



The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae)

Frederik Spindler, René Lauer, Helmut Tischlinger, and Matthias Mäuser

ABSTRACT

Metriorhynchidae are the only archosaurs that show adaptations to a highly pelagic lifestyle. This morphology is paralleled by ichthyosaurs and plesiosaurs, which share a streamlined, largely scaleless skin surface. Although published metriorhynchid material indicates a similar condition, no detailed description of their integument has been carried out. New data from several specimens representing at least three genera are shown here, revealing a uniform skin type lacking any traces of scales or scutes and instead showing folded and transverse fibers. A hypocercal tail fluke comparable to that of ichthyosaurs is present in metriorhynchids. Surface anomalies on metriorhynchid skin are interpreted as potential epizootic scars, similar to those from barnacles, or bite marks. A broad comparison implies deep homologies with plesiosaur and ichthyosaur skin. We also describe skin details of early (teleosauroid) thalattosuchians for the first time. Unlike Metriorhynchidae, their integument is demonstrated to be very similar to that of extant crocodylians, which can be partially explained by their inferred onshore behavior. There is generally a high threshold for extensive skin modifications in aquatic reptiles.

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INTRODUCTION

During the transition from terrestrial to a secondarily aquatic lifestyle, some amniote lineages underwent substantial modification of their integument, in large part to increase hydrodynamic efficiency. Cenozoic mammals, most dramatically cetaceans, lost their fur and evolved a smooth, highly streamlined skin (Themudo et al., 2020). This adaptation was somewhat paralleled by the Mesozoic ichthyosaurs (Fraas, 1888; Lingham-Soliar and Plodowski, 2007; Renesto et al., 2020) and plesiosaurus (Frey et al., 2017; Vincent et al., 2017), which lost the scaly integument of their terrestrial reptile ancestors in favor of smooth skin. Not all marine reptile groups became scaleless, however. Marine turtles retain scaly skin, although they exhibit a leathery, less keratinized skin around their major joints and scutes covering the shell have been lost in *Dermochelys* (Maderson, 1972). Exceptionally preserved specimens confirm that the integument of the Late Cretaceous, fully marine mosasaurs retained the typical scales of squamates (Lindgren et al., 2009, 2010), and a comparable condition is present in the Jurassic pleurosaurids, a group of highly modified aquatic rhynchocephalians (Broili, 1926). Several crocodyliform lineages became aquatic during the Mesozoic, of which the Thalattosuchia were most highly adapted for a marine lifestyle (Young et al., 2010). Thalattosuchia is composed to two major subclades, of which the Teleosauroidea was less specialized for marine life. Teleosauroids exhibit rows of osteoderms similar to those of the vast majority of other crocodyliforms (Johnson et al., 2020b), but their soft tissue anatomy is poorly known and has received only cursory review in the literature (e.g., Westphal, 1962). For the more specialized thalattosuchians, the Metriorhynchoidea, early researchers argued for a fully marine lifestyle and smooth skin (e.g., Fraas 1901, 1902), but with limited actual documentation of soft tissue preservation. Here, we describe extensive new soft tissue records for thalattosuchians from the Late Jurassic plattenkalk localities of Wattendorf and Painten (Bavaria, Germany), comparing them to other marine reptiles in order to shed light on the evolution and function of the metriorhynchid integument.

Reptilian Integumentary Terminology

Reptiles are usually associated with a ‘scaly’ appearance, which is often popularly assumed to reflect an ancestral condition. However, what are called ‘scales’ in different reptilian subclades are not identical in structure or evolutionary history. The overlapping, epidermally-defined scales of Lepidosauria (squamate lizards and snakes [including mosasaurs], as well as the tuatara and its fossil kin, see Maderson, 1968) differ fundamentally from the non-overlapping scales of crocodiles, turtles, and bird limbs. Scales in these latter taxa are covered with rigid β -keratin and interlinked by α -keratin hinges (Alibardi et al., 2009; Rutland et al., 2019) and are inferred to represent the more ancient condition. Whereas lepidosaurs perform singular ecdysis, these other reptiles shed their epidermis in fragmented flakes (Spearman and Riley, 1969). Variability in scale development can occur even within a single taxon; in crocodylians, for example, the ‘scales’ on the head are the result of rhomboidal fracturing of the skin during development (Milinkovitch et al. 2013), unlike the genetically-modeled scales elsewhere on the body.

In fossils, integumentary structures such as scales are infrequently preserved and can be difficult to discern. Their recognition in fossil material is often predicated on the presence of regular arrangements of discretely-bounded structures. However, similar structures in fossils can be produced by folding of the skin (either post mortem or as a natural condition in the living animal). Both fine squamation and detailed, regular folding occur in areas of increased skin movement in life. Differentiation of these in fossils can be problematic, but folds can generally be recognized by gradual fading of their edges, unlike the sharp boundaries present in all scales.

In the connective tissue of the integument, fibers occur, which also form the initial stages of osteoderm growth (Vickaryous and Sire, 2009). Dermal fibers are flexible, strengthening elements that would have maintained structural integrity in the skin of scale-less marine saurians (Lingham-Soliar and Plodowski, 2007; Lindgren et al., 2011), and are detectable in fossils as strong, discrete, straight-to-weakly curved elements arranged in parallel sets. Fossilized muscular fascia, which could be confused with skin fibers, appear less

sharp and exhibit broader stripes instead of unidimensional fibers.

Specimen Repositories

Fossil specimens, which contributed to our detailed analysis for this study, are housed in the following paleontological repositories: **LF** – Lauer Foundation for Paleontology, Science and Education, Wheaton, IL USA; **NKMB** – Naturkunde-Museum Bamberg, Bavaria, Germany; **DMA** – Dinosaurier Museum Altmühltal, Bavaria, Germany. Additional specimens referenced in this work are housed at: **NHUK** – Natural History Museum, London, UK; **SMNS** – Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany; **BMMS** – Bürgermeister Müller Museum Solnhofen, Bavaria, Germany; **JME** – Jura-Museum Eichstätt, Bavaria, Germany.

METHODS

The current study addresses macroscopic structures observed and photographed under daylight (herein visible light) and ultraviolet light (UV, or Ultraviolet Induced Fluorescence, UVIF). Frequent UV investigations during the past 20 years have shown that fossils from the Upper Jurassic limestones of southern Germany are often auto-fluorescent (e.g., Tischlinger, 2002, 2005, 2015; Tischlinger and Unwin, 2004; Frey and Tischlinger, 2012; Tischlinger and Arratia, 2013; Schwarz et al., 2019). This technique allows for more precise investigation of morphological details of both hard and mineralized soft tissue, including delicate structures that are poorly or not discernible in visible light.

UV investigations for DMA and NKMB specimens were carried out with the help of different high-performance UV-A lamps with a wavelength of 365–366 nanometers and intensities between 4000 and more than 50 000 microwatts per 10 mm², depending on the distance concerned and the number of lamps: 2 Benda UV-lamps, type N, 16 watt, UV A, 366 nanometers (nm), size of filter 200 mm x 50 mm. 1 Labino UV-lamp, spotlight S 135, 35 watt, UV-A, 365 nm with custom-made Midlight-reflector-inset. 1 UV-inspection lamp Convoy S2+ UV 365 nm with Li-ion 1865.

The photo documentation was done with Panasonic Lumix GX80 with Lumix G-Vario 3,5-5,6 /14-140 mm, Leica DG Summilux 1,4/25 mm ASPH and Panasonic macro lens H-HSO30E Lumix G macro 30 mm F2.8 O.I.S. Applying different filters allowed a selective visualization of some fine structures. Color compensation filters (yellow,

cyan, and magenta of different types and densities) made of special colored glass or gel were placed atop the camera lens. The furthestmost filter was a UV-filter, which blocked UV light up to 390 nanometers.

Ultraviolet Induced Fluorescence (UVIF) Digital Photography of LF specimens was utilized to identify and document mineralization of rarely seen soft tissue preservation, such as skin and muscle; and fine morphological details and structures of hard surfaces, such as teeth and bones. The technique also helps to identify areas of repair and restoration, which impact accurate analysis of fossil specimens and their enclosing matrix. All specimens were photographed under both visible light and UV light, results of which were provided as RAW files.

UVIF photographic documentation was performed with the use of the following photographic equipment: A Nikon D4 DSLR camera (without sensor modification), tethered to a 4K monitor, and a wireless shutter release. Camera lenses include: AF Nikkor 28 mm f2.8; AF-S micro Nikkor 60 mm 2.8G ED; and Nikkor 20 mm lens. Filters include: a linear polarizing filter, used for both visible light and UVIF photography: MidOpt PRO 32-62; (+ polarizing film on the lamp for some visible light images); and a color correction balancing filter, used for UVIF photography: (orange) MidOpt LAT20-62.

Lights/lamps utilized for visible light photography include: two Fotodiox ring lights, color temperature of 5500k, and use of diffusers (one diffuser fitted with polarizing film was used in combination with a linear polarizing lens filter (cross-polarization) to reduce unwanted glare and provide definition.) Lights/lamps utilized for UVIF photography include: a 95 watt Quad High-Performance UV Lamp; equipped with 3 – 95W bulbs: UV A (320 – 400 nm), UV B (280 – 320 nm), and UV C (280 – 100 nm) wavelengths; Hoya U-325 and Komodo UV-400 filters; and a remote control. UV wavelengths were used individually, and together, to identify specific UVIF responses. In this case UV A, B, and C wavelengths were used together. All UVIF images were captured in a darkened room with the UV lamp as the sole light source. Additional UV lights/lamps include: 2 - 9 watt, triple UV lamps: equipped with UV A, B and C wavelength bulbs, used individually and together, fitted with Hoya U325C and Kokomo UV-400 filters; 2 - 9 watt custom-designed triple UV Gooseneck lamps, and equipped with filters to utilize UV A, B or C individually; and 2 UV/LED flashlights were used for investigation: Convoy S2+ 365 nm UV with LG LED.

Additional equipment includes customized stands and mounts, designed to stabilize all elements during long exposure photography of UVIF images. They are fully adjustable to easily accommodate a wide variety of sized specimens, while also providing consistent and repeatable photographic results including: a custom-built lamp stand for the 95 Watt UV Quad lamp array; a camera stand, Manfrotto #806 Salon 190; a 3-way geared pan/tilt head with quick-release plate, Manfrotto #410 and #410PL; and a table with motorized lift. In addition, customized identification tiles and cubes (1 cm) were utilized to identify data not captured within the camera’s metadata such as the UV wavelengths, the specific filters, and provide scale.

Additional macro photography of specific details of specimens in the LF, DMA, JME, and NKMB collections were captured with a Canon EOS 600D, macro lens EFS 18-55 mm, a polarizing filter, and tripod.

GEOLOGICAL BACKGROUND

The sites of the Late Jurassic fossils discussed herein are located on the northern and southern Franconian Alb (Wattendorf and Painten, respectively; Figure 1), Bavaria, Germany. Both localities are outcrops of laminated carbonates

(plattenkalks), which are typical for the famous Konservatlagerstaetten of the Solnhofen Archipelago. The timeframe for their deposition ranges from upper Kimmeridgian to lower Tithonian. The Wattendorf Plattenkalk contains the oldest preservation of material, dated as early late Kimmeridgian age (Pseudomutabilis subzone, see Schweigert, 2007). The Painten Plattenkalk was also deposited earlier than the typical Solnhofen plattenkalk environment and dates to the late Kimmeridgian (Ulmense subzone).

Numerous hypotheses have been presented to explain the origin of these Konservatlagerstaetten (Viohl, 2015). The current understanding of this paleoenvironment is that laminated plattenkalk formed in restricted basins, so-called “wannen” (Fesefeldt, 1962), which were embedded in a relief of microbialite-sponge bioherms and biostroms. The undisturbed lamination and preservation of articulated vertebrate skeletons suggest anoxic conditions on the seafloor and in the sediment, in stagnant water conditions – some kind of a ‘dead zone’ hostile to higher life.

During the Late Jurassic these special conditions prevailed along a wide belt following the southern edge of the Central European shelf sea in delimitation to the deeper Tethys. The resultant

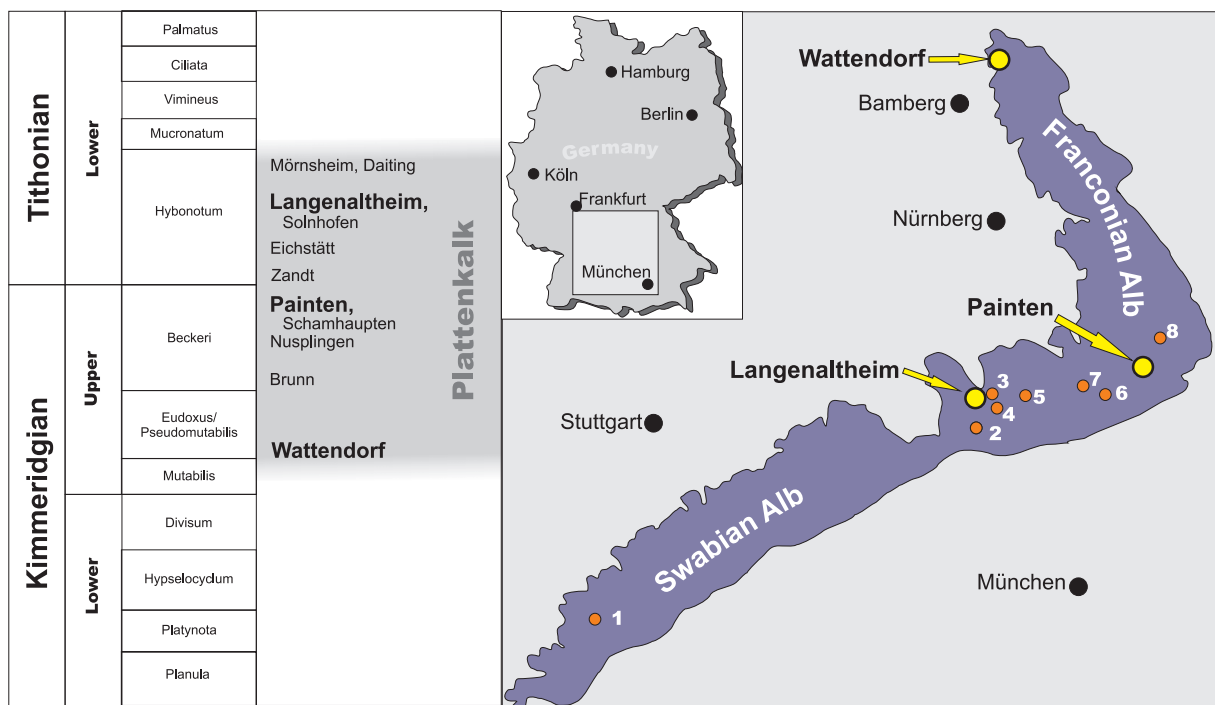


FIGURE 1. Stratigraphic positions and locations of different Upper Jurassic plattenkalk localities of the Franconian and Swabian Alb. 1 Nusplingen, 2 Daiting, 3 Solnhofen, 4 Mörsheim, 5 Eichstätt, 6 Schamhaupten, 7 Zandt, 8 Brunn. Stratigraphic positions after Schweigert (2007).

plattenkalk range extends from Wattendorf in the northeast across the Southern Franconian Alb and the Swabian Mountains to the French Jura in the southwest. The type of sedimentary rock and the quality of fossil preservation vary considerably along this depositional area. This variance is mostly due to local synsedimentary environmental conditions. The Wattendorf Plattenkalk was deposited within a cove of a microbialite-sponge reef, which opened towards the Wattendorf-wanne. The sediment of this cove consists of laminated plattenkalk facies, intercalated between graded turbidite beds and coarsely-grained detrital beds (Fürsich et al., 2007). The sequence measures about 7 m at its deepest point and thins toward the reef. In the immediate vicinity of the reef the plattenkalk limestone turns into a very thinly laminated dolobindstone. In the latter, *Dakosaurus* NKMB-P-Watt06/508 was found; whereas *Cricosaurus bambergensis* NKMB-P-Watt14/274 comes from a sequence of very finely-grained graded beds, microbial laminae, and ultra-thin clay laminae in the center of the cove. The latter beds of the Wattendorf section are particularly notable for their excellent preservation of vertebrates (Mäuser, 2015).

The stratigraphic horizon that yielded the herein-discussed crocodyliforms from the Painten-Quarry consists of a 5-meter-thick package of graded turbidite-beds, laminated limestone (bindstone) and coccolith-beds (Meyer and Schmidt-Kaler, 1984, Albersdörfer and Häckel, 2015). They were deposited in the northern area of the Painten-wanne. The carbonates have a considerable concentration of silica, as is common for like-aged carbonates of the Southern Franconian Alb. Both the high quality of preservation and the abundance of articulated vertebrates in these beds are outstanding.

DESCRIPTION OF NEW MATERIAL

Specific Morphology

Metriorhynchidae indet. (cf. *Dakosaurus*), LF 3474 (Figures 2–4). Proposed generic assignment is based on robustness of the skeleton and known presence of this taxon in the assemblage (Young et al., 2012). A new specimen from Painten, partially disarticulated and inferred to represent a burst carcass. The trunk, hip, and hind limbs, as well as most of the tail, are preserved in separate slabs with associated soft tissue. Single vertebrae and sets of dorsal ribs are disarticulated but still closely situated. Post mortem movement resulted in some flipped-over distal phalanges. The skull was

washed away in a turbidite, leaving only an impression (R. Albersdörfer, pers. comm.). Documentation was carried out under visible light and UV (directly compared in Figure 2).

Numerous skin patches are present. Some of them preserve sub-parallel folding (Figures 2, 3C, D, F), some have sets of folds in crisscross arrangement (Figure 3A), or with oblique zones of repeated onset of folds (Figure 3E). The latter indicates either a major zone of movement in life or early diagenetic compression. Patches with possible musculature are present (Figure 3E). A few larger areas are smooth, possibly representing the epidermal surface when tightened (Figures 2, 3C, F). Next to the knee, a single fold is sharp and deep for more than 20 mm (Figure 3D), suggesting small-scale flexibility of the outermost skin layers in life or post-mortem decay. Hinges in the form of crossing fold systems between even skin fields, usually keratinized in modern turtles and crocodylians, are not paralleled by reinforcements or scute rims (Figure 3A, B). Independent of the softly rounded folds, there are layers with long, sharp, sub-parallel fibers (Figure 2). These fibers occur in only one direction per area, transversal (perpendicular) to the long axis of the entire body.

Whereas certain pieces of the fossil cannot be rearranged with certainty, three slabs can be united to show most of the tail (Figure 4). Associated soft tissue gives an impression of relative thickness in life, although diagenetic compaction might have widened the area in question. Assuming that the skin retained a relatively rigid integrity throughout a certain perimeter, the relative height of the tail in life could be estimated as about two thirds of the transverse width of soft tissue in the fossil (a factor of 0.63, where the preserved width is treated as an approximation of half of the original circumference). The tail tapers constantly towards the bending zone of the column, where the soft tissue would have tightly wrapped the vertebrae. The dorsal lobe of the fluke is incomplete but can be estimated from its discrete, darkly colored front edge. The hypocercal ventral lobe is largely complete, showing a narrow front apron and a concave, tapering rear apron, which meet in a rounded, but discrete tip.

Irregularities are present on parts of the preserved skin of the trunk (but apparently not on the tail). Irregular skin structures include subcircular marks approximately 15 mm in diameter and incomplete 'curl' marks approximately 3 cm in diameter (Figures 2, 3C). The surface of these areas is sometimes broken and sometimes

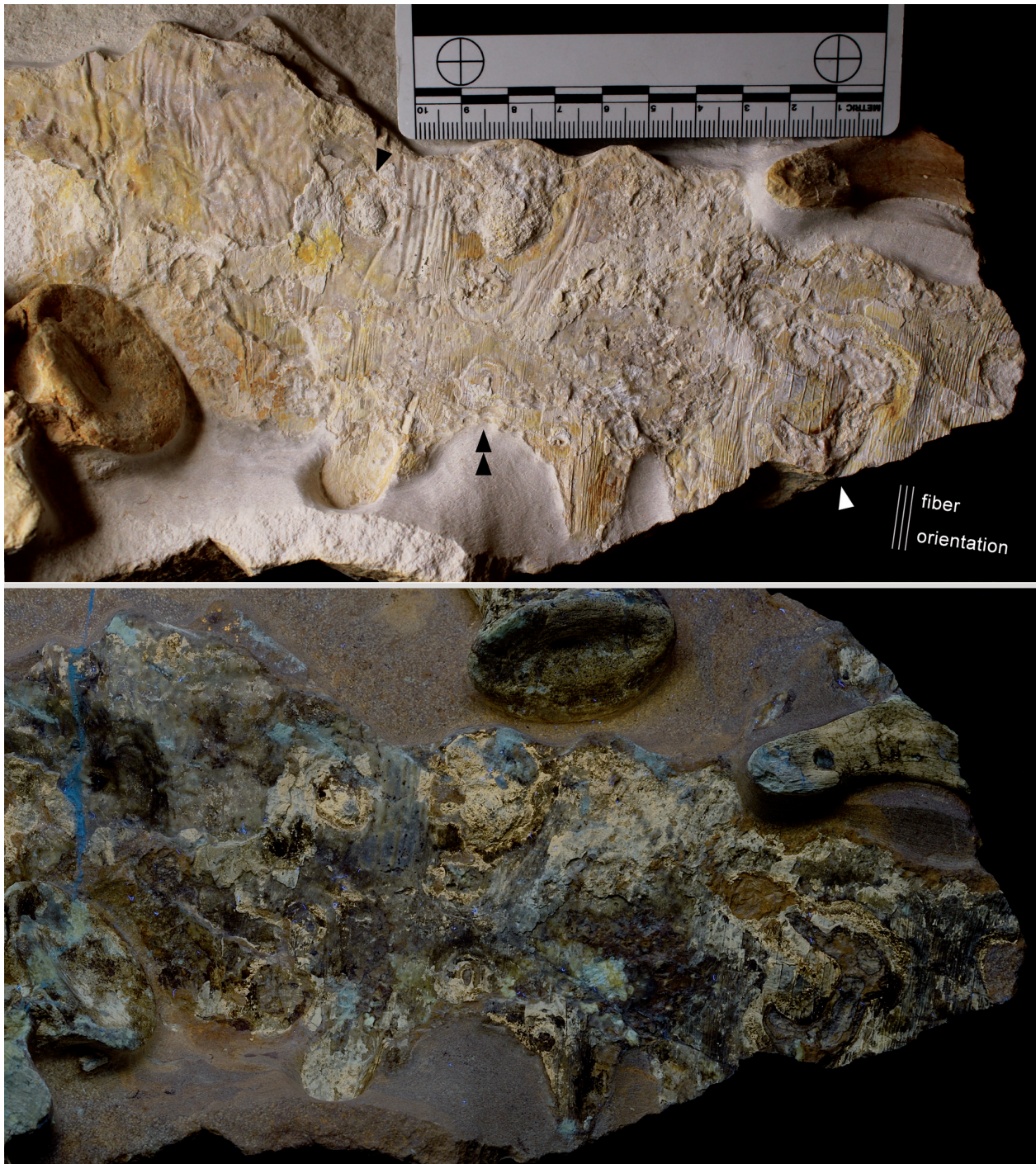


FIGURE 2. Metriorhynchidae indet., LF 3474, patch of trunk integument with displaced vertebrae and rib (uncertain position on body), same section photographed under visible light (above) and UV (below; UV A, B, and C, with orange filter and linear polarizing filter). Skin traits comprise soft-looking folds (left), sharp striae identified as fibers (right portion), and irregular skin scars (arrows pointing at three circular irregularities in the center, and curl-like structure in the right half; see discussion for interpretation). Scale bar for both parts equals 10 cm.

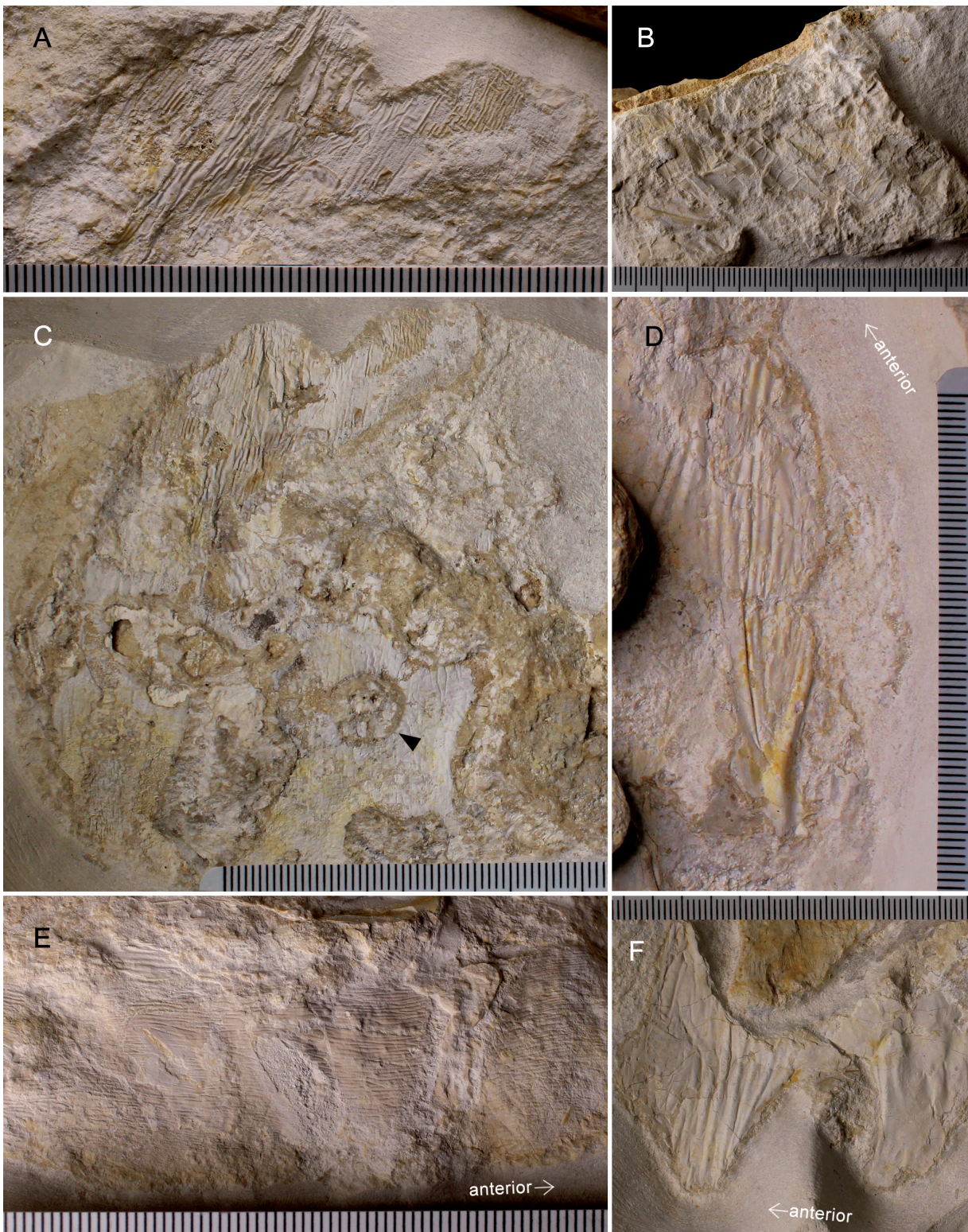


FIGURE 3. Metriorhynchidae indet., LF 3474, scattered patches of skin preservation in visible light, from partially disarticulated trunk. A: Fold systems with dominant and additional orientations. B: Sharp lines forming a net of cracks or distinctly flexed folds; displaced portion with unknown body orientation. C: Displaced patch as in A in a wider section, with at least one circular irregularity in the lower part (arrow). D: Soft folding of skin surface, exposed near to the knee. E: Potential bundles of muscle fibers (horizontal), with oblique crossing fold traces on the right (chest, anterior to pectoral girdle). F: Softly folded integument associated to the ischium (upper middle). All with mm scale.

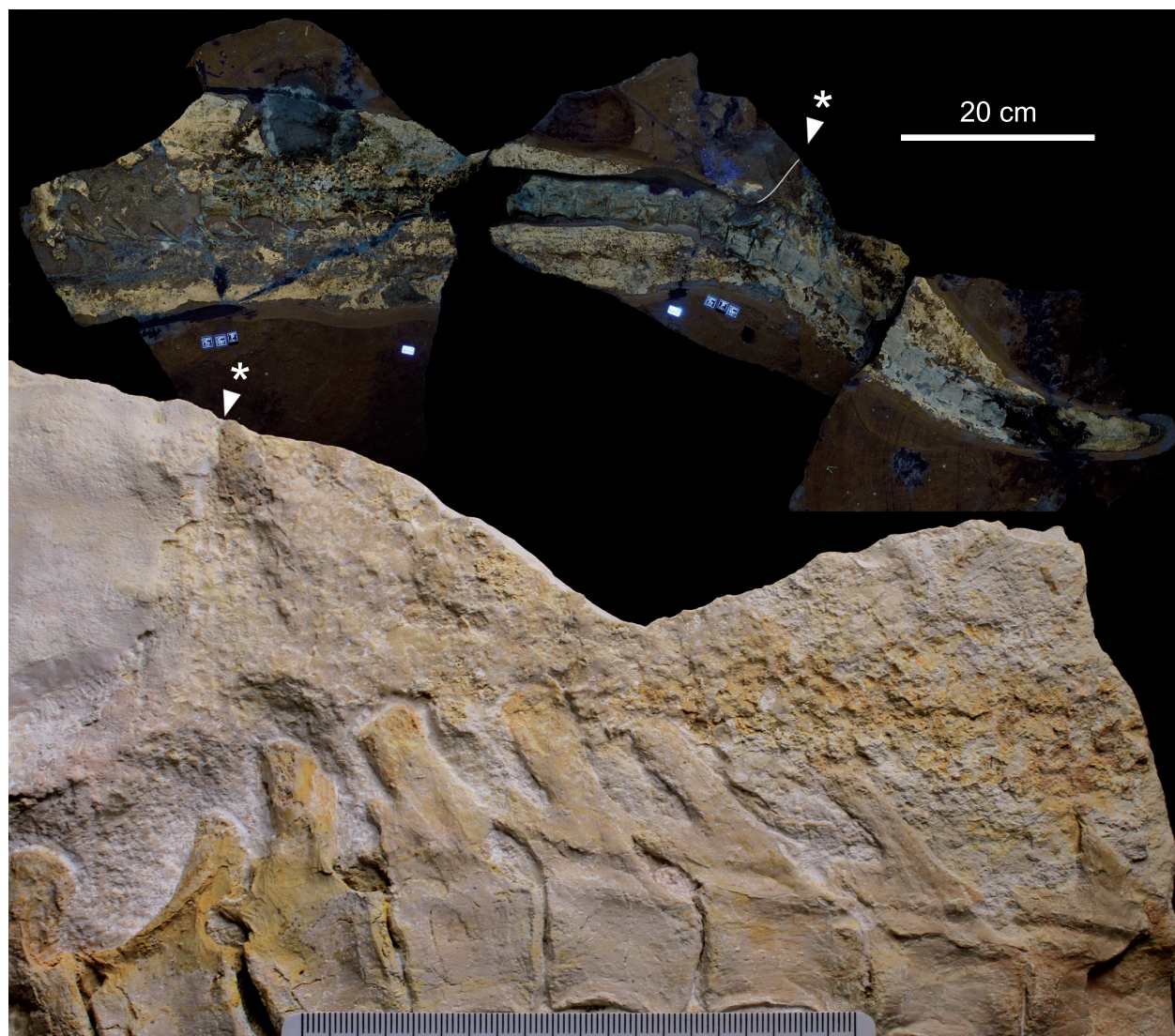


FIGURE 4. Metriorhynchidae indet., LF 3474, distal half of tail, photographed under UV A, B, and C, with orange filter and linear polarizing filter. Skin preservation mostly reacting as yellowish areas. Note the pronounced fluke. The edge of the base of the upper lobe is marked by a white line, as mapped from the below detail under visible light to demonstrate soft tissue distribution (arrow pointing to leading edge). Scale bar equals 20 cm; for inset in mm.

smooth. Sharp, transversal fibers cross the smaller irregularities, but are cut or superimposed by the larger curls. Smooth skin folds bypass or stop at these irregularities, implying that the latter were stiffened, maybe representing keratinized/callused scar tissue.

***Dakosaurus* sp., DMA-JP-2009/001 (Figures 5–10).** Nearly complete and articulated skeleton from Painten, osteology currently under description. Generic attribution based on the short, broad snout, characteristic of this genus within the Painten assemblage (Young et al., 2010). Skin preservation is present on most of the straight portion of the tail, dorsal to the trunk and around the

neck. Additional soft tissue, gut contents, and diagenetic mineralization blurs detail in many regions. Observations were made under visible light and UV (Figure 5).

The skin is preserved in layers (Figures 6A, C, 8), one of which is reddish-brown and extremely brittle, covered by whitish, most likely phosphatized matter. Fine, transversal striation is visible on the best-preserved areas (Figures 5, 6A, C, 7). Coarser, soft folds appear short, while straight folds are long and apparently closely related to the fiber layer. Oblique and crisscross patterns are rare, with one patch observed on the neck and one on the tail (Figure 6B, C). No scutes are observed;

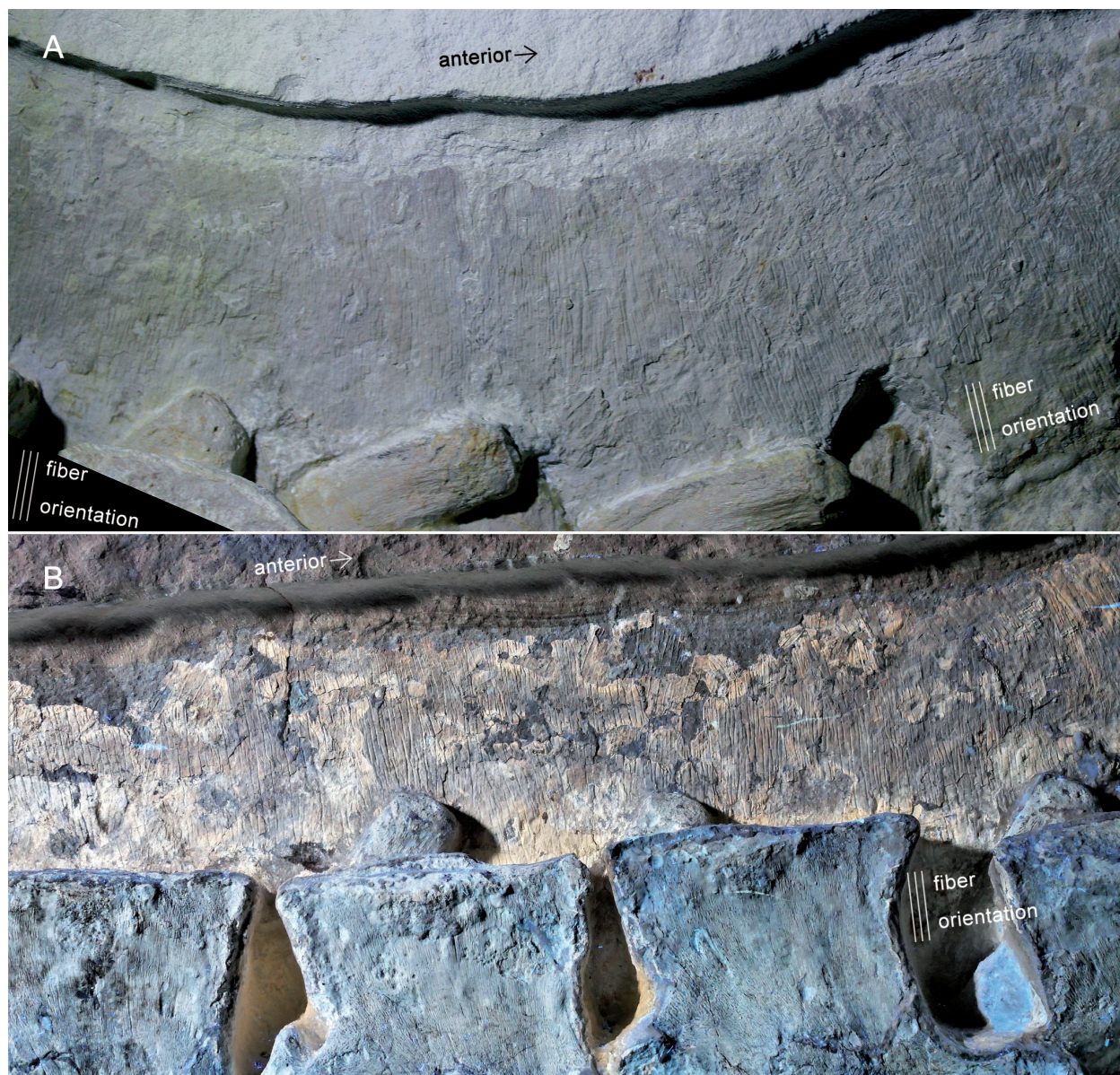


FIGURE 5. *Dakosaurus* sp., DMA-JP-2009/001, skin preservation on dorsal margin of trunk. A: Shoulder area, skin with transversal fibers and associated folding, visible light. Width of frame equals approximately 18.2 cm. B: Lumbar region, similar structures as in A, under UV. Width of frame equals approximately 20.5 cm.

all folds show free terminal points, not enclosed, discrete areas. Based on their positions, these patches likely represent areas of increased movement in life. On the proximal portion of the tail, sharp and discrete folds are observed, less densely parallel than in more anterior portions (Figure 8). The crisscross patch contains additional longitudinal striae (Figure 6C), which are loosely parallel and therefore likely folded, instead of indicating another layer of fibers.

Similar to the trunk of LF 3474, the tail and probably the neck of DMA-JP-2009/001 is associ-

ated with enigmatic skin irregularities in a 'nest-like' concentration (Figures 7-10). The smaller, rounded marks have a diameter of about 1.2 cm, while larger, less circular structures reach up to 3.5 cm, if retaining a discrete outline at all. Fibers and discrete folds partially cross these structures (Figures 8, 10) and soft-looking folds sometimes encircle the marks. The restricted compaction and shapes of these irregularities suggest a hardened structure prior to embedding.

Metriorhynchidae indet., NKMB-P-Watt06/508 (Figures 11–15). Complete and articulated poste-



FIGURE 6. *Dakosaurus* sp., DMA-JP-2009/001, integumentary details of various regions of the body, all under visible light. A: Patch on proximal tail, with widely spaced striation right-angled to vertebral column. Width of frame equals approximately 6.7 cm. B: Crisscross folding in neck region. Width of frame equals approximately 3.7 cm. C: Patch on proximal tail with rare occurrence of longitudinal folding, right-angled to transversal fiber system (section of the middle left of A, under different lighting). Width of frame equals approximately 5.3 cm.

rior half of a medium-sized, robust skeleton from Wattendorf. Soft tissue preservation is scattered over most of the body (Figure 11), but is disrupted by extensive diagenetic alteration. Observations were made under visible light and UV documentation. Although caudal vertebrae are large up to the bending zone, the soft tissue covering tapers constantly and is confluent with the trunk. Softly folded skin is also present on the ventral belly region.

Fine, transversal fluting and fibers similar to the Painten specimens are present (Figures 12, 14, 15). However, NKMB-P-Watt06/508 also preserves many more longitudinal striae. These are poorly defined, only sub-parallel, and are therefore interpreted as folding, not distinct fibers.

Little to nothing can be observed of the webbing of the feet (Figure 13). The scaleless skin type is visible on a patch associated with the right meta-



FIGURE 7. *Dakosaurus* sp., DMA-JP-2009/001, visible light photograph of dorsal region of anterior middle tail, with numerous dark irregularities on the skin. Width of frame equals approximately 12.1 cm.



FIGURE 8. *Dakosaurus* sp., DMA-JP-2009/001, anatomically proximal continuation of Figure 7. On the lower left and right, the dark patches (white arrows) expose a skin layer that is overlain by the bright matter in most of the preserved skin. Width of frame equals approximately 8.2 cm.



FIGURE 9. *Dakosaurus* sp., DMA-JP-2009/001, UV image of tail portion with the highest concentration of skin irregularities (arrows; see previous figures). Width of frame equals approximately 28.0 cm.

tarsal region or the webbing of the left foot. The outline of the leading edge around the first toe of the right foot is narrow and suggests that the terminal phalanx was encased by the outline of the hind flipper.

There are skin irregularities on the tail (Figures 12, 14, 15). These imperfections are only vaguely similar to those observed in the specimens described from Painten. In NKMB-P-Watt06/508, they are smaller, covering a range from 2 to 8 mm in longest extent. Instead of larger, curl-shaped structures, these marks are round-to-oval, mostly flared, sometimes inconspicuously concentric, and questionably hollow. Those irregularities that appear raised are from the exposed right side of

the body, while the flat or rimmed impressions represent the underlying left side. Compared to the surrounding skin folds, the irregularities appear rigid, sometimes smooth and inflexible, indicating greater resilience under the otherwise strong compaction of preserved soft tissue.

***Cricosaurus albersdoerferi*, BMMS-BK 1-2 (Figures 16–18).** Articulated skeleton from Painten. Generic attribution based on the combination of bicarinate teeth without enamel ornamentation, well-developed surangular and angular with anterior tips anterior to the orbit, rounded prefrontals, and external nares separated by the premaxillary septum (Sachs et al., 2021). The specimen includes moderate repair along the margins of



FIGURE 10. *Dakosaurus* sp., DMA-JP-2009/001, close-ups of skin irregularities, courtesy of Yanina Herrera, used with permission. A: Large oval scar, see also Figures 8 and 9. Width of frame equals approximately 4.5 cm. B: Circular scar representing the most abundant type and size of skin irregularities in this specimen, adjacent to blurred, open irregularity, see also Figures 6A, 7, and upper edge of Figure 9. Width of frame equals approximately 4.5 cm. C: Circular scar retaining the texture of uninterrupted skin, see also Figure 7 and 9. Width of frame equals approximately 5.5 cm.

pieces of the slab and the bones that were split between these pieces. Skin preservation is interrupted by cracks in the specimen. However, there is still a wide distribution of skin preserved which was observed under visible light and UV.

The largest skin patch, in the throat area (Figure 16), is smooth with minimal folding. Dorsal to the neck, a string of patches clearly indicates sub-transversal to diagonally forward-tilted striae made up of sharp grooves (Figure 18A, C, D). Some of these structures are curved, possibly resulting from

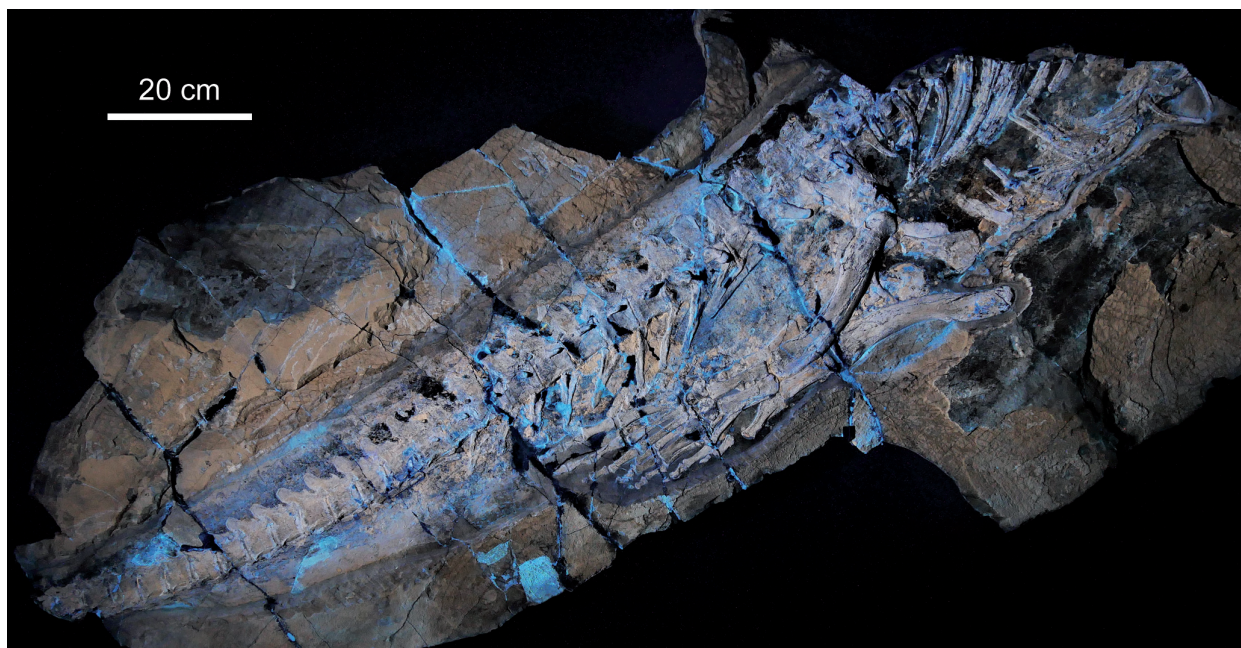


FIGURE 11. Metriorhynchidae indet., NKMB-P-Watt06/508, specimen under UV, with soft tissue preservation surrounding most of the skeleton. A separated piece containing the distal tail is not depicted here, since no soft tissue is exposed. Scale bar equals 20 cm.

overlap of both sides of the body subsequent to final compressive flaring of the soft tissue. Longitudinal sets of coarser fluting indicate musculature (Figures 17, 18A). Under a certain angle of light, a single dorsal patch reveals crossing sets of parallel folds, producing an acute rhomboidal pattern (Figure 18D).

Between some of the posterior trunk ribs, a single skin patch with a cell-like, sub-square relief pattern is present (Figure 18B). We tentatively interpret this structure as shrinkage or compaction under lateral narrowing, reflecting a pattern of crossing folds, rather than sharply outlined scutes. A blurred set of diagonal striae might be associated with the femur (Figure 18E). Although this striation texture is somewhat coarser, it is consistent with the remaining integument. A strip of soft tissue bearing squamous-appearing structures close to the femur is very diffuse, probably the result of overlaid soft tissues from the trunk and nodule-like diagenetic mineralization rather than actual scales.

One of the associated patches of skin on the ventral tail is very smooth (Figure 18F). Possibly, this type of preservation is more representative of the normal surface of the body, if not representing adipocere. The distal tip of a hemapophysis served as a pressure center for radial folds during compaction.

Tiny skin irregularities are best preserved on the chest (Figure 17). Blurred, round, crater-like structures of about 2 mm in diameter appear as a random 'nest.' They show no observable effects on the texture of the surrounding integument. A larger scar is present on the tail (Figure 18F).

***Cricosaurus bambergensis*, NKMB-P-Watt14/274 (Figures 19–21).** Largely complete and articulated skeleton from Wattendorf. Referral based on Sachs et al. (2019). Skin was preserved as reddish, delicate layers, occurring in fragmented patches from the shoulder region to the proximal tail. Observations were made under visible light, also checked under UV.

Fine, sub-transversal striation was observed anterodorsal and anteroventral to the shoulder (Figure 19). This striation is combined with folding that is apparently associated with certain bones, indicating a long-lasting flexible behavior during compaction.

Brownish, more brittle patches with criss-crossed fluting next to some gastralia may indicate uneven diagenesis, deserving closer investigation in the future. The current study also revealed crustaceans as gut contents (Figure 20), preserved in a similar manner.

Dorsal to the lumbar region, more oblique striation occurs in a large skin patch. Longitudinal ridges are branching and suggest some shrinkage

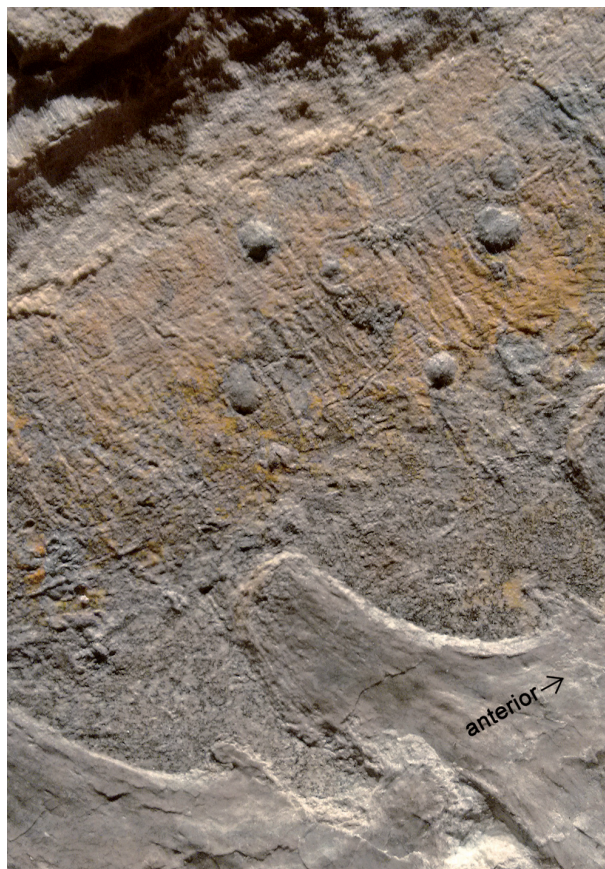


FIGURE 12. Metriorhynchidae indet., NKMB-P-Watt06/508, dorsal region of middle tail, with longitudinal and transversal skin folding, along with a nest of irregularities (grey knobs). Width of frame equals approximately 7.6 cm.

or flaring effects (Figure 20). This pattern is also interlinked with transverse processes of the neural arches, which implies that a considerable amount of flesh was present during compaction.

The area of the proximal part of the tail, anterior to the gap where the distal tail is dislocated (Sachs et al., 2019), retains the sub-transversal, fibrous striation of the anterior trunk, with some diagonal and slightly sigmoidal orientation (Figure 21). In the ventral portion, crossing layers can be observed, with a backward-tilted set of wider striae that preserve musculature. The outline of soft tissue preservation gives an impression of the amount of flesh surrounding the hemapophyses, indicating the presence of a typically powerful crocodyliform tail.

Cf. *Rhacheosaurus gracilis*, LF 2426 (Figure 22). Largely complete and articulated juvenile (tail is missing) from Langenthalheim. Referral made on the basis of the short temporal area and uncarnated teeth (Young and Andrade, 2009; Parrilla-Bel

et al., 2013). Patchy and fragmented skin remains are preserved from what is potentially a throat pouch to the tail. Observation under several UV wavelengths revealed no discrete scutes or osteoderms.

Cf. *Dakosaurus*, DMA-JP-2018/002 (not illustrated). A very young juvenile from Painten, complete skeleton currently under description. Generic attribution based on the short snout, unique to this genus among Painten metriorhynchids; although possibly related to allometry, coeval genera tend to show proportionally longer snouts even as juveniles (see cf. *Rhacheosaurus* specimen above). Its postcranial portion is completely surrounded by a delicate shadow of soft tissue. Observations under visible light and UV revealed no scales, implying that the metriorhynchid skin type experienced no major ontogenetic changes.

Metriorhynchid Integument: Summary

Our modern picture of metriorhynchid aquatic adaptations is largely the same as that determined by Fraas (1901, 1902), including a smooth skin surface and hypocercal tail fluke. No osteoderms were observed in any of the specimens. The metriorhynchid skin type was rather uniform, soft and scaleless, with internally fibrous tissue. It was tight and streamlined, somewhat like in dolphins. Repeated patterns of folding reflect zones of increased movement as well as common taphonomical effects. Dermal skull bones of the investigated taxa lack the osteoderm-like groove-and-ridge sculpturing (Figures 16, 22) that is commonly found in anamniotes (Clack et al., 2016) and other aquatic crocodyliforms (Wu et al., 2001; Johnson et al., 2020b). This implies that skin modification in metriorhynchids includes the cranial cover.

This skin morphology is in accordance with an impressive historical specimen of *Rhacheosaurus gracilis* (NHMUK R.3948; Figure 23) that contains a blurred “skin shadow” with informative outlines around the tail (the only described metriorhynchid that preserves an upper fluke lobe; Young et al., 2010). From this slab, Ammon (1906, figure 9) described a whitish, striated, phosphorite mass, which he interpreted as fossilized musculature (Reis, 1893). This is very similar to some portions of the Painten *Cricosaurus* BMMS-BK 1-2. (Figures 17, 18A).

Within the layered skin, only one set of fibers can be identified so far, with a clear sub-transversal orientation. Terminal phalanges in the foot of Metriorhynchidae are barely curved and lack pronounced tubercles, indicating they would be of

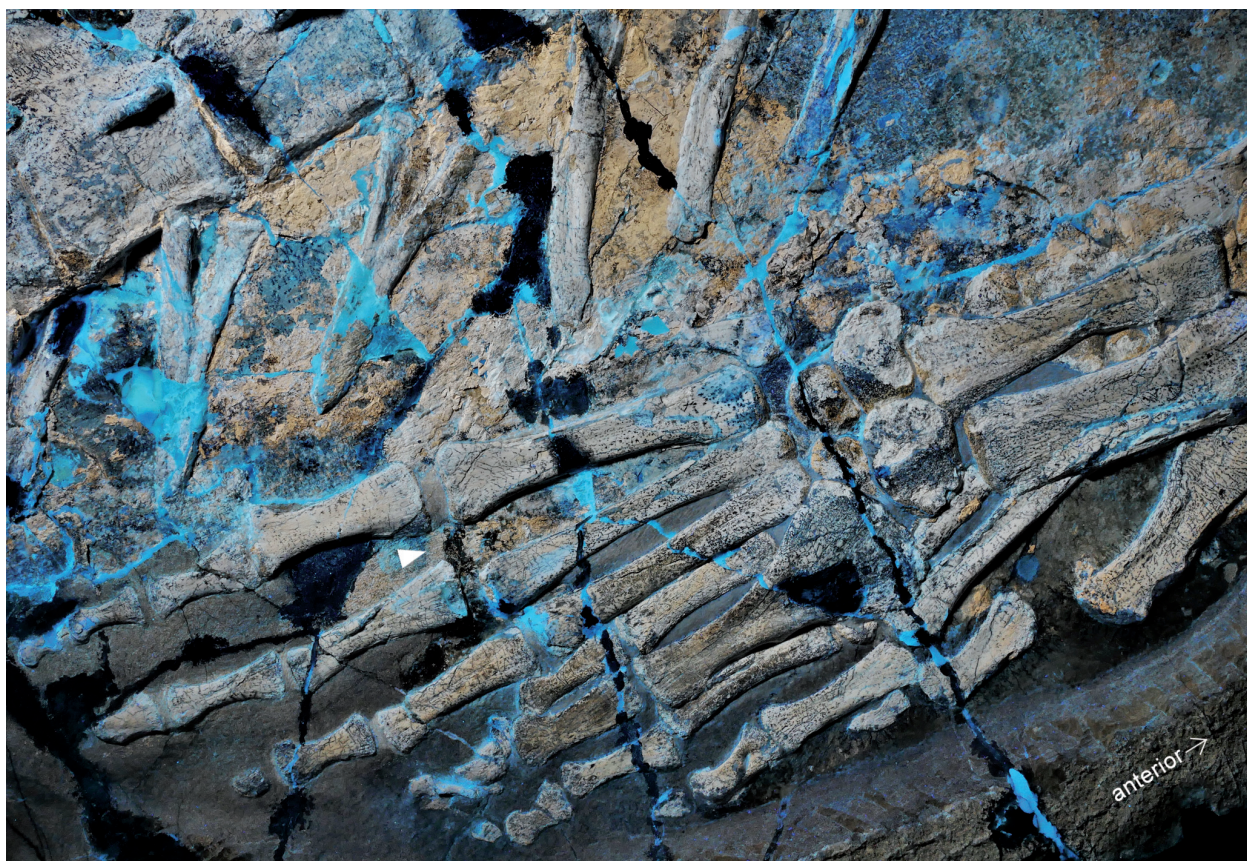


FIGURE 13. Metriorhynchidae indet., NKMB-P-Watt06/508, feet of both sides under UV. The caudal soft tissue ends slightly ventral to the hemapophyses. Minor patches of yellowish skin indication are uncertainly belonging to the webbing or metatarsal area of one of the feet (arrow). Width of frame equals approximately 35.5 cm.

minimal use in scratching. Some are remarkably shortened and reduced to tiny discs. Only a few longer terminal phalanges suggest the vague possibility for the formation of larger rigid skin structures, maybe analogous to the claw-bearing Trionychidae (softshell turtles), but unlike *Dermochelys* (leatherback sea turtle).

Additional spikes on the anterior edge of vertebral spines in the mid-caudals of many metriorhynchids seem to contribute to tail mobility. In the same region, some teleosauroids show elongated spines (pers. obs. of *Aeolodon*, JME unnumbered), possibly to support a crest immediately posterior to the dorsal caudal osteoderm shield. However, this region did not support a dorsal fin or seam in any thalattosuchian specimen, as confirmed by the new observations. Instead, the tail fluke is a constant structure (Figure 24). Elongated, forward-tilted spines in the bending zone of the caudal column are believed to attach with connective tissue fibers, similar to the anatomy of mosasaurs (Lindgren et al., 2010, figure 6 C). A complete fluke is present on an unpublished “Solnhofen” metriorhynchid

housed at the Wyoming Dinosaur Center (Cowan, 2010; pers. obs., HT; albeit with unknown degree of restoration). Its imperfect tail bend suggests that this is an immature individual.

Metriorhynchids lack osteoderm armor, which might also be relevant for habitat selection. Although metriorhynchid gastralia are more robust than those of ichthyosaurs, they do not differ much from the gastralia of extant crocodylians that bear ventral osteoderms. Ventral armor is present in teleosauroid thalattosuchians, turtles, and sauropterygians due to specialized gastralia and ventral girdle elements. Compared to these cases, Metriorhynchidae and Mosasauridae represent an opposing, ventrally less-protected pelagic bauplan.

Although not belonging to the integument in a narrower sense, scleral rings are ectoderm derivatives, formed via intramembranous ossification (Franz-Odenaal, 2005, 2008). Thalattosuchia and certain marine Mesosuchia are the only crocodylians that possessed scleral rings (Wu et al., 2001; Pol and Gasparini, 2009), representing a convergent feature comparable to that of ichthyosaurs,

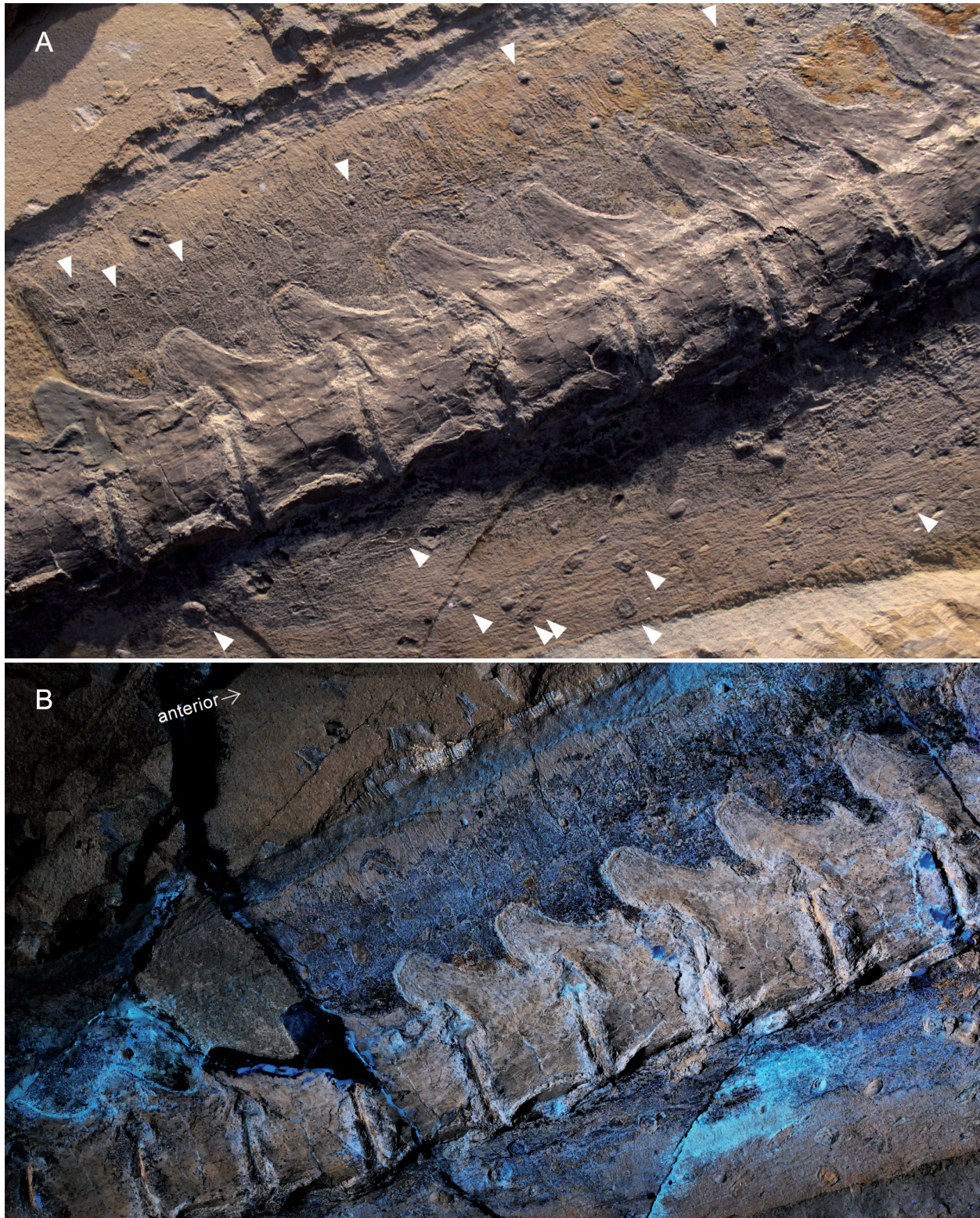


FIGURE 14. Metriorhynchidae indet., NKMB-P-Watt06/508, middle tail with soft tissue preservation. A: Visible light image with structural details of the skin, mostly folding, and knob-like irregularities (some indicated by arrows). Width of frame equals approximately 30.6 cm. B: UV image with darker bluish signals probably reflecting varnish. Width of frame equals approximately 33.9 cm.

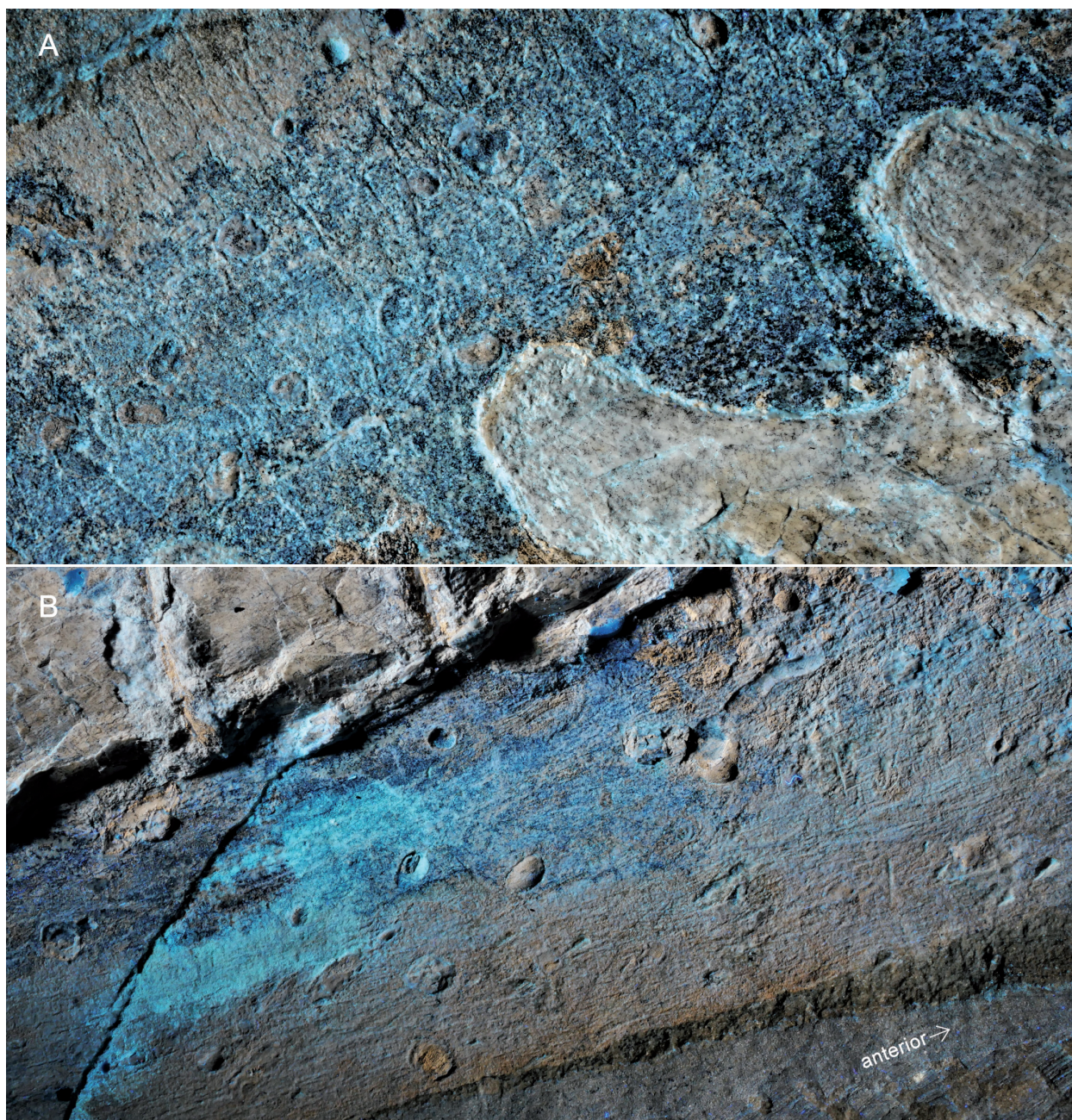


FIGURE 15. Metriorhynchidae indet., NKMB-P-Watt06/508, UV close-ups of skin surrounding the middle tail. A: Dorsal region with numerous knob-like irregularities. Width of frame equals approximately 10.1 cm. B: Ventral region with longitudinal folding (by skin substance preservation or imprints), and further irregularities. Width of frame equals approximately 18.0 cm.

and may represent an example of deep homology within Pseudosuchia (Nesbitt et al., 2013).

Observations from Non-metriorhynchid Thalattosuchia

Two specimens preserving considerable integumentary anatomical detail are known in the Teleosauroidea, the sister-group of the metriorhyn-

choids. SMNS 10985 (Figure 25) is a fragmentary skeleton historically referred to “*Steneosaurus*” *bollensis* from the Lower Jurassic locality of Frittlingen, Germany (for revised taxonomy see Johnson et al., 2020a; “*S.*” *bollensis* is currently placed in the genus *Macrospodylus*). This specimen was previously mentioned by Westphal (1962, figure 4) and Godefroit (1994, figure 28). Skin is preserved



FIGURE 16. *Cricosaurus albersdoerferi*, BMMS-BK 1-2, soft tissue patch under UV, with yellowish areas indicating skin preservation. The posterior skull can be seen on the left, the scapulocoracoid on the lower right. Width of frame equals approximately 23.0 cm.

along the rear apron of the femur down to the metatarsus. The soft tissue cover was obviously tight and narrow around the ankle, whereas external to the fourth metatarsal a narrow web can be assumed. The bent toes with broad terminal phalanges suggest that functional, somewhat 'hoof-like' claws resembling those of other crocodyli-forms (Brochu, 2013) were projecting over a potential paddle. Fine skin folding posterior to the knee indicates frequent movement in life. Strong compaction typical of black shales likely exaggerated the broadness of the preserved skin patch. That this broadness is partially a diagenetic effect is evidenced by the fact that the scute patterns on both sides are flattened and the impression of the underlying side can be traced through the exposed

side. The lower limb has a less pronounced soft tissue thickness. If compaction of the body was strictly vertical, this distribution would indicate strong musculature for femoral retraction, used in swimming, walking, or possibly nesting. The surface structure (Figure 26) consists of rectangular scutes with discrete and straight hinges, arranged primarily in chessboard (square) orientation, with locally sheared, rhomboid outlines, or an initial offset of neighboring rows. The quality of the integument is astonishingly similar to that of extant crocodiles, underlining a considerable continuity throughout crocodyli-form evolution. The only difference between the morphology of SMNS 10985 and extant representatives is that the latter feature a greater variety of scute sizes, including larger



FIGURE 17. *Cricosaurus albersdoerferi*, BMMS-BK 1-2, soft tissue patch on the ventral chest, posterior to pectoral girdle. On the middle left (below terminus of rib), horizontal striation reflects musculature. The covering layer exhibits soft skin folds. Circular irregularities (some marked by arrows) are interpreted in the text. Width of frame equals approximately 6.5 cm.

scutes, particularly on the outer side (in SMNS 10985 it is blurred by the overlaying internal side), which are partially associated with osteoderms. Detailed photographs did not indicate the regular dotting patterns of sensory pits, as would be expected from comparison with extant crocodylids.

Another teleosauroid taxon preserving skin, but from the Late Jurassic plattenkalk of the Solnhofen Archipelago, is *Aeolodon priscus* (Figure 27; for validity of *Aeolodon* see Young and Andrade, 2009; Ösi et al., 2018). In this taxon, as indicated by an unnumbered JME specimen, stretched, rhomboid-to-random polygonal shaped scales cover the webbed foot surface. Due to some restoration to the terminal phalanges, no clear information can be determined about the inclusion of claws in the paddle. Further observations include large, sub-rectangular scutes on the tail, with a longitudinal row of large dorsal scutes that form a fin-like edge, similar to that found in modern crocodylians. The middle portion of the tail is narrowly wrapped by soft tissue. The hind limbs show rhomboid scutes, consistent with SMNS 10985.

From our current knowledge, no semi-aquatic crocodyliform has secondarily achieved a smooth

and naked skin type (unlike certain turtles, hippopotamids, or modern amphibians, which contrast with the ancestral semi-aquatic tetrapod condition; Witzmann, 2011). Scutes seem necessary for protection during onshore basking, but such behavior is questionable in teleosauroids. Their scutes may have been retained as a constraint for osteoderm formation (see below). This could explain why an open-sea habitat, as inferred for the teleosauroids *Aeolodon* and *Machimosaurus* (Johnson et al., 2020b), does not automatically result in the evolution of smooth skin. In contrast, metriorhynchid skin was probably at risk from persistent exposure to sunlight, underlining that the shift to a cetacean level of integumentary adaptation was not possible until after completion of the transition to a pelagic lifestyle. This assumption is in accordance with the discovery that the metriorhynchoid tail fluke evolved prior to the loss of osteoderms (Ösi et al., 2018).

Although teleosauroids show a number of initial to derived marine adaptations, for example reduced front limbs and loss of air-borne hearing (Montefeltro et al., 2016; Schwab et al., 2020; Johnson et al., 2020b, figure 64), their integument

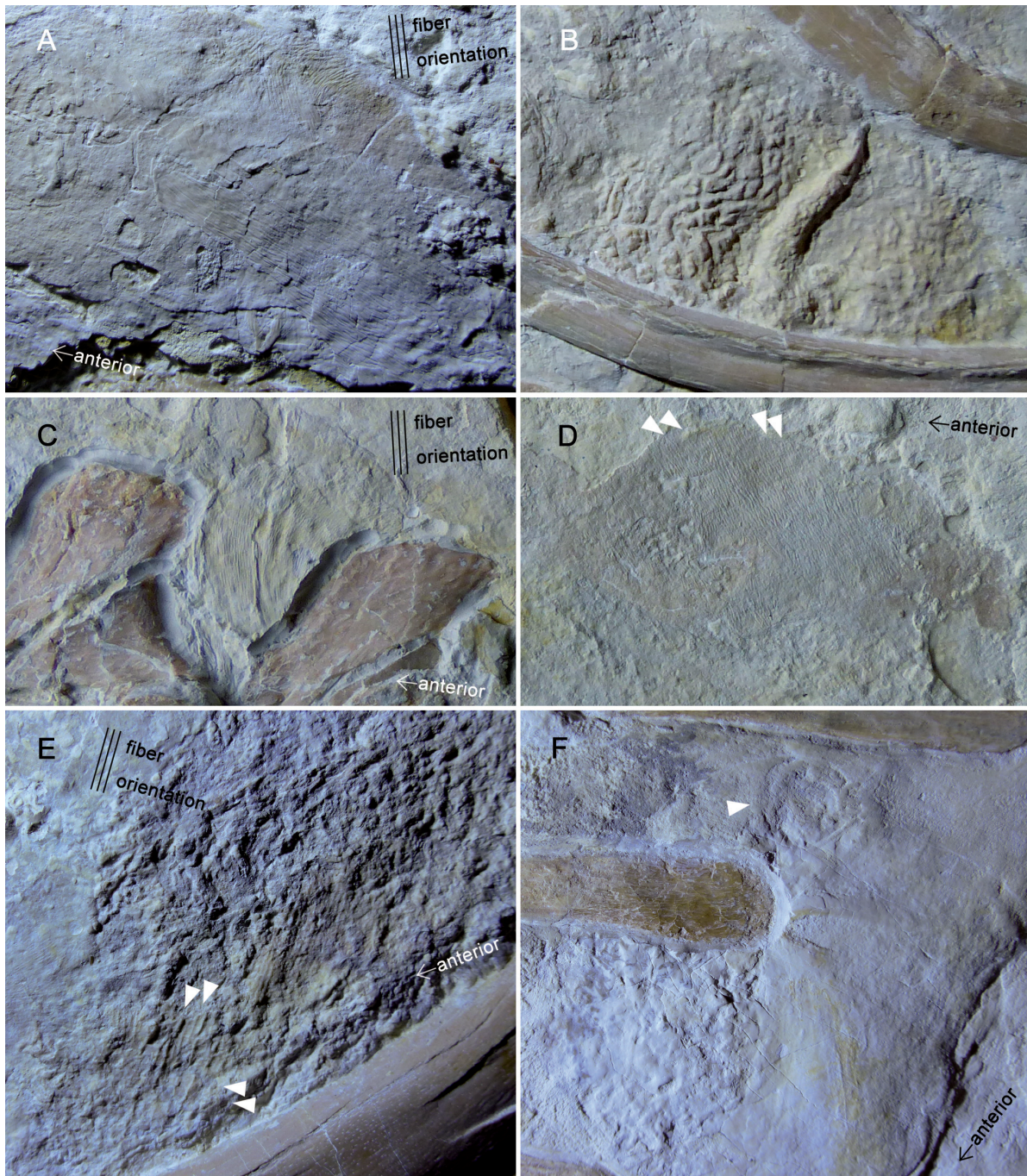


FIGURE 18. *Cricosaurus albersdoerferi*, BMMS-BK 1-2, details of skin preservation. A: Anterior part of dorsal edge of neck patch (Figure 16). From the center to the lower right longitudinal muscle fascia are exposed. In the upper part, sets of folds and possibly fibers overlap. Width of frame equals approximately 3.1 cm. B: Indistinct fragmentation of skin patch in posterior trunk, interpreted as potential taphonomic shrinking. Width of frame equals approximately 3.5 cm. C: Dorsal edge of neck patch (Figure 16) with curved striation (arrows indicate acute rhomboidal directions). Width of frame equals approximately 3.7 cm. D: Position little more posterior as in C. Additional to the dominant orientation of skin surface striation, another, acute-angled set crosses and is visible under a certain angle of light. Width of frame equals approximately 3.2 cm. E: Skin details associated to femur (lower right), with oblique striation and rhomboidal, superficially scale-like compaction pattern (lower left, indicated by arrows). Width of frame equals approximately 4.2 cm. F: Anterior hemapophysis with associated skin folds that radially spread from the bone terminus as an effect of load during compaction. A circular skin irregularity is seen above the bone (arrow). Width of frame equals approximately 5.4 cm.

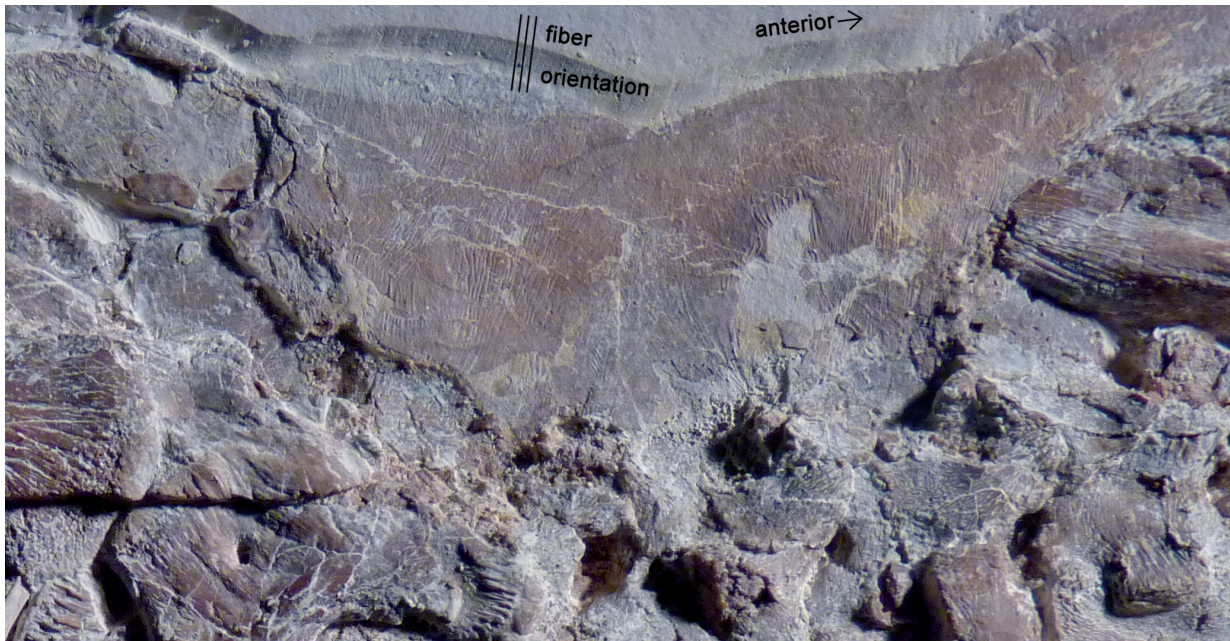


FIGURE 19. *Cricosaurus bambergensis*, NKMB-P-Watt14/274, skin preservation in dorsal neck, illustrating transversal fibers. Width of frame equals approximately 5.5 cm.



FIGURE 20. *Cricosaurus bambergensis*, NKMB-P-Watt14/274, body trunk portion with folded skin (upper red margin) embedding dorsal column. In the lower right corner, gut contents preserved a crustacean (arrow marking hinge between carapace and abdomen). Width of frame equals approximately 9 cm.



FIGURE 21. *Cricosaurus bambergensis*, NKMB-P-Watt14/274, proximal tail portion, column surrounded by skin patches with folds and fibers. The arrow points to a patch tentatively identified as musculature. Width of frame equals approximately 12 cm.

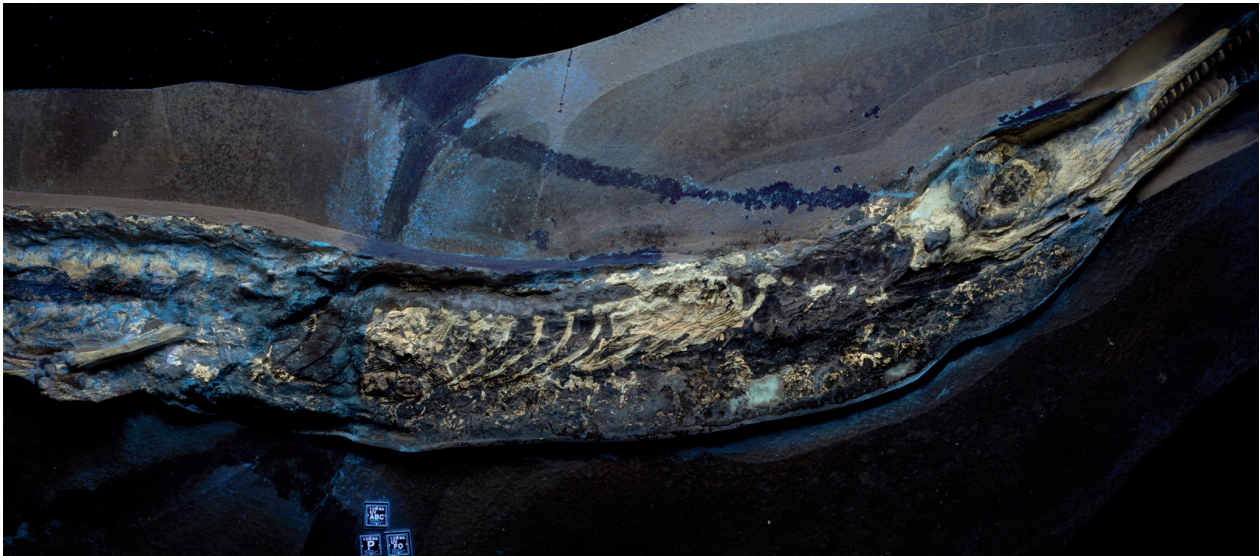


FIGURE 22. Cf. *Rhacheosaurus gracilis*, LF 2426, photographed under UV A, B, and C, with orange filter and linear polarizing filter. Yellowish areas represent skin preservation as well as bone. Cube length 1 cm; total width for frame equaling 57.8 cm.



FIGURE 23. *Rhacheosaurus gracilis*, NHMUK R.3948. A: Skeleton with soft tissue outlines. B: Detail of tail fluke. The outline of the upper lobe is blurred and not clearly indicated by darker color. Courtesy of Yanina Herrera, used with permission. Scale bar in cm.

appears to have been very much like modern crocodylians, including the texture of their osteoderms, some dermal skull textures, and soft tissue architecture. Thalattosuchians and the lineage leading to modern crocodylians had diverged by the early Jurassic at the latest. Based on this phylogenetic

bracketing, we can determine that the shared integumentary features of these groups would have applied to the majority of Crocodyliformes. Although the precise integumentary morphology of teleosauroids should not necessarily be used as a general plesiomorphic model for all Crocodyli-

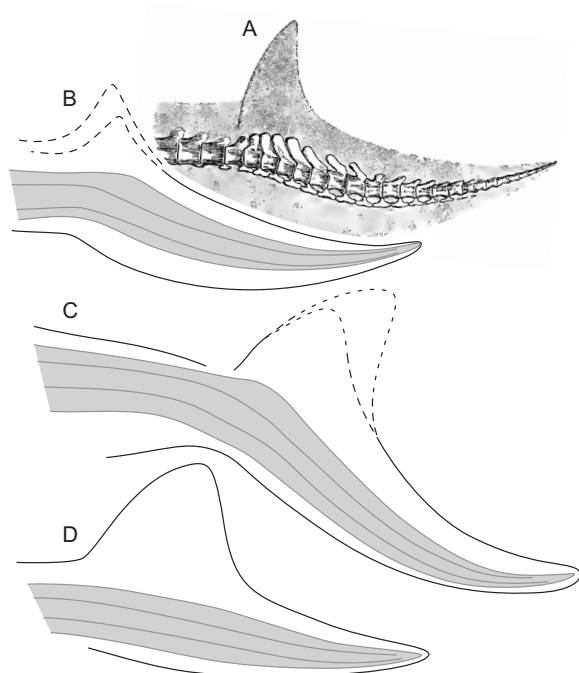


FIGURE 24. Schematic drawings of metriorhynchid tail flukes, distal caudal columns and integumentary contours. A: *Rhacheosaurus* NHMUK R.3948, historical reconstruction (Andrews, 1913, figure A). B: Same specimen, outline from photograph (Figure 23B), with potential outlines of the upper lobe evaluated from textures on the fossil in visible light. C: Metriorhynchidae indet., LF 3474 (new specimen, Figure 4), with possible outlines for the upper lobe inferred from preserved edges. D: Proposed outline in ontogenetic stages with less pronounced tail bending (generalized sketch comparable to unpublished specimen, see text for further information). All drawn to similar size.

formes, it is a useful example of how the ancestral crocodyliform skin type can react under semi-aquatic selection (applicable to e.g., Stomatosuchidae, Goniopholididae). A broader review of the integument across crocodile-line archosaurs would be useful to tease apart distinctions between semi-aquatic lineages and highly terrestrial lineages that also exhibit square osteoderm armor, like *Aetosauria* (Heckert et al., 2010) or *Simosuchus* (Hill, 2010).

DISCUSSION

Comparisons with Other Marine Reptiles

Smooth skin is known to occur in some other saurian clades. The arguably most highly specialized marine reptiles are the Ichthyosauria, which may have originated shortly after the Permian-Triassic transition (Huang et al., 2019). Skin impres-



FIGURE 25. Teleosauroid SMNS 10985 (formerly assigned to *Steneosaurus*), right hind leg with soft tissue preservation. Courtesy of Erin Maxwell, used with permission. Scale bar equals 10 cm.

sions and macrostructures of derived ichthyosaurs include large, hypocercal tail flukes (Bardet and Fernandez, 2000). Additionally, authentic dorsal fins and flippers of Lower Jurassic Holzmaden specimens show a low-angled radial striation. According to Lingham-Soliar (1999, 2001), ichthyosaur skin was composed of a number of sets of crisscrossed fibers of different sizes, and ranged in texture from rough interior to finer exterior layers.

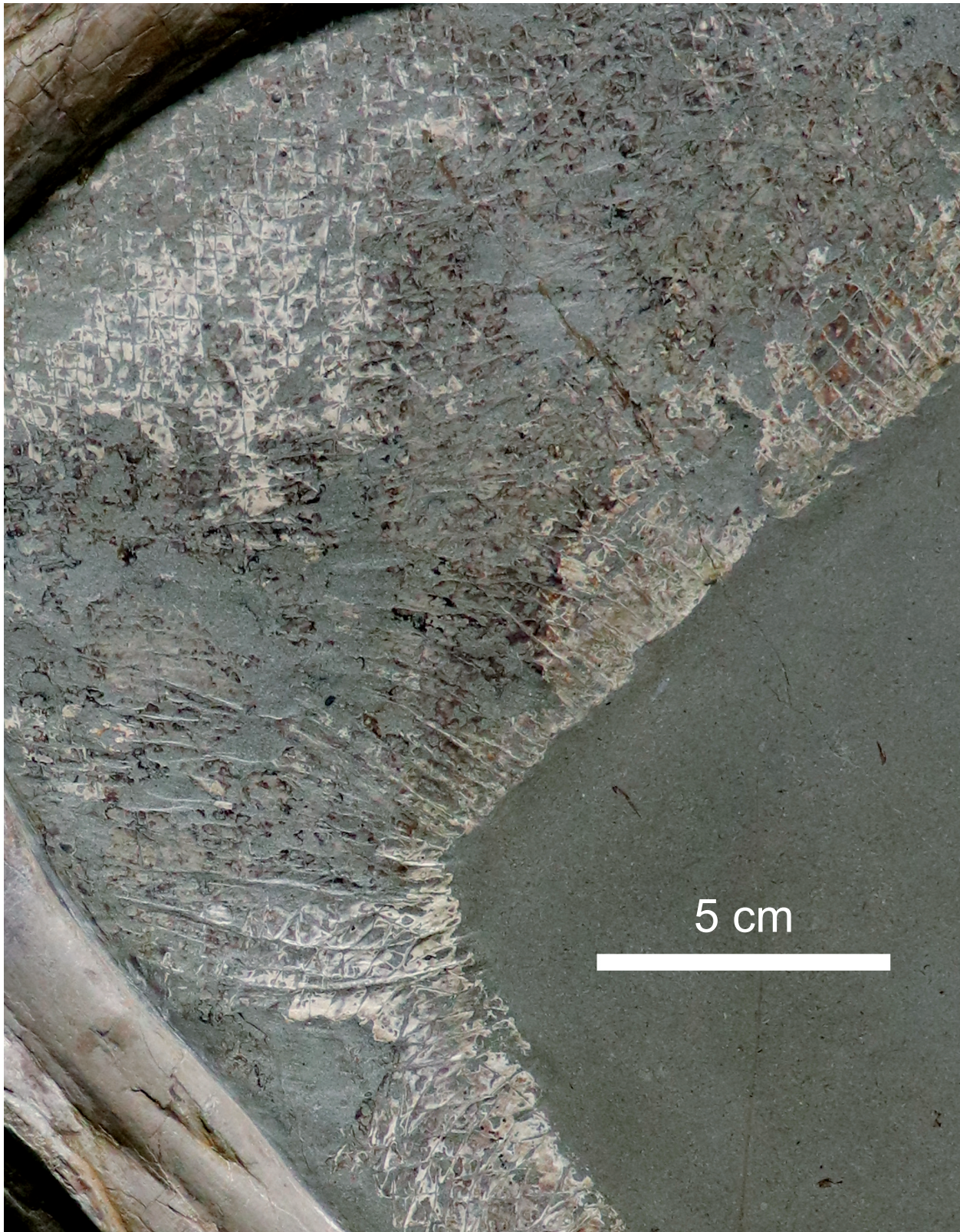


FIGURE 26. Teleosauroid SMNS 10985 (formerly assigned to *Steneosaurus*), detail of integument on rear side of hind leg, illustrating flexed joints and square to rhomboidal shaped scutes. Courtesy of Erin Maxwell, used with permission. Width of frame equals 16 cm.



FIGURE 27. *Aeolodon priscus*, JME (uncatalogued, firmly installed in the permanent exhibition). A: Distal tail portion preserving enlarged rhomboidal scutes on dorsal edge (arrows mark dorsal points of transversal hinges); width of frame equals 15 cm. B: Skin preservation around the hollow of the knee (femur visible in left lower corner), with patches of distinct rhomboidal scutes (arrows mark example of hinge orientation); width of frame equals 23.5 cm. C: Webbing of foot with stretched polygonal scutes; width of frame equals 15.8 cm.

This construction is interpreted as strong and flexible, mainly to support persistent hydrodynamic shaping and high-speed control (Lingham-Soliar and Plodowski, 2007). Tiny, polygonal scales have been documented on an ichthyosaur flipper (Fraas, 1888), though these could be artifacts of diagenetic shrinkage. Broili (1942) provided more details on these structures, which seem to be restricted to the leading edges of flippers and fins.

The next-appearing marine reptile radiation that evolved a smooth skin surface includes the Plesiosauria. One of the earliest integumentary structures recognized in this clade was a fluke-like, asymmetrical tail fin in *Seeleyosaurus* (Dames, 1895). Such structures might have been rather common among plesiosaurs, as reflected by a “pygostyle-like” tail tip in an elasmosaurid (Kubo et al., 2012). The skin preservation in *Seeleyosaurus* features a delicate, scaleless integument with interior striation similar to that of ichthyosaurs (S. Sachs, personal commun., 2020; including close-up photographs). Soft tissue around the anterior paddle of *Hydrorion* (= ?*Microcleidus*) was described by Huene (1923, plate 1, figure 1). The rear apron of the flipper has either extremely fine scales or is scaleless (according to photographs, courtesy of S. Sachs, personal commun., 2020). The best published material belongs to an indeterminate plesiosaur (Vincent et al., 2017) with crisscrossed fibers under various angles, a tail with transversal skin striation, and a hind paddle interpreted to contain rows of delicate, non-overlapping scales with fine epidermal ornamentation. The asymmetrical outline of the fluke of *Seeleyosaurus* suggests a vertical orientation in life. Unlike the fluke of metriorhynchids or ichthyosaurs, its small size implies a minor role for propelling (Sennikov [2019] argued for a horizontal fluke with vertical undulation, which contrasts with the results of Carpenter et al. [2010]). The general convergence of vertical flukes in marine reptiles can be explained by a predominantly horizontal undulation of the vertebral column shared with their terrestrial ancestors, unlike marine mammals with horizontal flukes (Cetacea, Sirenia), whose ancestors performed dorsoventral flexion. Given horizontal undulation in the ancestors of metriorhynchids, we predict the prevalent plane of motion for the fluke in this group to be dorsal/frontal.

Frey et al. (2017) reported a new plesiosaurian specimen (holotype of *Mauriciosaurus fernandezi*) with extensive soft tissue preservation including a very broad horizontal soft tissue apron around the proximal tail. Further observations

included: soft tissue aprons also occurring at the rear edge of the flippers, which may not have been fully covered with scales; skin surface characterized by crossed lines of small scales (square coordination); trunk integument exhibiting longitudinal rows of fine, transversely rectangular units, interpreted as scales; hip region including some larger scales; and adipocere deposition. Altogether, plesiosaur skin seems less perfectly hydrodynamically modified than that of ichthyosaurs, but with a clear reduction of macrorelief and surface texture compared to terrestrial reptiles.

Little can be said about the integument of plesiosaur outgroups. Early Eosauropterygia have not been discovered with well-preserved skin (Wachtler, 2018, p. 55). A reinforced integument in these aquatic reptiles has been inferred from taphonomic indicators, however (Renesto, 2006; Bearmore and Furrer, 2017). Placodontia reflect a generally scaly condition, as osteoderm patterns are usually reflected by scutes (Scheyer et al., 2012; Maderison [1972] noted the extant *Dermochelys* as an exception; there is also a general reduction of scutes in many Trionychidae). Considerable ornamentation in placodont osteoderms confirms this assumption, along with direct evidence from impressions of scute rims like those of turtles (Westphal, 1975). It is possible that a highly modified skin type did not occur before the sauropterygian shift to pelagic forms during the Triassic-Jurassic transition (Neenan et al., 2017). As osteoderms occur in early sauropterygians (Scheyer et al., 2017) and similar armor elements are found in early ichthyosauromorphs (Carroll and Dong, 1991), this could represent a common pattern, whether due to shared ancestry (if these clades are sister-taxa; e.g., Chen et al., 2014) or similar initial adaptations to semi-aquatic life.

The similarities of metriorhynchid, plesiosaurian, and ichthyosaurian transformations might be more than just superficial convergence (Kelley and Pyenson, 2015). Possibly, there are deep-homologous genetic patterns resulting in these convergent evolutionary modifications, as paralleled by marine mammals (Zhou et al., 2015). Unlike these other Mesozoic marine reptile radiations, the Late Cretaceous Mosasauridae (Squamata) retained scaly skin. Mosasaurs exhibit varying patterns of flat square, rhomboidal, or hexagonal coordination of overlapping and possibly osteoderm-bearing scales that show sculpture for hydrodynamic optimization (Williston, 1914; Lindgren et al., 2009, 2010). Mosasaur dermal fibers show a crisscross set of orientations, with a dominant longitudinal set

and others that parallel the diagonal scale rows (Lindgren et al., 2011). The unique combination of a scaly skin while being fully pelagic is probably linked to specialized features of the integument in squamates, with overlapping epidermal scales showing vertical keratin generations, unlike the horizontal alternation of α - and β -keratin in the archosaurian skin (Maderson, 1972; Rutland et al., 2019).

Secondary Loss of Osteoderms and Scutes

Osteoderms are the only direct skin feature that can commonly be traced through the fossil record. Crocodylian osteoderms are highly vascularized on their external surface to support heat absorption and radiation (Grigg and Gans, 1993; Clarac et al., 2018). The presence of such bony armor in early thalattosuchians, in particular its overall resemblance with that of living crocodylians, suggests a similar thermoregulatory use, maybe associated with prolonged onshore or surface-near basking.

Nearly all crocodylomorphs exhibit osteoderms, with rare exceptions represented by the Metriorhynchidae and some terrestrial forms (Clark et al., 2004; Godoy et al., 2016; Montefeltro, 2019). Apart from protective armor (Hill, 2010; Marinho and Carvalho, 2009), dorsal osteoderms yield attachment sites for the tendon apparatus of the neural arches (Frey, 1988; Dilkes and Brown, 2007; Buchwitz and Voigt, 2010), which is why osteoderms tend to be retained even under reduced armor in cursorial forms (Serenio and Larsson, 2009; O'Connor et al., 2010). A role for crocodylian osteoderms in acidosis buffering has also been hypothesized, with reserves of carbonates in the osteoderm serving to buffer elevated lactate levels in the blood during prolonged apnea (Clarac et al., 2018) performed during resting or ambush predation. It remains unclear whether or not transitional metriorhynchoids could have lost their scutes but retained subcutaneous osteoderms. *Dermochelys*, trionychid turtles, and occasional mammalian examples (McDonald, 2018) demonstrate that this morphology is possible, but it is rare.

A summary on osteoderm growth in modern crocodylians is provided by Vickaryous and Sire (2009). Prior to mineralization of an osteoderm, a knot-like aggregation of fibrous, cellular connective tissue appears in the keel of the associated epidermal scale, which is otherwise identical to the matrix of the stratum superficiale. This development is delayed as compared to the remainder of the skel-

eton. Juveniles lack bony skin armor until ossification spreads, beginning around the dorsal neck and shoulder. This suggests the following evolutionary scenario for the origin of the specialized metriorhynchid skin type:

1. It is assumed that the thalattosuchian armor was lost rather suddenly (on a geological timescale), not stepwise per region, and not with a continuous decrease of osteoderm size over a longer period of evolution. Teleosauroid juveniles smaller than 70 cm have not been recorded (Westphal, 1962), but larger juveniles resemble adults in their osteoderm morphology.
2. Instead of local fibrous aggregations of connective tissue, a more planar reinforcement might have been achieved in the stratum superficiale, which subsequently replaced the shaping function and tightening effect of keratin scutes in the entire dermis.
3. The inclusion of dorsal osteoderms into tendon attachment sites of the vertebral column is not an a priori feature in early ontogeny. Therefore, the tendon apparatus is modular and flexible from an evolutionary perspective.

The loss of osteoderms in Metriorhynchidae is a question of adaptive value. Possibly, bony armor simply became obsolete as an additional acidosis buffer after the transition to a fully pelagic lifestyle. It could be buffered by the common disposability of ions in the seawater, especially due to the pelagic incorporation of biocalcite common since the Jurassic (Aloisi, 2018). The relationship of this system to metriorhynchid osteoderm loss is uncertain, however, due to missing data on various aspects of metriorhynchid paleobiology (unknown diving habits, hypothetically increased oxygen absorption) and associated geochemistry (Ridgwell, 2005; Gothmann et al., 2015). Osteoderm loss could alternatively (or additionally) be a means of increasing mobility in the pelagic metriorhynchids. Increase of trunk flexibility as an explanation for metriorhynchid osteoderm loss also has problems, however, since this thalattosuchian trend was somewhat reversed by secondary stiffening in Metriorhynchidae (Molnar et al., 2015). Furthermore, the fact that armored teleosauroid thalattosuchians survived nearly as long as metriorhynchids suggests that their less specialized bauplan was not maladaptive for marine life.

Crocodylian scutes grow continually or annually, forming corneous layers underneath the latest generation (Alibardi, 2010, figure 7). This mode offers a potential model for evolutionary reduction

of scutes in Metriorhynchidae, which probably occurred over the entire body and decreased periodic keratinization. The remaining soft skin cover would have retained its function as a barrier for water and electrolyte exchange, contributing to euryhaline homeostasis (Grigg, 1981; Taplin et al., 1982; Grigg and Gans, 1993). As Metriorhynchidae share a smooth skin surface with other pelagic saurians, the ultimate adaptation is seen in hydrodynamic efficiency to optimize streamlining. However, the presence of some armored teleosauroid thalattosuchians in open-water habitats suggests that this was not the only viable approach, with parallel radiations occurring simultaneously between Teleosauridae and Metriorhynchidae (Young et al., 2011).

Interpretation of Skin Irregularities

Similar skin irregularities in the two larger specimens from Painten might be attributed to integumentary strengthening structures, but differ from *Cricosaurus* from the same locality and an indeterminate, medium-sized metriorhynchid (NKMB-P-Watt06/508) from Wattendorf. Moreover, there is no regular repeated distribution on the body. Therefore, these irregularities are unlikely to be regular anatomical features and are more parsimoniously interpreted as pathological. We tentatively interpret these structures as epibiont scars.

Epibiota encompass a diversity of taxa, of which some can be excluded as originators for the structures in question. Algae would have little potential of preservation or even settlement on a fast-moving marine predator. The attachment of brachiopods and goose barnacles (Pedunculata) is organic (chitinous cuticle of pedicle) or cemented. Although reported as having an epiplanktonic lifestyle since the early Jurassic (Gale and Schweigert, 2015), goose barnacles would be very uncommon on higher nekton, or require deep, skin-doming peduncles (as reported from certain sharks; Rees et al., 2014). Stalked epibionts would probably have been actively scrubbed off by nektonic reptiles. Although Stramentidae lived as closely attached epizoa, these mostly Late Cretaceous barnacles left characteristic, internally segmented traces (Ifrim et al., 2011; Gale, 2016) that would be readily recognizable and are dissimilar from that observed here. Slipper limpets (Calyptraeidae) have a record reaching back only to the Cretaceous (Sohl, 1987). Oysters (Ostreoidea) are byssate and interlock with structured hardgrounds, which do not produce rounded

attachment scars. Suckerfish or remoras (Echeneidae) are non-invasive and cannot be traced older than the Oligocene (Friedmann et al., 2013). Lampreys (Petromyzontidae) rip deeper wounds upon attachment, however, the scars in question appear to be very flat and superficial and sometimes do not affect the surrounding skin. On the other hand, healed wounds can show similar structures, as is reported from fossil examples (Rothschild and Depalma, 2013). Given the unordered arrangement and sometimes irregular shape of the structures in question, however, no gnathostome producer of potentially healed bitemarks is considered likely at this time.

Two possible epizoa show a closer match with the observed traces. First, limpets (Patellogastropoda) have been a common element in marine communities since the Paleozoic. They generate immense suction through the action of their muscular foot and adhering mucus. Long-term shell contact can cause subcircular troughs on intertidal rock (pers. obs.). Limpets are rarely found on whales today, but have been reported as epizoa on Cretaceous ammonites (Kase et al., 1998) reinterpreted records of mosasaur bites as limpet home scars, though such bites were later confirmed based upon other material; Tsujita and Westermann, 2001). Although referred scars (Kase et al., 1994) resemble some of the curl-shaped structures observed on Painten metriorhynchids, most limpets prefer stationary hardgrounds in surface waters. Extant limpets perform homing (Cook et al., 1969), which does not match with a regular epizoic lifestyle on agile apex predators. However, limpets cover a much greater ecological spectrum, traced back to the Mesozoic (Chen et al., 2019). Only one very questionable limpet fossil is known from the Bavarian Jurassic Solnhofen Archipelago (Nützel, 2015), likely due to rare hardgrounds in the surf zone.

Second, acorn barnacles (Sessilia) are the most abundant epibionts on extant sea turtles, as well as baleen and toothed whales (for overview see Hayashi, 2013). Integrative analyses have demonstrated their middle Jurassic origin and late Jurassic radiation (Pérez-Losada et al., 2004, 2008), but there is a lack of fossil evidence from the Jurassic (Schweigert, 2015). It appears attractive to link this hypothetical origin with a pelagic shift in turtles (new specimens from Wattendorf and Eichstätt [Joyce et al., 2021] as well as from Painten [pers. obs. of the authors] with marine adapted flippers suggest a late Jurassic occurrence of pelagic turtles; compare with Hirayama, 1998),

as well as speculative coevolution with Metriorhynchidae. However, known early acorn barnacles were solely epibenthic, and there is no record on older turtle fossils (for which Reolid et al., [2015] state possible taphonomic effects, such as post mortem loss of epibionts). Only a few lineages are adapted to penetrate the cutis of whales, with some evolutionary plasticity of anchorage mechanisms (Seilacher, 2005). Balanomorpha can be traced back to the Late Cretaceous (Yamaguchi and Newman, 1990; Gale and Sørensen, 2014), Neobalanomorpha and the epizootic Coronuloidea to the Eocene. Specialized whale barnacles (Coronulidae) are not recorded older than Neogene (Hayashi, 2013; Gale and Skelton, 2018). This result does not a priori exclude hidden, less specialized Mesozoic epizootic cases, but leaves this interpretation as pure speculation.

Although barnacles are usually treated as commensal on pelagic tetrapods, there might be a minor parasitic effect in terms of hydrodynamic costs (which is why ships are cleaned of barnacles). Whales are noted to actively remove barnacles during surface activity, causing characteristic scars (Scarff, 1986; Félix et al., 2006) that are admittedly more circular than the larger irregularities observed in the new metriorhynchid material. There is clear preference of host taxa (Hayashi et al., 2013), but Collareta et al., 2016 describe exceptional epibiont dispersal of barnacles from turtle to whale in the fossil record. Therefore, a flexible spectrum of hosts is conceivable, including barnacles on extant crocodiles and alligators (Cupul-Magaña et al., 2011; Nifong and Frick, 2011).

The inferred scars on metriorhynchid skin appear to be rather shallow, precluding any epizootic parasites that possessed deep anchoring adaptations. Cetacean hosts shed their skin regularly, against which barnacles have some defense. Similarly, such strong attachment prevents barnacles from being shed off during ecdysis of marine snake hosts (Key et al., 1995). If the scars on the two larger specimens from Painten are from older fouling, they might have been deformed during growth. In DMA-JP-2009/001, smaller scars look fresher due to a deeper relief and a sharp, circular outline. In LF 3474, smaller scars are less pronounced, while the largest curl structures appear to be a deeper and stronger incrustation, probably due to aging parasites. The presence of the largest scars on the biggest metriorhynchid specimens might reflect a lower frequency of skin renovation in mature animals.

The potential traces of epizoota reported herein would be the first documentation of coevolution with Mesozoic marine reptiles. Zangerl (1948) reported on bryozoans and a questionable barnacle on a Cretaceous turtle, but likely a freshwater form, hence epibenthic on allochthonous bones (see also Brownstein, 2018). Particularly for the Late Jurassic Solnhofen Archipelago, no match with known invertebrates could be recognized, implying a new ecological component (Figure 28). A major challenge to this interpretation is the lack of a confirmed identification of the producer of these skin irregularities, which requires further understanding and investigation of metriorhynchid biostratigraphy. If quick burial took place, lamprey bites could be more likely. Mesozoic lampreys are very similar to modern forms (Chang et al., 2006), although no certain Late Jurassic marine representative can be named. The fossil record of this group is overall poor, which is not surprising in the light of restricted biomineralization. However, well-sampled Konservat lagerstätten like the Bavarian Late Jurassic plattenkalk formations raise the potential for discovery of fossil lampreys, if present.

CONCLUSIONS

1. Metriorhynchidae share a uniform type of smooth and flexible skin that completely lacks scutes. Straight, mostly transversal fibers represent the only set of reinforcement structures. Evidence for this skin type, which is similar, though simpler than that of ichthyosaurs, comes from a series of metriorhynchid species. Current data suggest no dependence from size classes or metriorhynchid subclade.
2. Teleosauroid thalattosuchians had an integument very similar to that of crown crocodylians. Therefore, both living crocodiles and teleosauroids can serve as a model for the ancestral condition in Metriorhynchoidea. Coarse, square-shaped scutes could represent an adaptation to, or exaptation for, aquatic habitats. Although not unambiguous, this pattern accords with that of other aquatic archosauromorphs.
3. The skin type of Metriorhynchidae represents a convergence with Ichthyosauria and Plesiosauria. Apparently, there is a generally high threshold for extensive skin modifications in aquatic reptiles, linked to a significant transition to a pelagic lifestyle. Turtles, however, deviate from this discrimination, as there exist limnic forms with reduced keratinization and pelagic forms retaining scutes.

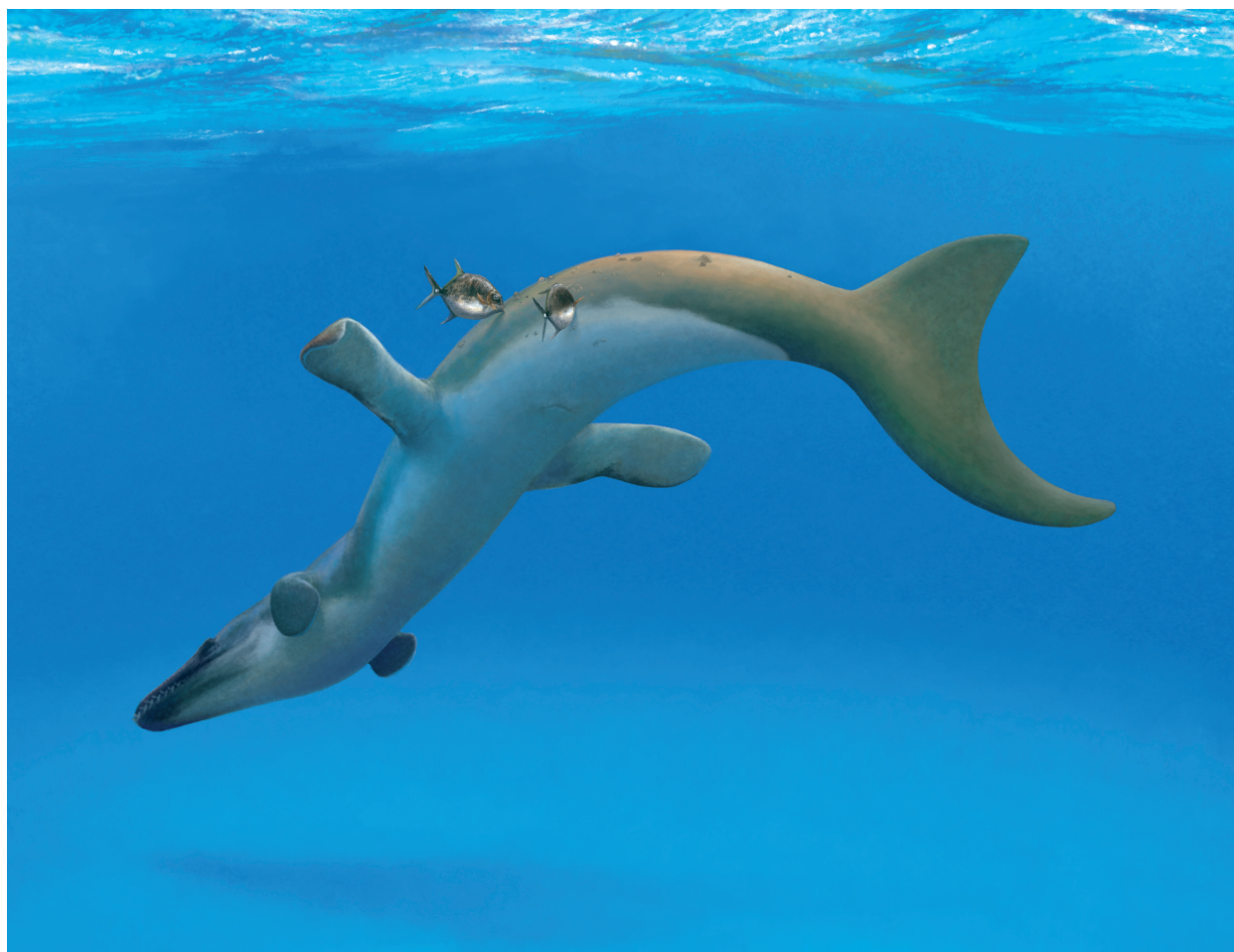


FIGURE 28. Life reconstruction of a *Dakosaurus*-like metriorhynchid, illustrating the skin surface, fluke outline, and potential epizoic parasites, according to new data.

4. Metriorhynchidae reached a degree of aquatic adaptation that is comparable to that of Ichthyosauria and probably the similarly built Mosasauridae. This comparability underlines the fully pelagic lifestyle of Metriorhynchidae, in accordance with current research.

5. Skin formation in extant crocodylians implies an evolutionarily sudden loss of osteoderms and scutes in Metriorhynchidae, linked to their fully aquatic locomotion and potentially their limited exposure to sunlight. It is believed that Teleosauroida performed onshore basking.

6. Frequent and irregular marks on the skin may represent traces of epizoa or scars comparable to those of lamprey bites. The trace marks are consistent with structures produced by barnacles or limpets, though this cannot be determined with certainty in the absence of

preserved tracemakers. Epizoic parasites on marine tetrapods would be a new addition to our knowledge of Jurassic ecology.

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