



Article

The Diet of *Metriorhynchus* (Thalattosuchia, Metriorhynchidae): Additional Discoveries and Paleoecological Implications

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Abstract: A new metriorhynchid specimen with stomach contents is described here. Assigned to *Metriorhynchus* cf. *superciliosus*, this specimen has a clear longirostrine form as indicated by its gracile and elongated mandibular rami. This is the second example of gastric contents described for Metriorhynchidae. This specimen's preservation allows the identification of the gill apparatus remains of *Leedsichthys*, the giant suspension-feeding osteichthyan from the Jurassic, including its gill rakers. The gastric contents also contain remains of invertebrates. This specimen indicates that *Leedsichthys* was not the direct prey of these crocodiles but more that its body was scavenged by them. Longirostrine metriorhynchids were piscivorous but also opportunistic and may have had more of a scavenging component in their lifestyle than previously understood, as all discovered fossils point in this direction.

Keywords: *Metriorhynchus*; Callovian; *Leedsichthys*; gastric contents; scavenging



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1. Discovery of the Specimen

In 1962, at the “Vaches Noires” cliffs of Villers-sur-Mer (Calvados, France) in the Marnes de Dives, Upper Callovian Athleta and Lamberti Zones, the late Jean-Claude Gaillard found a nearly complete skeleton of a specimen of Metriorhynchidae (Crocodylia, Thalattosuchia) thanks to the tide. This skeleton is nearly 2.5 m long, with a perfectly intact vertebral column (not sheared, as with many specimens from this area) and has all its gastric contents in place within the rib cage. Having been in a private collection, this specimen was only mentioned in [1] in a limited context for measurements used for its locomotor profile, and was first figured in 2008 as part of a crocodylian exhibition in Normandy (complete skeleton illustrated in [2], Figure 1). This specimen has been housed in Elbeuf, Fabrique des Savoirs (FBS) since 2012, under the accession number 2012.4.67.80. The aim of this study is not to provide a description of its postcranial material, as despite its excellent preservation, it does not contribute much to our knowledge of this taxon, particularly after previous skeletal studies from similar specimens [3–6]. It is, however, worth noting that the locomotor profile is nearly a perfect fit to our understanding of the locomotion of these genera and illustrates an appendicular skeleton which, like the ulna, was never before figured beyond outline drawings. Instead, we focus on the second known metriorhynchid gastric contents, which are rarely fossilized and provide new insights into the habits of such species. These remains allow us to make direct inferences of paleoecology, rather than make speculations based solely on tooth morphology.

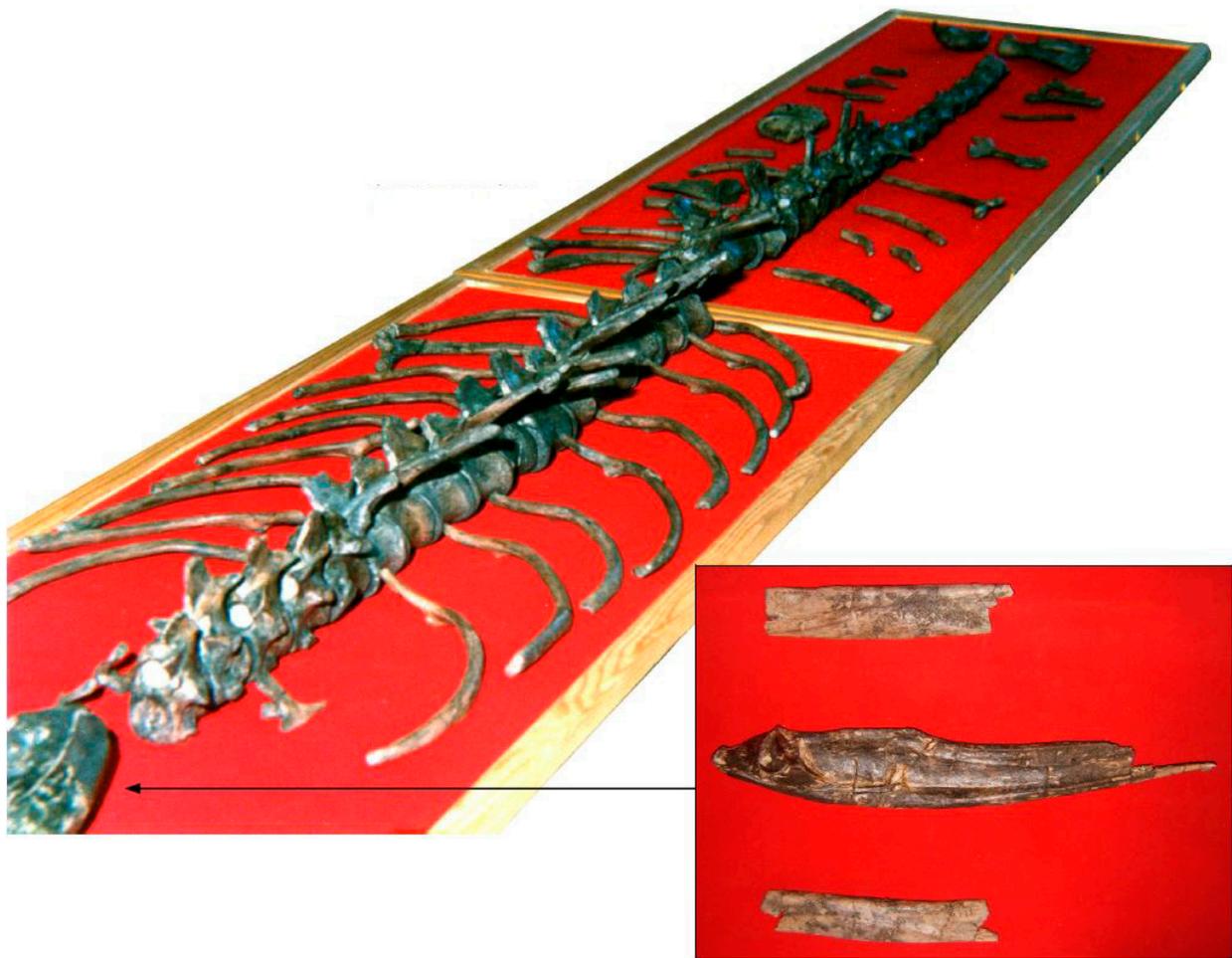


Figure 1. *Metriorhynchus* cf. *superciliosus* (FBS 2012.4.67.80) as figured in [2] and adapted—credits: J.C. Gaillard and Y. Lepage.

2. General Description

The skeleton itself is composed of the left posterior mandibular ramus, nearly thirty complete cervical and thoracic ribs, forty articulated vertebrae from the cervical to caudal areas, the right pectoral girdle, the right humerus, and both sides of the pelvic girdle ([2]).

The gastric contents, which are represented by a block of about 8×8 cm, has been found in place among the ribs and includes many small objects; therefore, it has been decided to not further prepare the separate fragile elements inside the block.

3. Systematic Paleontology

The amphicoelous aspect of the vertebrae indicates a mesosuchian (Figure 1). The lack of mandibular fenestrae is only seen in *Metriorhynchidae* (Figure 2). The humerus with a small deltoid crest has a length of 9.4 cm; its rectangular aspect is typical of the genus *Metriorhynchus*, as shown in [5] (Text Figure 70). The pelvic girdle (ischium, ilium, and pubis) is also similar to those illustrated in [4,5]. This specimen was diagnosed as *Metriorhynchus* cf. *superciliosus* [1,2].



Figure 2. *Metriorhynchus* cf. *superciliosus*: (A) left mandibular ramus, external view—FBS 2012.4.67.1 (total length, 36.1 cm; height at coronoid level, 7.5 cm); (B) left mandibular ramus, internal view (bm, bite mark); (C) right humerus, external view—FBS 2012.4.67.4 (dc, deltoideus crest; total length: 8.1 cm; length from deltoideus crest to upper diaphysis: 3.8 cm; proximal width: 2.1 cm; distal width: 1.7 cm); (D) right humerus, internal view; (E) right ulna, external view (total length: 4.8 cm; maximum width: 2.4 cm); (F) right ulna, internal view.

In this genus, two groups are present in the Upper Callovian: the longirostrine *Metriorhynchus superciliosus* and the brevirostrine *M. brachyrhynchus*. A recent study [7] attempted

to demonstrate that there were more genera and species than expected. However, Le Mort et al. [6] examined this more closely and showed that such results must be carefully re-evaluated, as diagnostic characters have been misinterpreted or shown across multiple genera, e.g., a *Dakosaurus* from Villers unknown from this Callovian locality.

Moreover, some arguments used to distinguish genera seem to be irrelevant or unjustified [6]; therefore, to avoid any confusion or misidentification, the classification used by the authors in [8] is used to ensure comparison of the same objects.

Returning to our specimen, the question arises as to whether it represents a long-snouted or a short-snouted form. As the postcranial remains of *M. brachyrhynchus* are poorly known, postcranial characters cannot be used to help us identify our specimen.

Nevertheless, short-snouted forms have a very massive and thick mandible that has even been historically confused with *Pliosaurus* (cf. *Pliosaurus trochanterius*, [9], corrected in [10]). This difference between the two mandibles of *M. superciliosus* and *M. brachyrhynchus* is figured in [2].

The slender aspect of the mandible of our specimen leads us to assign this specimen to *M. cf. superciliosus*.

Super-order Crocodylomorpha Hay, 1930 (*sensu* Nesbitt, 2011)

Order Mesoeucrocodylia Whetstone and Whybrow, 1983

Sub-order Thalattosuchia Fraas, 1901

Family Metriorhynchidae Fitzinger, 1843

Genus *Metriorhynchus* Meyer, 1830

Metriorhynchus cf. superciliosus de Blainville in Eudes-Deslongchamps, 1852.

4. Geology

This specimen was discovered by Mr. J.C. Gaillard at the beach level of the Vaches-Noires cliffs after high tide (pers. comm. 1998), between Villers-sur-Mer and Houlgate. According to him, the level of the “Marnes de Dives” (Athleta and Lamberti Zone) [11] is characterized by terrigenous sedimentary components (illite, kaolinite, and vermiculite) representing a calm environment with pyrite and some carbonate levels [12]. This area has already provided many vertebrate remains, in particular thalattosuchians, like teleosaurids (e.g., the *Steneosaurus heberti* holotype housed in Paris) and metriorhynchids (e.g., [2]), but also fishes (including coelacanths and *Leedsichthys*), other marine reptiles, and dinosaurs. The quiet sedimentary environment and hypoxic conditions permit the preservation of carcasses without physical or biological disturbance.

5. Description

As already noted, this nearly complete specimen allows for the illustration of some data otherwise poorly recorded, including the figuring of nearly unknown bones like the ulna, giving an added value beyond the main subject of this paper, which is the gastric contents.

Nevertheless, its state of preservation makes it one of only three candidates for the necessary measurements to determine this taxon’s locomotor profile (i.e., systematic measurement of the angle of aperture of the prezygapophysis articular surface along the vertebral column [1]).

This skeleton is nearly complete, allowing us to estimate its length at 2.50 m, representing a young adult, as indicated by the closed neurocentral sutures on the vertebrae [12].

This specimen, which is well illustrated in [2], includes: half of the left mandibular ramus (with a post- or peri-mortem bite mark on the splenial) (Figure 2B), small parts of the right mandibular ramus, anterior part of the atlas, five cervical vertebrae, seventeen dorsal vertebrae, three lumbar vertebrae, two sacral vertebrae, twelve caudal vertebrae, and cervical and costal ribs, along with chevron bones.

The appendicular skeleton includes the right coracoid, nearly all of the right pelvis, and part of the left pelvis. Rare elements that were not previously well illustrated are included here, such as the right humerus (Figure 2C,D) and the ulna (Figure 2E,F). The

ulna was identified as such by the authors of [5] and is here illustrated for the first time, although already drawn in outline in [3,4].

Such rarely preserved elements in anatomical connection suggest a fast burial. This is supported by the lack of fixed bivalves or serpulites on the bones (like the specimen of *Metriorhynchus* described in [6] from the same level).

A description of the gastric contents is shown in Figure 3.

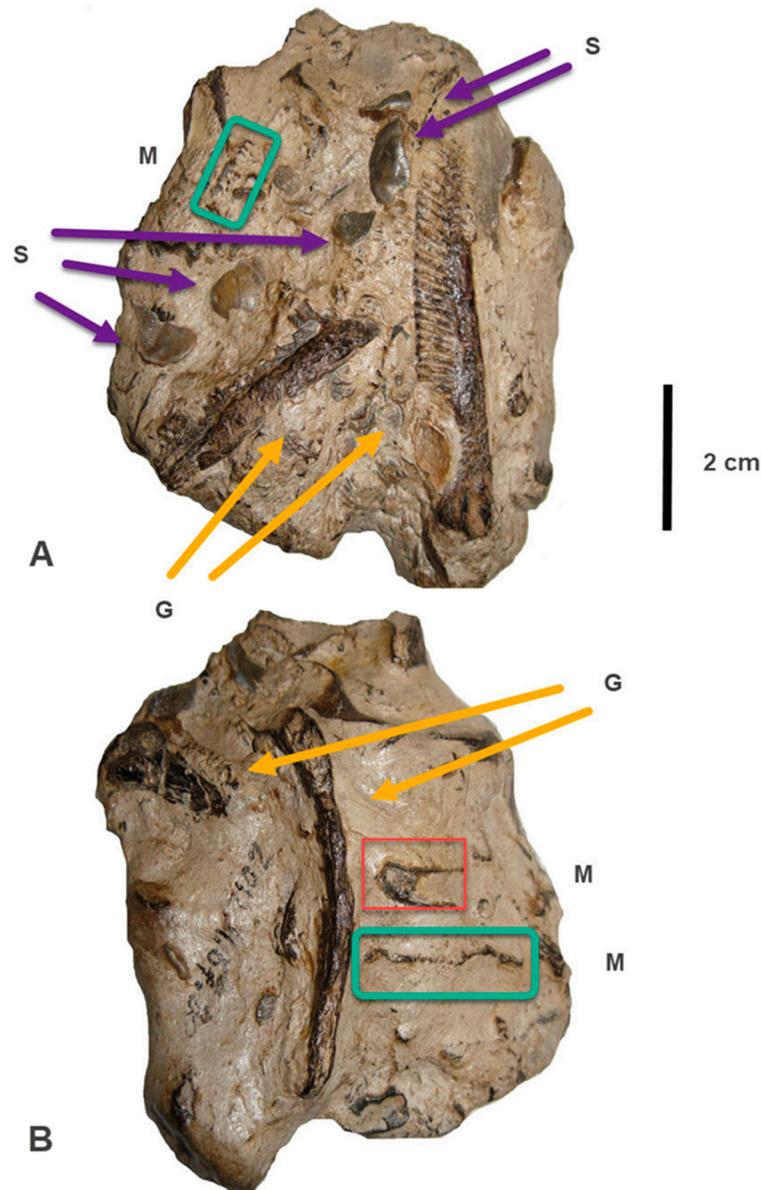


Figure 3. *Metriorhynchus* cf. *superciliosus* gastric contents block. FBS 2012.4.67.30 (Fabrique des Savoires), scalebar = 2 cm. (A) main surface view; (B) reverse surface view. G = gill raker fragments, showing signs of both physical and biochemical damage. The main surface shows both a raker with a chunk missing from its fimbriation series (sensu Liston 2013) and another with a partially dissolved appearance. M = interfanuncular mesh fragments (sensu Liston 2008, 2013). Green boxes highlight mesh fragments, and the red box indicates a vertical cross-section through a gill raker. S = shell elements.

The preparation of this part of the specimen has not been pursued, due to its rarity and the state of preservation of the material it contains. The gastric content occurs as a piece approximately 8×8 cm.

Inside, the most noteworthy components are the two gill raker fragments of 3.7 cm and 5.8 cm lengths.

The presence of the remains of *Leedsichthys* from this locality is consistent with previous discoveries [13,14], especially given the long history of remains assigned to this animal that have been found from this same shoreline [15].

On the slab, there are several evident pieces of *Leedsichthys* gill raker present, along with fragments of the interraker fanuncular mesh that linked the gill rakers together in life to form a functional sieve [16]. The main surface of the preserved gastric contents block features two distinctive pieces of gill rakers from a lateral view, with several invertebrate shells scattered amongst them. One of the two raker fragments is approximately 58 mm long with distinctive fimbriations (see Figure 6 in [16] for comparison), with an embayment containing one of the invertebrate shells. The other raker fragment is around 37 mm long and exhibits a more ragged character on its upper margin. The embayed feature and the ragged character are interpreted as signs of physical and biochemical digestion of these components.

The reverse surface of the slab has a centrally-placed gill raker that is roughly 50 mm long. Only its ventral view is exposed, thus no indications of its fimbriations are visible. To the right of this raker lies a vertical cross-section of a raker, with the tip of another raker lying to the upper left.

Both surfaces also have isolated fragments of the fanuncular mesh [16] scattered across them, the disaggregations of which are similarly interpreted as the product of mechanical and biochemical processing following ingestion.

The gill rakers preserved here are incomplete. The largest of these fragments has a preserved length of 58 mm, with its profile [17] indicating that it represents roughly three quarters of the complete length. This would place its estimated full length within the taxon's typical adult gill raker length of 75 mm [17]. This implies that the stomach contents contained remains derived from an average adult-sized individual, which has been estimated at 8–12 m standard length (SL; measured from the tip of the snout to the posterior extent of the vertebral column) [18], which was recently confirmed as a physiologically viable size [19]. Liston [17] reviewed considerations of the paleoecology of this animal as a suspension feeder, also discussing the degree to which it was a detritivore as indicated by feeding traces [14], which has been supported by recent discoveries of pedomorphically delayed crushing maxillary dentition emerging in the largest adult individuals [20]. There have been specimens of *Leedsichthys* that display signs of callus bone regrowth following the attack of would-be predators, including pliosaurs [21,22]. However, a metriorhynchid tooth embedded in a *Leedsichthys* bone that was previously interpreted as showing signs of bone regrowth [23] was found to have resulted from a misinterpretation of a finely disrupted periosteal surface at the point of tooth puncture. This interpretation was supported by the identification of the bone as a hyomandibula, a deep structure within the skull, from which it would be hard to imagine the animal surviving any attack that would leave such a mark long enough for bone regrowth to occur.

This specimen of stomach contents therefore produces further evidence for metriorhynchids scavenging on the remains of *Leedsichthys*, as has been recorded for hybodont sharks [18]. An unexpected component in these stomach contents is the presence of small invertebrate shells, which could be confused with small gastroliths present among some crocodylians [24], as invertebrates would appear strange in an exclusively piscivorous/scavenging animal. Moreover, the fast burial process (attested to by the preservation of small skeletal elements such as the ulna, humerus, ribs, and chevrons) precludes the hypothesis of a post-mortem assemblage. Liston [17] noted a similar concentration of bivalves on the dorsal surface of both known basiocciputs of *Leedsichthys* that, in combination with this specimen, might indicate that such a carcass could provide a hypothetically rich food source [25] and short-term ecosystem, which a carcass of this animal would represent with both bivalves and metriorhynchids feeding from it.

6. Paleoecology

The first challenge in paleoecological reconstruction is to correctly identify the material: one cannot compare or interpret the ecology of animals when one is not sure of the determination.

As noted earlier, one study [7] attempted to show that there were more genera and species than commonly accepted. But, aside from a need to reevaluate the results, this creates instability and confusion due to increasing genera and species within already-identified material. As already demonstrated for the other family of thalattosuchians [26], the teleosaurids, this is prohibited by the Zoological Code without a submitted presentation to the commission (International Commission on Zoological Nomenclature, article 13). A stable classification is essential in order to obtain a better understanding of how metriorhynchids could have coexisted with other marine reptiles that were arguably better adapted for marine life.

Returning to “pure” paleoecological reconstruction, Vignaud [27], based on tooth morphology, proposed a classification of the diet of thalattosuchians; Massare [28] completed this work to help understand the paleoecology of such crocodylians. Nonetheless, even Massare, in a less cited but still important article [29], attempted to include all possible data to produce the best possible picture of the lifestyle of such animals.

Hua [30] tried to integrate all of the data then available—actualism, body shape, histology, and tooth morphology—proposing a model of an epipelagic ambush predator capable of coexisting with more massive and active predators such as ichthyosaurs and sauropterygians.

The bone histology of complete skeletons of adult and subadult metriorhynchids shows that ectothermy was still present, despite strong anatomical modifications due to the adoption of a marine lifestyle (reduced front limbs, hypocercal tail, loss of osteoderms, lateral vision) [31]. This morphological adaptation precedes the biological and, more precisely, the physiological (except for the salt gland for metriorhynchids discovered by the authors of [32] in the prefrontal area, present in modern crocodylians). This statement is illustrated in the four families of marine mesosuchians: Teleosauridae, Metriorhynchidae, Pholidosauridae, and Dyrosauridae. All of these families include marine or fluviatile species that do not show any skeletal evidence of physiological modifications [33].

Subsequent to this study, metriorhynchid remains have been discovered around the world outside Europe, from North America [33] to South America and Russia [34]. One Russian specimen, a single isolated tooth that may have been reworked from other sediments, has led to a broader paleolatitudinal distribution for the group [35].

This is not especially surprising for crocodylians, or even for cold-blooded organisms: it has already been shown for another marine mesosuchian family, the dyrosaurids [36], which also have a broad paleolatitudinal distribution. Curiously, the comparison with this other marine mesosuchian family has been forgotten in recent metriorhynchid reconstructions, as in [35]. The distribution of dyrosaurids exactly matches extant crocodylians: always in tropical water, and colonizing islands always in accordance with the oceanic current [36]. In any case, such distribution is an indication of hyperthermic physiology, as argued in [35].

Moreover, such paleolatitudinal partitioning must be interpreted carefully, as it is derived from specimens from different ammonitic zones that were separated by millions of years.

Recent studies have concentrated more on tooth morphology, particularly on zymphodonty, to create the concept of “hypercarnivory” initiated by the authors of [37] and followed by several papers from the same team (e.g., [38]). But such papers focused only on tooth morphology and are rarely integrated with other morphological data (e.g., [38,39]). As already noted, [25] was the first author to concentrate on tooth morphology but has continued this line of study with subsequent works [28,29].

Actualistic comparisons, e.g., with a marine crocodile like *Crocodylus porosus*, considering intramandibular, individual, and ontogenic variation [8], could drive interesting intraspecific analysis. A fossil organism is a mosaic of data that must be integrated to avoid

speculation and achieve the most parsimonious interpretation. In the present case, we can see that in fact these species were also scavenging during life when possible, a result that would not be anticipated through “classical” piscivorous tooth morphology analysis.

Recently, a new and independent geochemical approach was used to determine the metabolism of metriorhynchids [40] and seems to indicate a more active metabolism than that evoked in [30]. The interest of such an approach is its independence from the purely descriptive approach used in classical paleontology but its strong dependence on actualistic data. Such data evolve with precision, and it seems according to Seon (comm. pers. 2023) that, in fact, metriorhynchids can be regarded as closer to ecto-poikilotherms than previously indicated as a result of this geochemical study, due to revision of the previous actualistic model.

Ectothermic metabolism in metriorhynchids that is lower than predicted by further geochemical studies and paleolatitudinal paleobiogeography (separated by millions of years) has been interpreted by the authors of [35] as an indicator of an elevated metabolism.

This conclusion is not currently supported by the available evidence; remains more complete than one tooth, as well as from the same time period and location and ammonitic zone (same time period and same location), are needed to be certain of the congruency of the geochemical results, subject to confirmation via bone histology.

Martill [23] described the stomach contents of a specimen of *Metriorhynchus* sp. as containing fish scales, belemnites, and pterosaur bones, showing a piscivorous and opportunistic diet. Moreover, a tooth indicated in a *Leedsichthys* hyomandibular bone was interpreted to have represented an act of predation with subsequent bone repair; but, as shown in [17], this in fact represented a bite on a carcass, as indicated by the bone being identified as lying deep within the skull.

Subsequently, Forrest [41] described a scavenging act by a metriorhynchid on a large pliosaur humerus, which seems too large to represent a target for a predatory attack by a 2.50 m animal.

Hua and De Buffrenil [31] have shown that a *Metriorhynchus* skull was lightened by more than 60% due to bone resorption. Such osteoporosis (in the structural meaning, not pathological) must imply a structural weakness when compared to contemporaneous sauropterygian skulls, a weakness likely to be deadly during active hunting, especially for a longirostrine animal.

Bivalves are not at all part of an ichthyophagous longirostrine crocodylian diet and this seems to indicate, as shown previously, that these were fixed upon a floating carcass.

The size of the crocodylian (2.5 m) could be compared against that of its prey (8–12 m), and consequently appears a bit small.

For all of these reasons (skull “osteoporosis”, longirostrine shape, bivalves ingested accidentally, and size difference), these gastric remains are considered to represent an act of scavenging, as shown for the third time in this taxon.

Such data seem to indicate that, in fact, metriorhynchids must have been opportunistic ichthyophagous predators that engaged in more scavenging than previously understood.

What could actualism teach us? In fact, as already noted in [33], extant crocodiles that feed in the open sea (such as *Crocodylus porosus*) [42] are opportunistic and will scavenge when possible.

This opportunistic and scavenging behavior allows this species to survive an epipelagic life alongside sharks and odontocetes, despite having a less active metabolism, alongside ichthyophagous predators capable of sustained swimming. Such open-sea predators create a more important interspecific competition than in freshwater for those crocodylians.

This observed contemporary lifestyle could easily explain what has been found here, and it could indeed be the specialization that allowed metriorhynchids to coexist with other Mesozoic marine reptiles with higher metabolisms, such as sauropterygians or ichthyopterygians.

As already noted, the postcranial anatomy of short-snouted forms in Callovian and Oxfordian seas are poorly known, despite the fact that many complete skeletons of long-

snouted forms are known from such sites (e.g., [5]). This apparent disparity between the preservation of short- and long-snouted forms has not been emphasized sufficiently in the literature. The reason for this may be due to the brevirostrine species, like *M. brachyrhynchus*, having different habitats (such as juvenile forms preferring more fluvial habitats where fossilization might be less common) or due to them more commonly becoming competitors with other predators.

7. Conclusions

Due to their highly modified condition as crocodylians, many studies over the past two centuries have attempted to improve interpretations of their paleoecology. An organism is a mosaic of data that becomes blurred and partial once fossilized.

The description of the second-known stomach contents of a *Metriorhynchus* allows us to better determine their diet and, moreover, their role within Mesozoic marine ecosystems.

In order to achieve a reliable interpretation, it is necessary to take all facts into account and integrate them through all scientific disciplines (actualism, histology, geology, geochemistry, and academic description, among others). It is only in this way that one can build a robust model.

Such discoveries show that metriorhynchids were not simply sustained high-speed purely ichthyophagous predators but were more opportunistic and scavenging in nature. This difference would have allowed this family to coexist with other marine reptiles such as sauropterygians and ichthyosaurs, making them more efficient, from a morphological and physiological point of view. This fossil seems to exhibit precisely the same habits as living *C. porosus* in the open sea, feeding on whatever they might find, without any specialization.

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