

Article

New Information on the Madagascan Middle Jurassic Sauropod *Lapparentosaurus madagascariensis*

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Abstract: The systematic position of the Middle Jurassic sauropod *Lapparentosaurus madagascariensis* is not fully understood due to a lack of useful anatomical detail. Despite many new bone fragments from the axial skeleton, post-cranial skeleton, and a hind limb having been previously unearthed, its systematic position has not yet been satisfactorily established. Although this Malagasy taxon is only recognised by two autapomorphies located in the scapula and coracoid, two features of the neural spine, which are reported here, provide additional information on the common autapomorphies shared with the British genus *Cetiosaurus*. A full description of the femur and neural spine helps to determine some aspects of its relationship to other similar taxa. Remains of *Lapparentosaurus madagascariensis* have been recovered from mixed facies that may have been deposited in a shallow water lagoon during a transgressive period in the Isallo IIIb subunit in the Majunga Basin.

Keywords: autapomorphy; Cetiosauridae; Brachiosauridae; Bathonian; Isalo; Majunga

1. Introduction

1.1. Historical Background of the Cetiosauridae Group

The sauropod dinosaur *Lapparentosaurus madagascariensis* from the Middle Jurassic of Madagascar (Bathonian) has been a subject of controversy relating to its systematic position in addition to its paleoecology. Historically, the Malagasy form has been assigned to the genus *Bothriospondylus*, but Bonaparte [1] concluded that the Malagasy form is a junior synonym of *Lapparentosaurus* [2]. He noted that the generic assignment of the Bathonian sauropod remains from Madagascar to *Bothriospondylus* from England based on the vertebral centra has no serious basis, as the deep pleurocoels, the only character used by Lydekker [3] to recognize the same genus for the vertebral centra of Madagascar, have no systematic value [2,4,5]. Although evidence suggests that sauropods underwent a major radiation in the Middle Jurassic [6–8], the cetiosaurids are best known from that time. They are also well distributed in Algeria (*Chebsaurus algeriensis*, Callovian), England (*Ornithopsis leedsi* (= *Bothriospondylus magnus*), Callovian), and Argentina (*Volkheimeria*, Bathonian-Callovian), providing a glimpse of the early diversification of that family [8–10]. However, the Cetiosauridae is supposedly composed of a large number of species from Middle to Late Jurassic, and ambiguity in the determination of the systematic position of the Malagasy form is problematic because the species mostly does not share any recognized autapomorphies. Only *Cetiosaurus oxoniensis* only is considered to be a valid species and is the type species of the genus [11–14], the debate on whether the Malagasy form belongs to Cetiosauridae or Brachiosauridae results from Bonaparte [1] who regarded it as basal member of Cetiosauridae, but later workers, such as McIntosh [15] and Upchurch [16,17] suggested that it represented a member of the Brachiosauridae based on anatomical characters such as the steeply

inclined ischial shaft and the elongate humeri [1,2]. Additional material presented here elucidates further the relationship of the Malagasy form, mainly focused on neural spines and/or vertebra, with the Cetiosauridae and targets on solving partially its taxonomic status.

Lapparentosaurus belongs as part of the paraphyletic Cetiosauridae [1], to a multifurcation of similar Middle Jurassic cetiosaurids that include *Chebsaurus*, *Ferganasaurus*, and *Cetiosaurus*. This polytomy may be due to missing data causing their relationships to remain unresolved [10].

But since the Titanosauriforms are thought not to exist prior to the end of Jurassic [18,19] and that *Bothriospondylus* is thought to be at best a nomen dubium [2], the Madagascan form most likely belongs to the Family Cetiosauridae. The detailed analyses by Bonaparte [1] and Mannion [2,18,20] of the axial skeleton anatomy of the Madagascan form was based mostly on material unearthed from the same place and horizon where Buffetaut [21] had discovered the jaw of his genus *Archaeodontosaurus*.

1.2. Geological Setting

The fossil sites are located between Ambondromamy and Ambalanjanakomby, about 170 km east-southeast of Mahajanga, and extend through the National Road to Antananarivo (RN4) (Figure 1). They outcrop in badlands locally known as Tanety [22], and correlate to the Middle Jurassic. These outcrops are equivalent to the upper levels of the Isalo ‘Group’ (W Madagascar) and named ‘Isalo III-Facies Continental’ by Besairie [23]. The Isalo III subgroup is divided into two subunits: Isalo IIIa and Isalo IIIb. Besairie [24] recognized the top of the series as ‘Isalo IIIb-Bathonien Facies Mixte Dinosauriens’ because of its heterolithic nature, which was supported by Boast and Naim [25] (Figure 2). According to Besairie [24] this subunit is about 190 m thick and consists of alternating, variegated sandstones and siltstones arranged in cross-bedded layers, calcareous paves and multicoloured claystone banks [4,5,24]. Silicified wood is sometimes present. Besairie [24] suggested a Bathonian age for Isalo IIIb (ICS stage Bathonian 168.3–166.1 Ma [26]) on the basis of its rich invertebrate fauna including the index echinoids: *Nucleolites amplus* and *Acrosalenia colcanap* [27–31]. The Bathonian age of the Dinosaur-bearing layers (Isalo III) is also consistent with the presence of a bivalve of the genus *Corbula* [32,33].

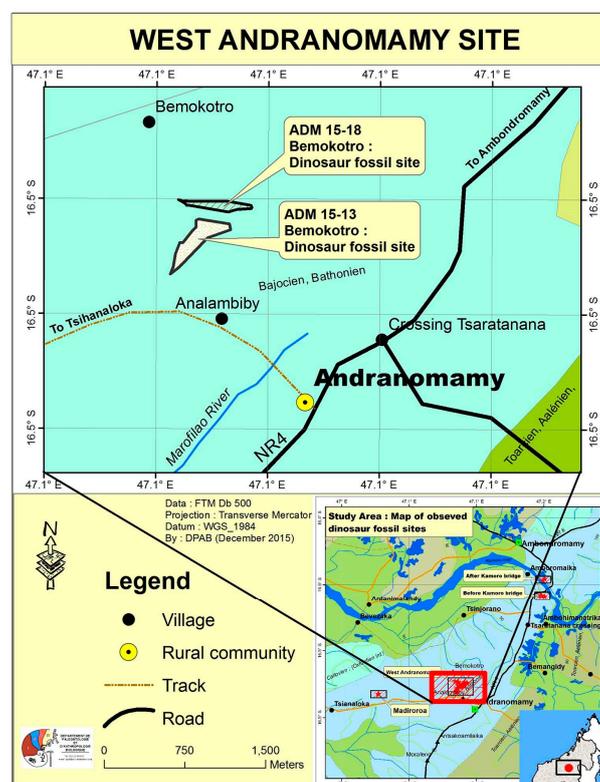


Figure 1. Area of study with modification from the Geographical System Information GSI analysis.

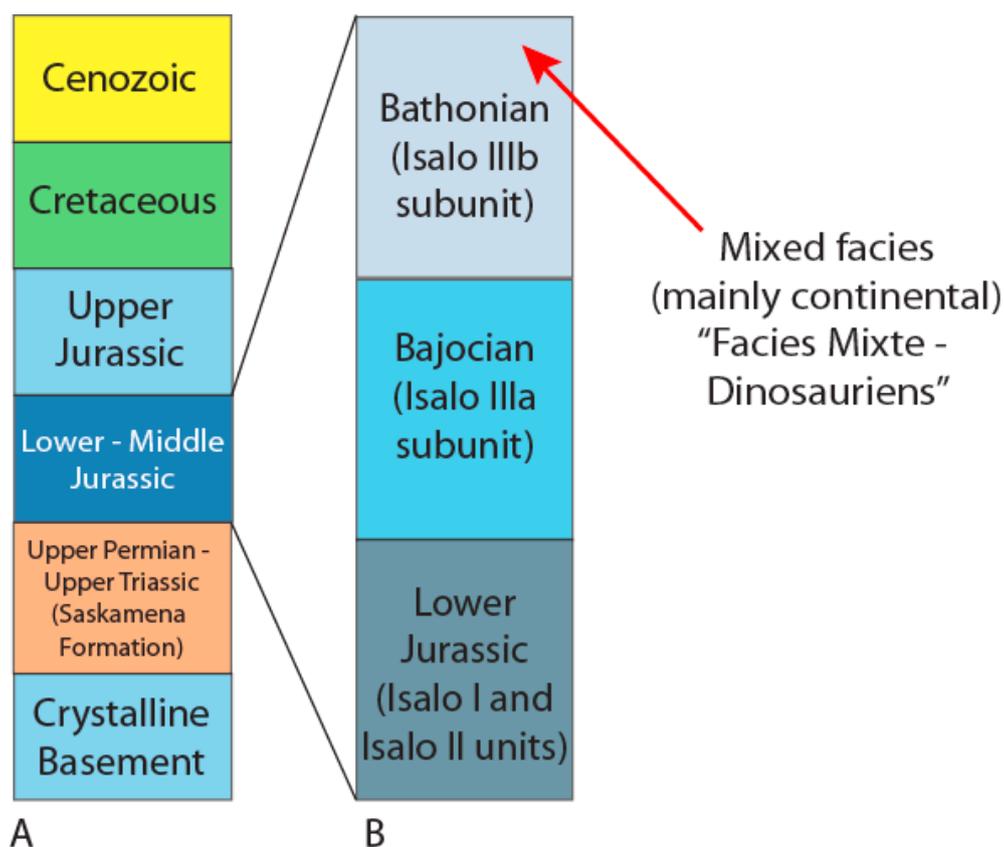


Figure 2. Geological sections of the whole Majunga Basin (A) and detail from near the village of Andranomamy (B). The arrow indicates the Bathonian Isalo IIIb Subunit “Facies Mixte Dinosauriens”, sensu Besairie [23]. (Redrawn from [24]).

2. Materials and Methods

The materials used for the morphological description include one broken left femur (Figure 3), one broken neural spine (Figure 4) thought to have belonged to a dorsal vertebra, and a caudal vertebra (Figure 5). The three bones belong to the hind limb and axial skeleton. The three bones are catalogued according to the locality name and the year of discovery (AND = Andranomamy; 15 = 2015) and deposited at the “David Krause” Collection Room at the Department of Paleontology and Biological Anthropology, University of Antananarivo (AND 15-001 for neural spine, AND15-002 for the middle distal caudal vertebra and AND 15-003 for the femur). Although the three bones are partly broken, some diagnostic features can be observed. The identification and assignment of the bones to any sauropod taxon still remains ambiguous but shared common autapomorphies with some taxa located from England can be identified [13]. However, more diagnostic material would need to be recovered before a full higher level systematic position can be determined with confidence. The identification of the common features between the two forms from England and Madagascar is the best and simplest way to support family level assignment of the bones. The main debate is about the systematic issue of *Lapparentosaurus madagascariensis* and the reliability of Ogier’s material (disarticulated, partial juvenile skeleton). This was later reinvestigated by Bonaparte [1], where he refers the material to his genus *Lapparentosaurus* with which he also includes the remains studied by Lydekker [3] and Thevenin [34]. This, despite a difference in the descriptions of the femur by Bonaparte and that of Mannion of the type material of *Bothriospondylus madagascariensis* (mainly based on Lydekker material) [2]. If it is to be shown that the two taxa are valid then there needs to be further study on some other aspects of the anatomy of the sauropod taxa from the Middle Jurassic of the Majunga Basin [35–38]. To recognize the systematic affinities of the Madagascan sauropod, a search of shared autapomorphies with *Cetiosaurus*

is an alternative method for identifying the family to which *Lapparentosaurus madagascariensis* belongs. However, the neural spines offered the only useful autapomorphy as the femur and the middle distal caudal vertebra do not show any significant autapomorphies. As *Lapparentosaurus madagascariensis* is considered as a non-neosauropod eusauropod by Mannion [20], the necessity for finding shared autapomorphies is critical for the determining partly the taxonomy issue at the family level, and to be confident with the relationship of the Madagascan taxa to the putative cetiosaurids located in other continents.

3. Results

Systematic Paleontology:

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Eusauropoda Upchurch, 1995

Cetiosauridae Lydekker, 1888

Lapparentosaurus madagascariensis, Bonaparte, 1986

Short diagnosis: Axial skeleton with tall dorsal vertebrae, posterior dorsals with elevated neural arches, and well-developed neural spines formed from four divergent laminae and with a massive dorsal region. Pneumatic fossae of dorsal vertebrae positioned on the anterior two-thirds of the lateral surface.

3.1. Anatomical Description

Characteristics of the Femur

In the description of Ogier's material by Bonaparte [1], the anterolateral surface of the proximal end of the femur bears two distinct ridges that extend ventrally and slightly medially across the femoral shaft. However, the material studied by Lydekker [3] has been redescribed by Mannion [2], who made the following statement: "The femoral head is a prominent, dorsomedially directed process (as in most sauropods) which is slightly anteroposteriorly wider than the greater trochanter. The greater trochanter is considerably lower than the femoral head, resulting in fairly steeply inclined greater trochanter surface." The absence of a prominent bulge in the lateral surface of the proximal end is considered to be the different from the femora of titanosauriforms [2,35]. In addition, according to the description of Lydekker [3], "the distal end of the femur has two distinct condyles for the tibia and fibula that are separated from one another by an intercondylar groove which shallow on the anterior and distal surfaces but becomes considerably more prominent on the posterior surface". A similar condition can be seen in the Rutland specimen of *Cetiosaurus* [13,14], but possibly found in other sauropod taxa. Furthermore, the presence of the slight bevelling of the distal end of the femur (Character coding: 201) [39], with the tibial condyle extending further distally than the fibular condyle (Character coding: 200) [39] is remarked on with regard to the Madagascan taxa [40], while the articular surface shape is restricted to distal portion of the femur (Character coding: 202) [39]. Such features are also present amongst a number of other sauropods (*Shunosaurus*, *Diplodocus*, *Cedarsaurus*, and *Tastavinsaurus*) [41], however, the identification of these features common to the Cetiosauridae and the Madagascan material supports the possibility that the Cetiosauridae are present in the Middle Jurassic of the Majunga Basin. Those features could represent shared autapomorphies between the two genera *Lapparentosaurus* and *Cetiosaurus*. That latter feature is also seen on the freshly recovered specimen in Andranomamy. It therefore seems that the new bone belongs to *Lapparentosaurus madagascariensis* and may be assignable to the Cetiosauridae (Table 1). The features in common between the femur of both *Lapparentosaurus* and *Cetiosaurus* are as follows:

- The great trochanter is considerably lower than the femoral head;

- No prominent bulge is present in the lateral surface on the proximal end (same as *Cetiosaurus*), different from femora of Titanosauriforms;
- Lesser trochanter is absent (Character coding: 197) [39];
- The 4th trochanter is supposed to be reduced to a low ridge possibly (character coding: 196) [39] located in the middle shaft but is expected to be straight (Character coding: 199) [39] and where the transverse diameter is subequal to 125%–150% anteroposterior diameter (character coding: 198) [39], which is also a missing part in Figure 3 (lies at the posteromedial margin of the shaft in *Haplocanthosaurus* and neosauropods).

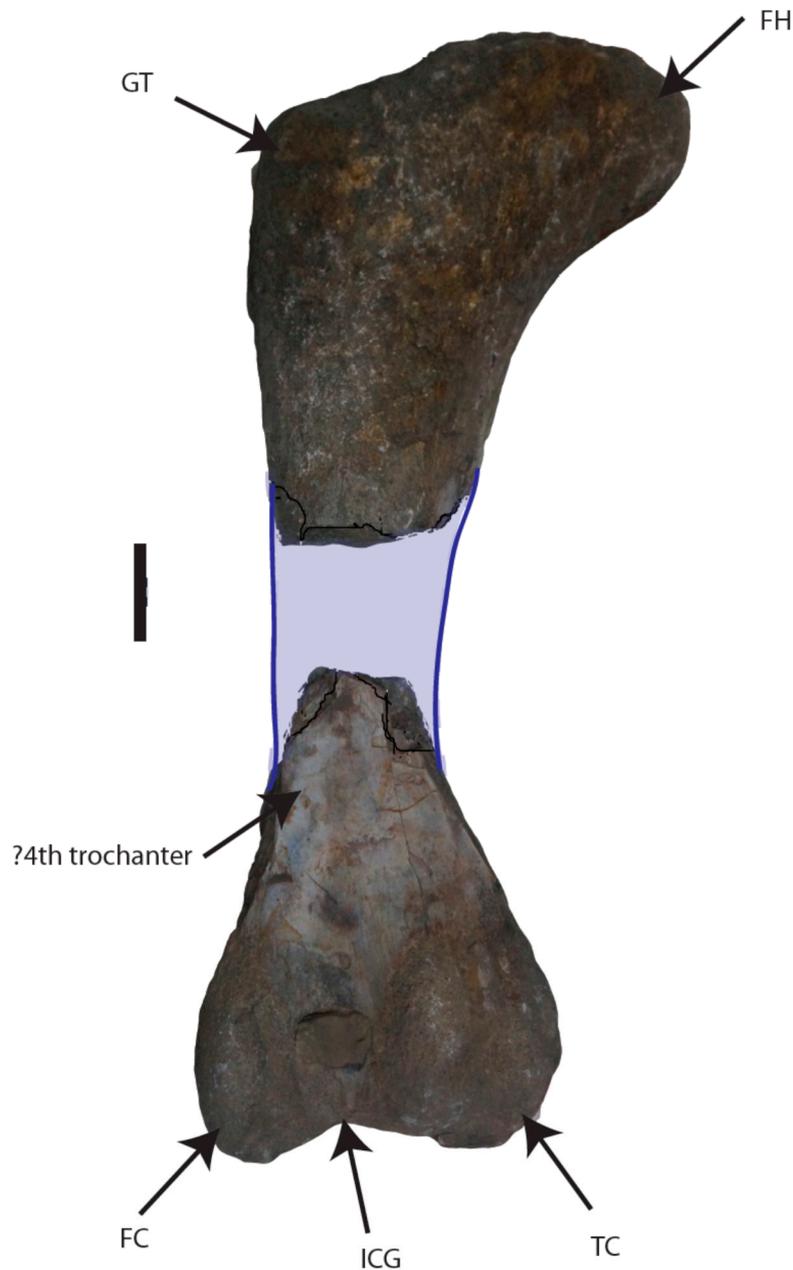


Figure 3. Left Femur in caudal view *Lapparentosaurus madagascariensis* missing the mid-shaft section; FC = fibular condyle; FH = femoral head; GT = greater trochanter; ICG = intercondylar groove; TC = tibial condyle. Scale = 10 cm.

3.2. The Neural Spine

The neural spine of the dorsal vertebra (Figure 4) in anterior view has a vertical orientation (character coding: 104) [39] and shows no spinopostzygapophysial lamina (spol) joining the spinodiapophysial lamina (spdl), which means no contact between them (character coding: 101) [39], while the latter lamina is absent (Character coding: 99) [39]. The spinoprezygapophysial lamina (sprl) is prominent in dorsal vertebra where it joins the prespinal lamina (prsl) on the neural spine to form a composite median lamina. A similar feature is also seen in the posterior view of the dorsal neural spine: the median spinopostzygapophyse lamina (spol) is simple (character coding: 100) [39] and probably prominent (worn part) and joins the postspinal lamina (posl) to form a composite median lamina (Table 1). As the spinodiapophyse lamina is restricted to dorsal and sacral vertebrae, and posteriorly reinforced by the branch of spinopostzygapophyse lamina to the most derived sauropod taxa such *Apatosaurus*, *Dicraesaurus*, and *Brachiosaurus* (Neosauropoda) [42], it is considered that *Lapparentosaurus madagascariensis* should be placed in the most basal group of eusauropods.

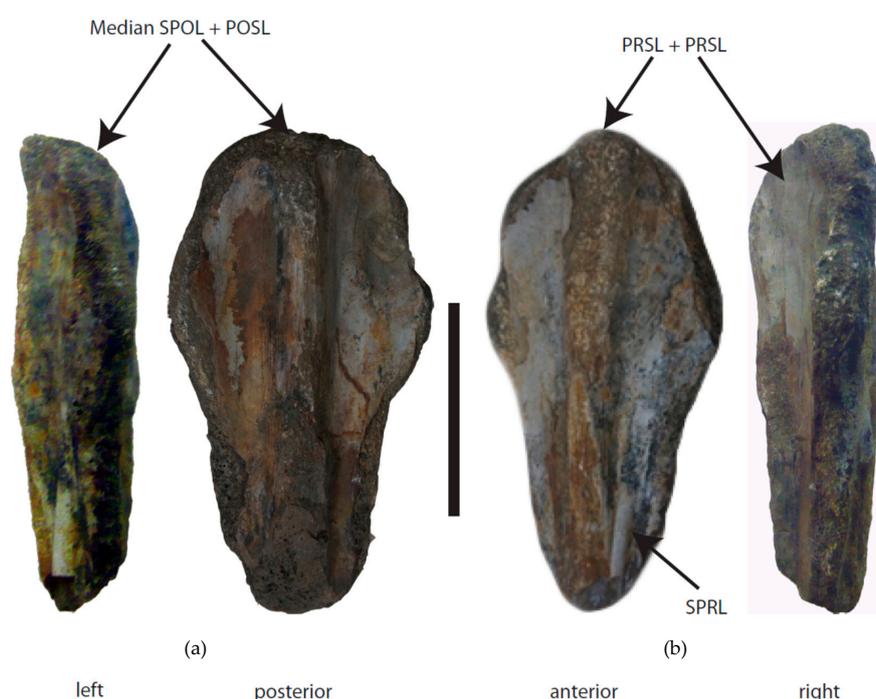


Figure 4. Posterior (a) and anterior (b) views of the neural spine of *Lapparentosaurus madagascariensis*; POSL = posterior median composite lamina; PRSL = anterior composite lamina; SPDL = spinodiapophysial lamina; SPOL = inferred position of the lateral laminae [42]. Scale = 10 cm.

3.3. The Vertebra

Although the vertebra is seriously damaged (Figure 5), some features can be observed with careful study. So, it is likely supposed that the both surfaces of the centrum are concave that helps to determinate the amphicoelous state of the vertebra (Character coding: 105) [39] if the view is oriented on the posterior or caudal side. It is likely to belong to an anterior caudal position [43] as the neural arch fossa is just above the centrum. However, in left lateral view and posterior view, an invaginated area which is identified as a fossa, following the nomenclatural system adopted by Wilson [43]. No neural spine has been recognized above the centrum. The vertebra has no neural spine preserved so the presence of a cdf (centrodiapophyseal fossa) or cpaf (centroparapophyseal fossa) can be seen. In the case of basal sauropods, non-neosauropod eusauropods, and macronarian dinosaurs, neither of those fossae occur in the lateral view of caudal vertebrae. We therefore consider the invaginated

area of the centrum equivalent to the cpaf which is in the correct position relative to the neural spine. Therefore, it is likely that the vertebra is a posterior dorsal rather than anterior caudal (Table 1).

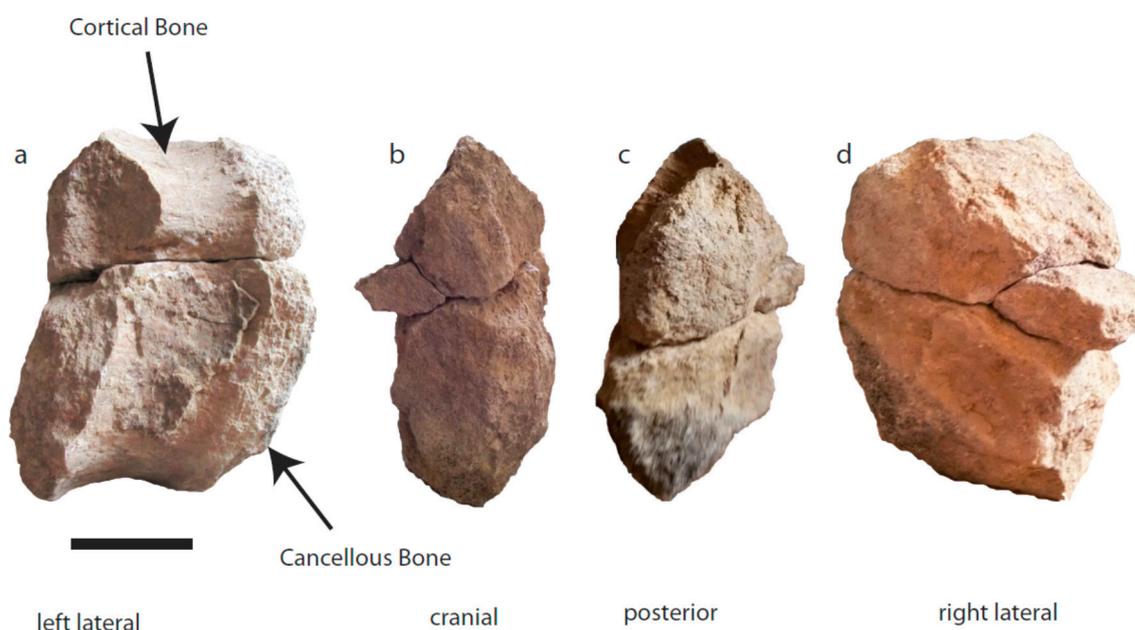


Figure 5. Left lateral (a); cranial (b); posterior (c); and right lateral (d) view of posterior dorsal vertebra of *Lapparentosaurus madagascariensis*. Scale = 10 cm.

Table 1. Resume of the main anatomical features of the three new materials.

Anatomical Element	Measurement	Short Detailed Description
Femur	Length: 710 mm from the tip of femoral head until the tip of the distal part of the femur	A short-sized femur but heavy and no 4 th trochanter which is supposed to be located in the main area of the shaft (Missing part length roughly to be 210 mm)
Neural spine	Length: 225 mm from the top of the neural spine until the border tip of the centrum.	A relatively flat neural spine in lateral view with different orientation of laminae
Vertebra	Height: from the top of the centrum until the base of the centrum 170 mm	A low-heighted centrum which is supposed to belong to a posterior dorsal.

4. Discussions

4.1. Affinities with the Genus *Cetiosaurus*

Five potential autapomorphies are recognized to be belonged to the Middle Jurassic species from UK, and according to the paleogeographical world map, the Madagascan form should not get separated from the features which are identified to the other Middle Jurassic dinosaur sauropods encountered in other province areas. Here are the autapomorphies which are related to the Genus *Cetiosaurus*.

- Pyramid-shaped neural spines in posterior cervical and anterior dorsal vertebrae;
- Loss of the spinodiapophysal lamina on dorsal vertebrae;
- Anterior chevrons with anteroposteriorly compressed distal shaft;
- Distal caudal centra have a tongue-like projection at the dorsal midline of their articular ends;
- A distinct hollow on the lateral surface of the ilium at the base of the pubic process.

Among the five autapomorphies, two have been identified between the two taxa (*Cetiosaurus oxoniensis* and *Lapparentosaurus madagascariensis*); a pyramid-shaped neural spine from the anterior dorsal vertebrae with tapering in shape or not flaring distally (Character coding 102) [39] and loss of the spinodiapophyseal lamina on the dorsal vertebrae. Among five listed autapomorphies encountered in the genus *Cetiosaurus*, two are recognised [13] also to be present in the Malagasy form.

4.2. Family Affinities of the Madagascan Form

Bonaparte [1], during the reinterpretation of the material described by Ogier [35], did not recognize any autapomorphies in common between the English and Malagasy forms. He did, however, mention morphological characters in relation to the humerus and the femur. As the material described by Ogier [35] belongs to a juvenile, he did not consider potential ontogenetic variation whilst studying the autapomorphies encountered in the Malagasy form. Material studied by Lydekker [3] from Narinda Bay is thought to be sub-adult to adult and exhibits later ontogenetic characters with some autapomorphic features which are somewhat easier to recognize. Most of the anatomical character analysis, based on these very few fragmentary specimens, aims at resolving the additional information related to taxonomic issue of *Lapparentosaurus madagascariensis*. Even the large polytomy of the cetiosaurids produced using the phylogenetic analysis by Lang [10] was largely unresolved, with only two recognized autapomorphies among five for the genus type *Cetiosaurus*, it would be better to consider *Lapparentosaurus madagascariensis* a basal cetiosaurid. The scope of taxonomic resolution is very restricted here, allowing the identification of only two recognized autapomorphies with only one related to the neural spine (Pyramid-shaped neural spine and loss of the spinodiapophyseal lamina in dorsal vertebra).

The Patagonian cetiosaurid *Volkheimeria chubutensis* also considered to be a primitive cetiosaurid due to its vertebral structure [40]; the dorsal neural spines are relatively flat in lateral view with straight anterior and posterior borders of the axial lamina, both of which are also considered to be similar to the Malagasy form *L. madagascariensis*.

L. madagascariensis was considered by Mannion to be a titanosauriform (Mannion 2005) [2], despite not recognizing the existence of the Middle Jurassic titanosauriform body fossil [20].

Although long bones are not usually diagnostic to genus or family level in sauropods (Upchurch, pers. comm.), some characters support the assignment of the Malagasy Bathonian form to the Cetiosauridae.

4.3. Reliability of the Taxonomic Affinities of the Madagascan Form

The strict consensus cladistics analysis by Lang [10] based on 16 parsimonious trees allows the members of the paraphyletic group of cetiosaurid dinosaurs to be easily distinguished. Further resolution of this will require more detailed analysis of the skeletons based on better material. Finally, more studies need to be undertaken on the fossa of the vertebrae of *Lapparentosaurus madagascariensis* and comparing those of *Cetiosaurus*, *Chebsaurus*, *Ferganasaurus* (phylogenetically close relatives) and the coeval *Volkheimeria* focusing on cervical, dorsal, and anterior caudal vertebrae. This is a critically important to ensure reliability in the determination of the full systematic position of *Lapparentosaurus madagascariensis*.

5. Conclusions

Two anatomical details have been identified as potential autapomorphies encountered to the Malagasy form—a pyramid-shaped neural spine from the anterior dorsal vertebrae and loss of the spinodiapophyseal lamina on the dorsal vertebrae. These are specifically identified to only one anatomical part of the axial skeleton. That is a basic approach to confirm the position of *Lapparentosaurus madagascariensis* to be nested within the clade of the Cetiosaurids.

However, among the 13 surveyed coding characters [39], only three have primitive state of characters. That is one another proxy to confirm the position of the *Lapparentosaurus madagascariensis* to be placed in the basal non-Neosauropod eusauropod dinosaurs.

As the Ogier material pertaining to MNHN MAJ 289 [35] can and should currently be considered as belonging to *Lapparentosaurus*, these three postcranial specimens recently recovered (described above) can help towards determining the familial relationships of the Malagasy taxa. The material studied by Ogier [35], and redescribed by Bonaparte [1] (especially with reference to the femur), and those described by Lydekker [3] could belong to the same species but important characters may have been absent due to the material being of a juvenile. Although the femur (Figure 3) is not complete, because the central shaft is missing, the freshly recovered material (femur and neural spine) from the Bathonian of Andranomamy fits well with the redescription of '*Bothriospondylus*' by Mannion [2,36]. As *Bothriospondylus* is now considered an invalid taxon not formally registered by the ICZN [12], the ontogenesis of the Madagascan sauropod form has not been fully studied and no additional sauropod taxa have been found from the Middle Jurassic of the Majunga Basin. Nevertheless, the newly recovered material most likely belongs to *Lapparentosaurus madagascariensis*. The numerous similarities shared between the Malagasy form and the following genera: the Patagonian *Volkheimeria*, the Indian *Barapasaurus*, and the British *Cetiosaurus* strongly suggest that the Malagasy form also belongs to the Cetiosauridae. As valid British cetiosaurids range in age from the Bajocian to Bathonian [7], and the Malagasy form shares a similar niche and ecology to those from the Middle Jurassic of Europe, the Malagasy form should be included in that family.

However, further discoveries of Middle Jurassic sauropods and better anatomical survey of characters of *Lapparentosaurus madagascariensis* will be needed to allow a more reliable position of Madagascan non-Neosauropod eusauropod [20] within the Cetiosaurid taxa. The survey of the Indian, Pentagonian, and English forms which is related to the identification of the autapomorphies and the biomechanical aspect of the femur will be directed to the study of the systematics, paleoprovince, and paleoecology of the Cetiosauridae family.

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