesize that the osteoderm ornamentation might be linked to lifestyle: it would allow a greater surface of exchange in aquatic to semiaquatic environments, to account for a greater temperature loss in those environments. Conversely, this morphological trait would have been ultimately lost in terrestrial notosuchians.

However, this issue remains open, and further studies are needed to better understand the impact and function of osteoderm ornamentation in crocodylomorphs. A better sampling of extinct forms would also be of interest, to better tackle the evolution of this trait throughout Crocodylomorpha's history.

AUTHOR CONTRIBUTIONS

Yohan Pochat-Cottilloux: conceptualization; investigation; writing – original draft; visualization; writing – review & editing; software; formal analysis; data curation; project administration. **Jeremy E. Martin:** conceptualization; funding acquisition; validation; writing – review & editing; project administration; supervision; resources. **Romain Amiot:** writing – review & editing; conceptualization; validation; project administration; supervision; resources. **Jorge Cubo:** conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review & editing; project administration; data curation; supervision; resources; formal analysis. **Vivian Buffrénil:** investigation; writing – original draft; validation; writing – review & editing; supervision; methodology.

ACKNOWLEDGMENTS

We thank Ronan Allain (MNHN) for access to the *A. wegeneri* material, Damien Germain (MNHN) for access to the histological collections of the MNHN, Séverin Morel (MNHN) for preparing the thin sections of the osteoderm of *Iberosuchus*, as well as Matthias Starck (University of Munich) and an anonymous reviewer for insightful comments that greatly improved the quality of this manuscript. This work was supported by the Agence Nationale de la Recherche (SEBEK project no. ANR-19-CE31-0006-01 to JEM) and by Sorbonne Université (project Emergences 2019 n° 243374 to JC).

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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How to cite this article: Pochat-Cottilloux, Y., Martin, J. E., Amiot, R., Cubo, J., & de Buffrénil, V. (2022). A survey of osteoderm histology and ornamentation among Crocodylomorpha: A new proxy to infer lifestyle? *Journal of Morphology*, e21542. <https://doi.org/10.1002/jmor.21542>