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The taxonomic content of *Machimosaurus* (Crocodylomorpha, Thalattosuchia)

Le contenu taxinomique de Machimosaurus *(Crocodylomorpha, Thalattosuchia)*

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ABSTRACT

Machimosaurus is a large teleosaurid thalattosuchian, a marine crocodylomorph historically recovered from Upper Jurassic strata of Europe. Several fragmentary remains are assignable to this genus but only four complete skulls have been reported, two of which are currently unavailable for study. A recent revision of the material assigned to *Machimosaurus* recognizes four valid species in this genus. Following a critical review of the diagnostic features of the various species, we confirm that the genus *Machimosaurus* is monospecific with *Machimosaurus hugii* as the sole and unique representative.

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RÉSUMÉ

Machimosaurus est un grand thalattosuchien de la famille des téléosauridés, un crocodylomorphe marin historiquement découvert dans les strates du Jurassique supérieur d'Europe. De nombreux restes fragmentaires sont identifiés comme appartenant à ce genre mais seulement quatre crânes complets ont été décrits, dont deux ne sont pas disponibles pour étude. Une révision récente du matériel attribué à *Machimosaurus* dresse un inventaire de quatre espèces valides dans ce même genre. Suite à un bilan critique des diagnoses de ces différentes espèces, nous confirmons que le genre *Machimosaurus* est monospécifique, *Machimosaurus hugii* étant le seul et unique représentant du genre.

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1. Introduction

The genus *Machimosaurus*, a teleosaurid thalattosuchian known from several European specimens as well as a single instance from Ethiopia (Bardet and Hua, 1996) has a long heritage in vertebrate paleontology but to the present day, no consensus has been reached toward its species content. A recent contribution (Young et al., 2014a) attempts such a taxonomic revision. The work of Young et al. (2014a) takes its roots in the hypothetical "*unusual subjective species synonymies for the type species* Machimosaurus hugii" and "*confusing statements about the type specimen of this species*" made by Pierce et al. (2009) and Martin and Vincent (2013) as well as the question on the availability of *Machimosaurus mosae* as a taxonomic name (Martin and Vincent, 2013). Young et al. (2014a) conclude that the species name *M. mosae* is available and identify three other species of *Machimosaurus* distributed in the Kimmeridgian deposits of Europe. For this, these authors erected a new species, *Machimosaurus buffetauti* Young et al., 2015, the holotype of which (SMNS 91415) comes from the Lower Kimmeridgian of Germany.

Machimosaurus was initially erected on the basis of teeth (Meyer, 1837), the morphology of which characterizes the genus. This was recently confirmed by Young et al. (2014b) who did not notice major differences between the studied specimens, despite the presence of intra-individual morphological variations. Further work at the level of Teleosauridae is pending and may prove useful for their taxonomy (Schaefer, 2012). Many fragmentary specimens of *Machimosaurus* have been reported but only two nearly complete crania are still available to scientists, namely, the specimen curated in Stuttgart (SMNS 91415) described by Martin and Vincent (2013) and the specimen curated in Bourg-en-Bresse that was described by Buffetaut (1982). The holotype described by Sauvage and Liénard (1879) as *Machimosaurus mosae* is apparently lost and the whereabouts of the neotype designated by Hua et al. (1993) are unknown. The aim of this note is to review the arguments set by Young et al. (2014a) and Martin and Vincent (2013) and discuss the rationale for the presence of several species of *Machimosaurus* during the Upper Jurassic.

2. Valid name and authorship of *M. mosae* and *M. buffetauti*

Among the contentious issues discussed by both Martin and Vincent (2013) and Young et al. (2014a) are the availability of the species name *Machimosaurus mosae* and its potential consequences on the taxonomy of the genus. Martin and Vincent (2013, p. 193) claimed indeed that the name *Machimosaurus mosae* is unavailable. It was published for the first time in a memoir (Sauvage and Liénard, 1879), in which a manuscript work (Liénard, 1876) is explicitly credited with the authorship of the species, funded at the time as *Teleosaurus mosae*. Because this work is not published according to articles 8 and 9 of the Code (ICZN, 1999), Martin and Vincent (2013) felt justified to declare *Teleosaurus mosae* and its later citations and combinations as invalid – nomenclaturally and therefore taxonomically.

Fig. 1. The skull and mandible of *Machimosaurus hugii* from the Kimmeridgian of Montmerle, Ain, France in A, dorsal and B, right lateral views. The specimen was partly covered in plaster by Eugène Eudes-Deslongchamps.
Fig. 1. Le crâne et la mandibule de *Machimosaurus hugii* du Kimméridgien de Montmerle, Ain, France en vues A, dorsale et B, latérale droite. Le spécimen fut en partie couvert de plâtre par Eugène Eudes-Deslongchamps.

However, the conclusion of Martin and Vincent (2013) is strongly contested by Young et al. (2014a, p. 32). They object notably that the erection of the name *M. mosae* by Sauvage and Liénard (1879) did fulfill the requirements of articles 8, 11, and 12 of the Code (ICZN, 1999), regardless of the credit originally given to Liénard (1876). The conclusion of Young et al. (2014a) about this matter is correct. In addition, Young et al. (2014a) refer to articles 11.6 and 50.7 of the Code (ICZN, 1999) to further justify the availability of *Machimosaurus mosae* and its authorship in spite of its use as a junior synonym of *Teleosaurus mosae* by Sauvage and Liénard (1879). However, this appeal is unnecessary. As defined in the Glossary of the Code, a synonym is indeed "*Each of two or more names of the same rank used to denote the same taxonomic taxon*" (ICZN, 1999). *M. mosae* and *T. mosae* are therefore not synonyms, but different "combinations" of the same specific name, even if the latter is a mere manuscript name. As such, *Teleosaurus mosae* is a *nomen nudum* and the species name *Machimosaurus mosae* is not a new combination as per the Code and retains Sauvage and Liénard, 1879 as original authorship.

In fact, another interesting issue has been raised by the creation of the new species name *Machimosaurus buffetauti* by Young et al. (2015), as defined by Young et al. (2014a). Besides the holotype SMNS 91415, the authors assign to this species the complete skull and mandible in occlusion from the Kimmeridgian of Montmerle, Ain and curated in the Musée de Brou, Bourg-en-Bresse (Buffetaut, 1982; Chanel, 1905 and complementary views in Fig. 1). The latter specimen is of special interest because it has been a source of dispute during the decades following its discovery (see Buffetaut, 1982; Chanel, 1905 for a detailed history). In particular, it has been given several species names which have been since considered as unavailable, notably by Buffetaut (1982) and Young et al. (2014a). Nevertheless, a careful re-examination of the available literature reveals that the nomenclature of the Bourg-en-Bresse specimen is more complex than previously thought.

The specimen was first trusted by the Société d'Émulation de l'Ain to E. Eudes-Deslongchamps for

preparation and study. As recounted by Jarrin (1870), the palaeontologist identified it as a new species of *Steneosaurus* and asked for advice to the society, proposing the epithet "*burdigalensis*". This offer was turned down by the members, who instead suggested "*burgo-bressiensis*" then the more simple "*burgensis*" for species name. Three years later, Jarrin (1873) provided a brief and rather lyrical account about the Bourg-en-Bresse skull in which it is designated as "*Steneosaurus burgensis*". He also included portions of the correspondence of E. Eudes-Deslonchamps who explained the progress of the preparation. The same "*Steneosaurus burgensis*" is again cited by Jarrin (1876) in a short passage.

Later, the history of the Bourg-en-Bresse skull was published in detail by Chanel (1905) who included extended citations of the local press and various exchanges that occurred between the Société d'Émulation de l'Ain, Eudes-Deslongchamps, and the mayors of Bourg-en-Bresse. The repatriation of the skull to Bourg-en-Bresse was announced in 1875 in the *Courrier de l'Ain* in which the author ended regretting that the *Steneosaurus* had been named *S. burgensis*: "*Pourquoi* Burgensis*? Bourg est à 3 lieues de Montmerle et les terrains jurassiques qui contiennent les Sténéosaures s'arrêtent à moitié-chemin, à Jasseron. Pourquoi ne l'a-t-on pas appelé tout simplement* Steneosaurus Montmerli *ou* Chanuti*? Ce dernier nom eût rappelé le généreux donateur d'une pièce paléontologique d'une grande valeur.*" (Chanel, 1905, p. 16). The municipality agreed with this opinion and decided to make a concession by renaming the Bourg-en-Bresse specimen "*Steneosaurus Burgensis Chanuti*".

Now, what is the respective status of "*Steneosaurus burdigalensis*", "*S. burgobressiensis*", "*S. burgensis*", "*S. montmerli*", "*S. chanuti*", and "*Steneosaurus burgensis chanuti*"? *S. burgensis* and *Steneosaurus burgensis chanuti* have been explicitly considered as *nomina nuda* by Buffetaut (1982) and recently by Young et al. (2014a)–who misspelt it "*chanti*" – and in their addendum (2015). The latter authors, in particular, appeal to Article 12 of the Code (ICZN, 1999). They claim that neither Jarrin (1876, 1873) nor Chanel (1905) followed the requirements (Young et al., 2014a, p. 30, 2015, p. 3). However, a close examination of Article 12 indicates that, in fact, Chanel (1905) established correctly – albeit involuntarily – the name *Steneosaurus burgensis chanuti*. Article 12 first states that: "*12.1. Requirements. To be available, every new name published before 1931 must satisfy the provisions of Article 11 and must be accompanied by a description or a definition of the taxon that it denotes, or by an indication*." If we agree with Young et al. (2014a) regarding the absence of a description or a definition in Jarrin (1876, 1873, 1870) and Chanel (1905), the latter nevertheless included an indication as per Article 12.2. Eight kinds of indication are listed under this article, among which is "*12.2.7. the proposal of a new genus-group name or of a new species-group name in association with an illustration of the taxon being named, or with a bibliographic reference to such an illustration*" (ICZN, 1999). Hence, the presence of a plate on which the Bourg-en-Bresse skull is figured as "*Steneosaurus Burgensis Chanuti*" is alone sufficient to warrant its availability and to credit Chanel (1905) as its author. Conversely, the six other names appear to be actual *nomina nuda*.

It is still necessary to settle a few points before applying the name of Chanel (1905). According to the Principle of Coordination, alias Article 46, indeed, the erection of the species name "*burgensis*" and infraspecific name "*chanuti*" by Chanel (1905) implies that an infraspecific and a specific equivalents, respectively, have been created at the same time (ICZN, 1999). Also, both "*burgensis*" and "*chanuti*" have been funded in the same publication, so their relative precedence needs to be determined. Fortunately, Article 24.1 clearly indicates that, "*When homonyms or synonyms are established simultaneously, but proposed at different ranks, in the family group, genus group or species group the name proposed at higher rank takes precedence*" (ICZN, 1999).

As a consequence, the first available and valid name assigned to the Bourg-en-Bresse specimen is *Steneosaurus burgensis* Chanel, 1905 with *Steneosaurus chanuti* Chanel, 1905 as an objective senior synonym. Both names take therefore priority over *Machimosaurus buffetauti* Young et al., 2015, in the case SMNS 91415 and the Bourg-en-Bresse skull are conspecific as concluded by Young et al. (2014a). Conversely, the names "*Steneosaurus burdigalensis*", "*S. burgobressiensis*", and "*S. montmerli*" and the citations of the names "*Steneosaurus burgensis*" and "*S. chanuti*" predating the publication of Chanel (1905) are all *nomina nuda*.

3. Are SMNS 91415 and the neotype of *M. mosae* different?

The specific distinction of *M. mosae* from SMNS 91415 is questionable. Young et al. (2015) designated the holotype of *Machimosaurus buffetauti* on specimen SMNS 91415, originally described by Martin and Vincent (2013) and referred to *M. hugii*. The central argumentation of Young et al. (2014a) establishing differences between the *M. mosae* neotype and SMNS 91415 essentially rests in their paragraph 4.2. but other differences can be found in their diagnoses of the different proposed species of *Machimosaurus*. Their argumentation for the difference between the *M. mosae* neotype and SMNS 91415 is structured around four main points:

- ontogeny;
- geological age;
- cranial features;
- postcranial features.

These are discussed below.

3.1. Ontogeny

SMNS 91415 and the neotype of *M. mosae* are not juveniles as explicitly stated by Martin and Vincent (2013). Although Young et al. (2014a) also list a suite of non-juveniles characters in these specimens, they alleged as well that Martin and Vincent (2013) are at the origin of a so-called 'juvenile hypothesis'–an erroneous claim. Martin and Vincent (2013) highlighted that the complete skulls

known for the genus *Machimosaurus* have comparable dimensions (see Table 6 in Martin and Vincent, 2013), and did not acknowledge any juvenile characteristics in any of the complete skulls referred to the genus *Machimosaurus*. Martin and Vincent (2013) and Young et al. (2014a) recognized the presence of exostoses in the specimen described by Hua (1999). However, the presence of these exostoses does not permit to determine the ontogenetic status of the specimen as they may have resulted from an infection (Rothschild, 2009), in which case they would have little bearing on the ontogenetic stage of the neotype of *M. mosae*.

3.2. Geological age

Relying on different geological ages (Uppermost Kimmeridgian, and Lower Kimmeridgian, a temporal gap of some 3–5 million years) is irrelevant to decipher the taxonomic status of specimens. There are several instances in the fossil record showing that a single species can exist for a few million years. For example the oldest known *Crocodylus niloticus* are between 2 and 3 Ma old (Tchernov, 1986) and the oldest *Alligator sinensis* are Pleistocene in age (Shan et al., 2013) (see also review in Brochu, 2003). Biological features, rather than temporal distributions, should be the central point in order to delineate species and these are examined below.

3.3. Cranial features

The outline of the orbits has been considered diagnostic so as to differentiate three *Machimosaurus* species with sub-rectangular, sub-circular and transversely ellipsoidal orbits (Young et al., 2014a). Nevertheless, the possible differences in skull proportions are difficult to establish considering the dorsoventral compaction of specimens and the resulting changes in the outlines of skull openings.

The basioccipital morphology has been used as a character to delineate *M. mosae* from other species of *Machimosaurus* (e.g. Young et al., 2014a, p. 31). However, the right portion of the basioccipital is broken in the neotype of *M. mosae* (see Fig. 18A, B in Young et al., 2014a) and, for this reason, the difference between the U and the V-shaped outlines of the basioccipital is considered to be dubious.

The presence of depressions on the dorsal surface of both quadrates of SMNS 91415 is intriguing, but has so far been exclusively described in this specimen. Their nature remains uncertain and care should be taken before it could be used as a diagnostic feature.

The loss of the prearticulars cannot be interpreted as a specific character for *M. mosae* (contra Young et al., 2014a, p. 19), as, as acknowledged by the same authors, its absence may result from a preservational artifact. Prearticulars are known in metriorhynchoids since at least the beginning of the XXth century (e.g. Andrews, 1913, part II, text-Fig. 60 p. 157). Young et al. (2014a) also establish the presence of a prearticular in the teleosaurid *Steneosaurus larteti*. Together with the description of a prearticular in *Machimosaurus* (Martin and Vincent, 2013), we predict that a prearticular will be found in other teleosaurids. Because this bone is present in both teleosaurids and metriorhynchoids, a reasonable assumption is that the possession of a prearticular is in fact a symplesiomorphy of Thalattosuchia.

In their species diagnosis of the *M. mosae* neotype, Young et al. (2014a) refer to a maxillary count of 17–18 alveoli. This count should not appear in a diagnosis because the maxilla of the *M. mosae* neotype is damaged and incomplete according to Hua (1999).

In the diagnosis of the new species *M. buffetauti* (SMNS 91415), the dentary is given a total count of 24–25 alveoli (Young et al., 2014a) but this appears to be in contradiction with the count of 22 maxillary alveoli presented in their Table 2. Martin and Vincent (2013) described, figured, and measured 21 alveoli on the left dentary row and 22 alveoli on the right dentary row of SMNS 91415.

Whether a smaller number of alveoli comprised at the level of the post-symphyseal dentary bone of SMNS 91415 compared to that of the neotype of *M. mosae* can be considered an autapomorphy (Young et al., 2014a) is questionable. It is difficult to draw a generality because, although this area is visible in SMNS 91415, it is not in the Bourg-en-Bresse specimen preserved with the occluding mandible. Moreover, the right post-symphyseal dentary bone of the neotype of *M. mosae* is only slightly longer by one alveolus. Considering such a character as diagnostic for a separate species is not solid.

Whether a difference in symphyseal length for distinguishing species of *Machimosaurus* is diagnostic (Young et al., 2014a, p. 33 and Table 1) is also questionable. This claim is based on the comparison of three specimens, one being an estimate from the poor illustrations of Sauvage and Liénard (1879) dixit Hua (1999, p. 143), and a second specimen, the neotype of *M. mosae*, for which the posterior mandibular rami are broken according to the Plate 2 of Hua (1999). The difference used to delineate the two species is about 4% and could represent the margin of error due to the breakage seen in the specimen described by Hua (1999).

3.4. Postcranial features

Young et al. (2014a) recognized diagnostic characters in the postcranial skeleton that allow discerning the neotype of *M. mosae* from SMNS 91415. They use three diagnostic characters taken from the morphology of the coracoid. However, the *M. mosae* neotype was preserved in clay, and experienced deformation. Moreover, Hua (1999, p. 159), in his description of the coracoid of *M. mosae* neotype states that it is fractured and deformed: "*Il a la forme d'un éventail bien qu'il ait été fracturé et déformé post-mortem*". According to the figures of Hua (1999), the proximal region of the coracoid seems incomplete. In this context, the three diagnostic characters identified by Young et al. (2014a) on the coracoid are questionable. Moreover, in their study of the morphologic variation of scapula-coracoid pairs in different species of extant crocodilians, Chamero et al. (2013) showed that intraspecific variation is large and equivalent to interspecific variation.

Young et al. (2014a) noted that the dorsal margin of the axis neural arch of SMNS 91415 is strongly concave whereas it is weakly concave in the neotype of *M. mosae*. However, the atlas-axis complex of the neotype of *M. mosae*

is heavily damaged as acknowledged by Hua (1999, p. 155). Furthermore, Young et al. (2014a) observe a difference in postzygapophyses reach, stating these structures are shorter in the neotype of *M. mosae* than in SMNS 91415. But this statement is problematic for two reasons. First, these postzygapophyses appear damaged or incomplete in the neotype of *M. mosae*. Secondly, Hua (1999) described long postzygapophyses in the neotype of *M. mosae*, reaching posteriorly 4 cm beyond the posterior surface of the axis centrum: "*la base de cette épine neurale dépasse de la face postérieure du centrum de l'axis de 4 cm*" (Hua, 1999, p. 156). In fact, the postzygapophyses of SMNS 91415 have a ventral length of 2.3 cm and reach further posteriorly than the posterior surface of the axis centrum for 1.4 cm. These figures are therefore contradicting the statement of Young et al. (2014a) that postzygapophyses in the neotype of *M. mosae* are shorter than in SMNS 91415 but are supported by Hua (1999, Plate 3 Figs. 1–3)'s figures, in which the left lateral view of the atlas-axis closely resembles those of SMNS 91415 in the reach of the postzygapophyses.

Therefore, we do not find compelling evidences from comparative cranial and postcranial morphologies for differentiating SMNS 91415 from the neotype of *M. mosae*. Following the conclusions of Martin and Vincent (2013), we maintain the referral of SMNS 91415 to *M. hugii* and consider the specimen from Bourg-en-Bresse as well as the neotype of *M. mosae* as belonging to *M. hugii*.

4. Ethiopian *Machimosaurus*

There is a single known occurrence of the genus *Machimosaurus* in the Late Jurassic of Ethiopia, which consists of the rostral end of sutured dentary ramii (Bardet and Hua, 1996). In their revision of *Machimosaurus*, Young et al. (2014a) recognized two diagnostic characters and erected the species *M. nowackianus*. These characters are based on relative dimensions of the inter-alveolar spaces compared to the size of the alveoli and to the transverse width at the level of the dentary tooth #4. Young et al. (2014a) state that in *M. nowackianus*, the inter-alveolar spaces between dentary alveoli #2 and #3 and between alveoli #3 and #4 is less than half the length of dentary alveolus #2. Although this seems right on the left dentary ramus, the inter-alveolar space appears to be as long as the length of dentary alveolus #2 on the right ramus. According to the figures available in Bardet and Hua (1996) and in Young et al. (2014a), the left dentary alveolus #2 in the Ethiopian specimen appears twice as large as the right dentary alveolus #2. Moreover, there exists some variability in the right versus left inter-alveolar space between dentary alveoli #1 and #2 in SMNS 91415 (see Fig. 7A in Martin and Vincent, 2013), thus questioning the validity of this character as diagnostic.

The second character used to diagnose *M. nowackianus* concerns the transverse width at the level of the large fourth dentary alveolus. Young et al. (2014a) state that this distance is smaller in the Ethiopian specimen than in other species of *Machimosaurus*, when the dentary is known. To quantify comparisons, we express this character as the ratio of the distance between the lingual margins of the opposing dentary alveoli #4, over the distance between the maximal widths of the dentary at the level of the alveoli #4. We find that SMNS 91415 has a ratio of 0.54 whereas the Ethiopian specimen has a ratio of 0.4, which are not substantially different. In addition, the lingual margin of the right and left alveoli #4 in the Ethiopian specimen are clearly damaged, giving the false impression that the alveolar outline is larger that it is actually in this specimen. According to the preserved labial contour, reconstructing the outline of the alveoli #3 in the Ethiopian specimen allows us to estimate a ratio of 0.5. Therefore, based on this only known specimen, we find no compelling evidence warranting a distinct species of *Machimosaurus* in Ethiopia. Certainly, this will have to be reevaluated with more complete discoveries.

5. Conclusion

To sum up, we recognize that the only significant differences between SMNS 91415 and the *M. mosae* neotype are the depressions on the quadrates of the former and the exostoses in the latter, but the taxonomic utility of such features appears unlikely if they result from pathologies. Moreover, individual variability and preservation should be taken into account. We consider the genus *Machimosaurus* as having a single valid species, *Machimosaurus hugii* Meyer, 1837, and we follow the revised diagnosis established in an earlier study (Martin and Vincent, 2013) for *Machimosaurus*. The holotype of '*Simolestes*' *nowackianus* Huene (1938) is also too incomplete and should be referred to *Machimosaurus* sp. as originally proposed by Bardet and Hua (1996). As stated previously in Martin and Vincent (2013), we do not exclude the presence of other species of *Machimosaurus*, but a larger sampling of diagnostic specimens is currently lacking or await restoration and subsequent study.

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