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Phylogenetic analysis of Gondwanan basal eusauropods from the Early-Middle Jurassic of Patagonia, Argentina

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ABSTRACT

Gondwanan Jurassic non-neosauropod eusauropods are key for the understanding of sauropod evolution, although their phylogenetic interrelationships remain poorly understood. However, following the revision of the holotype of a key taxon from the early Middle Jurassic Cañadón Asfalto Formation Patagonia, Argentina, *Patagosaurus fariasi*, the phylogenetic affinities need to be tested with new osteological information gathered during the redescription of the holotype of *Patagosaurus*. A new phylogeny presented here shows a close affiliation of *Patagosaurus* with *Cetiosaurus* from the Middle Jurassic of the UK. The close relationship of *Patagosaurus* with *Barapasaurus*, often found in previous phylogenies, was not recovered here. Instead, *Patagosaurus* is retrieved as more derived than most Early and Middle Jurassic sauropods, although more basal to *Mamenchisaurus*, *Omeisaurus*, turiasaurians, and neosauropods. Another sauropod taxon found together with *Patagosaurus*, *Volkheimeria*, is retrieved several nodes more basal than the former, which shows, together with evidence of several other sauropod taxa in

RESUMEN

Los eusaurópodos no neosaurópodos del Jurásico de Gondwana son especies clave para la comprensión de la evolución del clado Sauropoda, aunque sus relaciones filogenéticas siguen sin estar bien resueltas. Sin embargo, gracias a la revisión del holotipo de uno de los taxones más importantes del Jurásico Medio temprano de la Formación Cañadón Asfalto, *Patagosaurus fariasi*, bastantes de sus hipótesis filogenéticas han de ser puestas en duda, basadas en la nueva información osteológica recogida durante la redescripción del holotipo de *Patagosaurus*. La nueva hipótesis filogenética aquí presentada muestra una relación cercana entre *Patagosaurus* y *Cetiosaurus*, del Jurásico Medio del Reino Unido. La cercanía filogenética de *Patagosaurus* con *Barapasaurus*, publicada en numerosos análisis filogenéticos, no se obtuvo en este nuevo análisis. En este caso, *Patagosaurus* aparece como un taxón más derivado que la mayoría de saurópodos del Jurásico Medio y Superior, aunque más basal que *Mamenchisaurus*, *Omeisaurus*, Turiasauria y Neosauropoda. Otro taxón que se encuentra normalmente emparentado con *Patagosaurus*,

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the Cañadón Asfalto Formation, that a high evolutionary diversity existed in Southwest Gondwana in the early Middle Jurassic, a pattern which is also seen in fossil groups other than sauropods (e.g., theropods).

Keywords: Middle Jurassic, Gondwana, Patagonia, sauropod, phylogeny.

Volkheimeria, en nuestro análisis aparece varios nodos más basalmente que *Patagosaurus*. Esto muestra, junto con la presencia de otros taxones de saurópodos de la Formación de Cañadón Asfalto, que una diversidad evolutiva alta existió en el suroeste de Gondwana en el Jurásico Medio temprano, un patrón que también está presente en otros grupos fósiles (e.g., terópodos).

Palabras clave: Jurásico Medio, Gondwana, Patagonia, saurópodo, filogenia.

1. INTRODUCTION

Non-neosauropod sauropods are thought to have emerged in the Late Triassic of South Gondwana, although remains of a basal sauropod are known from possible Triassic sediments of Thailand (Buffetaut *et al*., 2000, 2002; Racey & Goodall, 2009) and recently described ichnofossils suggest the presence of sauropods in the Late Triassic of Greenland (Lallensack *et al*., 2017). After their initial appearance in the fossil record, sauropods achieved a worldwide distribution by the Early Jurassic (Raath, 1972; Jain *et al*., 1975; Cooper, 1984; McPhee *et al*., 2015, 2016), with non-neosauropod eusauropods first appearing in the fossil record in the early Middle Jurassic of Gondwana and Laurasia, with most material coming from South America (e.g., *Patagosaurus, Volkheimeria*) (Bonaparte, 1979, 1986a), Africa (e.g., *Spinophorosaurus, Lapparentosaurus, Bothriospondylus*) (Bonaparte, 1986b; Läng, 2008; Remes *et al*., 2009; Mannion, 2010), and India (e.g., *Barapasaurus*) (Jain *et al*., 1975; Bandyopadhyay *et al*., 2010). Other forms are known from Europe (e.g. *Cetiosaurus* and Asia (e.g. *Shunosaurus*) (Zhang, 1988) but they are found in younger sediments of late Middle Jurassic age, or even early Late Jurassic (Wang *et al*., 2018). By the Late Jurassic boundary (~ 150Ma) all major clades were established (McIntosh, 1990; Upchurch *et al*., 2004; Barrett & Upchurch, 2005; Wilson, 2005). The Gondwanan taxa are especially important for the study of sauropod evolution, as they are represented by the most complete record to date of early eusauropod body fossils. *Patagosaurus fariasi* is one of the best-preserved taxa with a plethora of referred material (Bonaparte, 1986a) found in two localities of the Cañadón Asfalto Formation near the Cerro Cóndor village in central Patagonia, Argentina. Though used in many phylogenies, it has not received much revision since it was named and first described in 1979 and 1986 by Bonaparte, and therefore its current phylogenetic position is unclear. Moreover, the strata from whence *Patagosaurus* and *Volkheimeria* were unearthed contain at least three other (as yet unnamed) sauropod taxa (Pol *et al.,* 2009; Rauhut, 2003a; Holwerda *et al*., 2015; Becerra *et al*., 2017; Carballido *et al.,* 2017). This shows a higher taxic diversity than elsewhere in Gondwana or Laurasia in contemporaneous beds. Finally, the Cañadón Asfalto Formation has recently been redated and found to be much older than previously assumed; roughly ranging between Toarcian–Bajocian (Cúneo *et al*., 2013), placing the fossils from the Cañadón Asfalto Formation right at the time of the early eusauropod diversification and radiation (Bonaparte, 1986b; Barrett & Upchurch, 2005; Cúneo *et al*., 2013).

Traditionally, *Patagosaurus* is retrieved as a basal eusauropod, more derived than *Shunosaurus*, and more basal to *Mamenchisaurus*, *Omeisaurus*, turiasaurians and neosauropods (see, for instance, Upchurch, 1998; Wilson, 2002; Harris, 2006; Carballido *et al*., 2011, 2012). In some phylogenetic analyses, *Patagosaurus* has come out either as sister taxon to the Indian Early–Middle Jurassic taxon *Barapasaurus* or the Middle Jurassic *Cetiosaurus* from the UK (Allain & Aquesbi, 2008; Remes *et al*., 2009). Other phylogenies recover *Patagosaurus* as more derived than either *Barapasaurus* or *Cetiosaurus* or one or other as more/less derived. The analysis of Läng & Mahammed (2010) recovers *Patagosaurus* as more derived than *Barapasaurus*, *Cetiosaurus oxoniensis*, and *Cetiosaurus mogrebiensis,* but more basal to the Rutland *Cetiosaurus*. The differing results of several phylogenies, which incorporate more basal sauropods reflect on the paucity of information on Early and Middle Jurassic sauropods.

Bonaparte (1986a) traditionally grouped *Barapasaurus*, *Cetiosaurus* and *Patagosaurus* together as ‘cetiosaurs’ based on morphological similarities, primarily in posterior dorsal vertebrae. With new information on the osteology of *Patagosaurus*, these relationships can be revisited. *Volkheimeria*, found together with *Patagosaurus* in the Cerro Cóndor localities, Patagonia, Argentina, was thought to be closely related to the Malagasy taxon *Lapparentosaurus* by Bonaparte (1986a, 1986b), however, in some phylogenies *Volkheimeria* is retrieved as more basal than *Patagosaurus* (e.g., Pol *et al*., 2011) and *Lapparentosaurus* has rarely been included in phylogenetic datasets, save for the analyses of Läng (2008) and Mannion *et al*. (2013). Recoding these specimens may further elucidate the interrelationships of Gondwanan eusauropods, which in turn will aid in sauropod evolutionary and biogeographical research.

Here, we present a new phylogenetic analysis focusing on Jurassic Gondwanan sauropods, together with an updated systematic review of all major Jurassic sauropod taxa that provide osteological information for phylogenetic analysis.

2. METHODS

2.1. Coding

Coding was done based on first-hand observations of the holotype of *Patagosaurus* (Instituto Miguel Lillo, Tucuman, Argentina), *Cetiosaurus oxoniensis* (OUMNH, Oxford, UK) and the Rutland *Cetiosaurus* (New Walk Museum and Art Gallery, Leicester, UK), *Lapparentosaurus* (MNHN, Paris, France), *Amygdalodon* (Museo de La Plata, Argentina), *Bothriospondylus* (NHM, London), *Cetiosauriscus* (NHM, London), *Tazoudasaurus* (MNHN, Paris), *Spinophorosaurus* and *Jobaria* (NMB, Naturhistorisches Museum Braunschweig, Braunschweig, Germany). All other sauropods in this matrix were coded using photographs, publications and information from previous matrices.

The matrix used is based on Carballido *et al*. (2012), to which characters were added by McPhee *et al*. (2014) as well as new characters which were added by the authors. See Supplementary Data for a list of characters and their coding.

2.2. Software

The data matrix was coded using Mesquite version 2.75 (Maddison & Maddison, 2010).

The resulting data matrix was analysed in TNT (Goloboff *et al*., 2008) in TNT version 1.5 (Goloboff & Catalano, 2016).

3. RESULTS

3.1. Systematic revision of Middle Jurassic Gondwanan sauropods

An updated systematic overview of several relatively well represented Early and Middle Jurassic sauropods used in this analysis is given below.

Patagosaurus fariasi was found in the late 70's and early 80's, it was named in 1979 and more fully described in 1986 (Bonaparte, 1979, 1986a). Several specimens were found from two localities, Cerro Cóndor Norte (which yielded the holotype specimen) and Cerro Cóndor Sur, both in the Cañadón Asfalto Formation, west-central Chubut Province, Patagonia, Argentina. The age is probably Aalenian–Bajocian, which is significantly older than the original Callovian age given (Bonaparte, 1986a; Cúneo *et al*., 2013). It is now believed that the material originally assigned to *Patagosaurus* includes at least one other taxon, and, possibly, two further taxa (MACN-CH 934, MACN-CH 230; Rauhut, 2003a). For this analysis, however, only the holotype PVL 4170 is coded.

Barapasaurus tagorei is an Indian taxon from the Early Jurassic Kota Formation, Pranhita-Godavari basin, Deccan, India (Bandyopadhyay *et al*., 2010). It was first described in the 1970's (Jain *et al*., 1975; Jain, 1980) and was recently redescribed (Bandyopadhyay *et al*., 2010). Next to the basal sauropod *Kotasaurus* (Yadagiri, 2001; Kutty *et al*., 2007), it is the only Indian Early Jurassic taxon known to date, and is therefore important for the study of Gondwanan sauropod evolution. It is known from several specimens, and includes teeth, as well as axial and appendicular material including pelvic and pectoral elements.

Cetiosaurus oxoniensis is historically speaking the oldest sauropod to be described, despite being deliberately omitted from the first paper naming Dinosauria, as it was thought to be a marine animal. Although not completely described until 1871 (see Owen, 1841, 1842; Phillips, 1871; Upchurch & Martin, 2003; Taylor, 2010), its first description dates from 1841 (the same year that *Cardiodon* was first described but based only on an isolated tooth (Owen, 1841; Taylor, 2010). The genus has, unfortunately, become a wastebasket for many *nomina dubia* and *nomina nuda* over the years. The type species under ICZN regulations was *Cetiosaurus medius*, which is a very incomplete series, however in 2009 the *Cetiosaurus* specimen known as the Bletchingdon specimen, from near Oxford, which is a large individual with many more skeletal elements than *C. medius*, was designated as the type species after an ICZN case was made (Taylor, 2010; Upchurch *et al*., 2009; Upchurch & Martin, 2003). It is from the Forest Marble of Oxfordshire, UK, which is Bathonian in age (±168 Ma). The specimen includes a caudal series, one partial cervical, a partial dorsal, and many appendicular elements, as well as pectoral and pelvic elements.

The "Rutland *Cetiosaurus*" is a sauropod found in Rutland, Leicestershire, UK, in 1968 in a brick pit, the sediments of which are dated as upper Bajocian (±175 Ma). The specimen is the most complete sauropod from the UK to date, consisting of a well-preserved cervical and dorsal series, several caudals, and several (though more fragmentary) appendicular elements. It was originally ascribed to *Cetiosaurus oxoniensis* (Upchurch & Martin, 2002), however, recently several differences have been found between the Rutland *Cetiosaurus* and *Cetiosaurus oxoniensis*, which could mean that the Rutland *Cetiosaurus* is in fact a different species from *C. oxoniensis*, which has previously been proposed (Läng, 2008).

Volkheimeria chubutensis is a sauropod from the locality of Cerro Cóndor Sur, Cañadón Asfalto Formation, west-central Chubut, Patagonia, Argentina. It is known from several vertebral and appendicular elements, as well as pelvic elements. It was found together with *Patagosaurus*, and described in 1979 and 1986 by Bonaparte.

Amygdalodon patagonicus is an Early Jurassic sauropod from Patagonia, Argentina. It was found in the Cerro Carnerero Formation at Pampa Agnia, Patagonia, Argentina, which was thought to be Bajocian, but may be as old as Pliensbachian-Toarcian (see Rauhut, 2003a; Cúneo *et al*., 2013). It was first described in 1947 (Cabrera, 1947), redescribed in three subsequent papers (Casamiquela, 1963; Rauhut, 2003b; Carballido & Pol, 2010). The material consists of isolated teeth, several appendicular elements and some fragmentary axial elements. It has been retrieved as a sauropod basal to *Tazoudasaurus*, *Vulcanodon*, and eusauropods. The dentition, in particular the enamel wrinkling pattern, thus far has been found to be unique amongst other basal sauropods (Carballido & Pol, 2010).

Tazoudasaurus naimi was found in the High Atlas Mountains in Morocco, North Africa, from the Azilal/Wazzant Formation, which is thought to be Toarcian to Aalenian in age, with *Tazoudasaurus* coming most probably from the Toarcian layers (Allain *et al*., 2004; Allain & Aquesbi, 2008). It is known from several individuals, both juveniles and adults, which sheds light on early sauropod ontogenetic variation. The material consists of dentition, cranial, axial, and appendicular material. A reconstruction of *Tazoudasaurus* has also been recently attempted (Peyer & Allain, 2010).

Spinophorosaurus nigerensis is a recently described basal eusauropod from the Middle Jurassic of Niger, Africa (Remes *et al*., 2009). It is known from several specimens, most of which are still under preparation. A full osteology is currently in the making (F. Knoll, pers. comm.). The holotype consists of several axial elements, cranial elements, teeth, and several pectoral, pelvic and appendicular elements. A braincase was described in 2012, drawing attention to a combination of primitive and derived characters (Knoll *et al*., 2012), which is not unusual for basal eusauropods. Lastly, this sauropod is peculiar for Jurassic sauropods in that it probably possessed tail spines (Remes *et al*., 2009).

Shunosaurus lii was found in 1977, named in 1983 and further described in 1988 (Dong *et al*., 1983; Zhang, 1988). It was found in the Lower Xiashaximiao Formation near Dashanpu, Zigong, China, which was thought to be Bathonian to Oxfordian in age (±168-157 Ma), however, recent redating of the depositional sediments yields a maximum age of 159 ±2 Ma, giving it an Oxfordian age (Wang *et al*., 2018). It is the most common sauropod from the Xiashaximiao Formation. It was thought to be a euhelopodid sauropod by Upchurch (1995, 1998), however, Wilson (2002) retrieved it as a basal eusauropod. A redescription of cranial material was published more recently, which found a unique curvature in both the maxillae as well as the dentaries (Chatterjee & Zheng, 2002; Zheng, 1996). A more recent description of the postcranial material, however, has not been performed. More redescriptions of Chinese sauropods from the Middle Jurassic will give more information on the phylogenetic position of *Shunosaurus*. Currently, it is usually found at the base of the eusauropods, being more basal than *Cetiosaurus, Patagosaurus*, and all other sauropods, but more derived than *Vulcanodon, Tazoudasaurus, Amygdalodon*, and *Spinophorosaurus* in phylogenetic analyses. Finally, it is peculiar amongst Jurassic sauropods due to the presence of a tailclub, something found otherwise (thus far) only in *Spinophorosaurus, Mamenchisaurus*, and potentially *Kotasaurus* (Xing *et al*., 2009; Ouyang & Ye, 2002; Remes *et al*., 2009).

Mamenchisaurus is a generic name for many different species, the most important for this study being *Mamenchisaurus youngi* and *Mamenchisaurus hochuanensis* (Young & Zhao, 1972; Russell & Zheng, 1993; Pi *et al*., 1996; Ouyang & Ye, 2002). The Mamenchisauridae is a group of Laurasian sauropods with extreme neck elongation, and their remains have been found in China, Thailand, and Mongolia (Suteethorn *et al*., 2012; Xing *et al*., 2015). The *Mamenchisaurus* fauna, unlike the *Shunosaurus*-*Omeisaurus* fauna, is Middle Jurassic in age (Wang *et al*., 2018). Their interrelationships are a work of ongoing progress, as in many eusauropod phylogenies they emerge as more derived than most derived non-neosauropod eusauropods, like *Cetiosaurus* and *Patagosaurus* (e.g., Wilson, 2002; Upchurch *et al*., 2004; Allain & Aquesbi, 2008; Remes *et al*., 2009). This could, however, be due to only one species of *Mamenchisaurus* generally being used for sauropod phylogenies (and then it usually is retrieved as sister-taxon to *Omeisaurus*) since within a mamenchisaurid-based phylogeny they are retrieved as more basal than most non-neosauropod eusauropods (Xing *et al*., 2015).

Omeisaurus is a generic name for species that include *Omeisaurus maoianus, Omeisaurus junghsiensis*, and many others. It was found in the Shaximiao Formation of Sichuan Province, China, which was dated to the Bathonian-Callovian (±178-168 Ma), however, like *Shunosaurus*, it is recently found to be Oxfordian in age (159 ± 2 Ma) (Wang *et al*., 2018). It was first described in 1939, and more specimens were added to the genus in the 1970's and 1980's, several of them supposedly representing different species. The most recent descriptions are from the early 2000's, however (Young, 1939; Dong *et al*., 1983; He *et al*., 1984, 1988; Tang *et al*., 2001; Wings *et al.,* 2011).

3.2 Phylogeny

The matrix used consists of 350 characters and 75 taxa. Pruning was done for unstable taxa after the tree searches by using IterPCR (Pol & Escapa, 2009; Goloboff & Szumik, 2015). Taxa to be pruned a-posteriori were *Cetiosauriscus stewarti* and *Klamelisaurus gobiensis*. Both sauropod taxa are either in need of revision or are currently under revision (see Heathcote & Upchurch, 2003; Moore *et al*., 2017). The resulting consensus tree with Bremer support is shown in Figure 1.

Patagosaurus is retrieved as sister taxon to the Rutland *Cetiosaurus*, and nested within *Cetiosaurus*, (see Table 1 for a list of synapomorphies). Furthermore, *Barapasaurus*, the other 'cetiosaur', is retrieved as less derived, being sister-taxon to the node of *Spinophorosaurus+Volkheimeria*, which all together are more basal to *Shunosaurus* and *Patagosaurus+Cetiosaurus*. Moreover, it takes 14 steps to force *Barapasaurus* to nest within *Cetiosaurus oxoniensis* and it takes 15 extra steps for it to go into a sister-group with *Patagosaurus* and the Rutland *Cetiosaurus* (Table 2). In a previous analysis by Remes *et al*. (2009), *Patagosaurus+Barapasaurus* were only one step away from the shortest trees. The main characters that differ between *Patagosaurus* and *Barapasaurus* are the ventral surface of the dorsal centra (ch.153) and the projection of the neural spine of anterior caudal vertebrae (ch.221). *Spinophorosaurus*, on the other hand, needs only two steps to be nested with *Cetiosaurus*, and 3 steps to be sister taxon to *Patagosaurus*. Other than this, the tree does not change much from previous analyses, in that *Tazoudasaurus* and *Vulcanodon* come out as sister-taxa, and more basal to *Barapasaurus*, as was previously also found (Allain & Aquesbi, 2008; Läng, 2008). *Patagosaurus* is also still found to be more basal to mamenchisaurs, turiasaurians, and neosauropods, which was also found in previous analyses (e.g., Wilson, 2002; Harris, 2006; Carballido *et al*., 2012, 2015; Carballido & Sander, 2014) Neosauropoda. However, the re-coding of *Volkheimeria* retrieves this taxon as more basal than *Patagosaurus,* forming a sister-group with the North African Middle Jurassic taxon *Spinophorosaurus.* In the current analysis, only takes one additional step to undo this grouping, however, it takes eleven steps to force *Volkheimeria* as sister taxon to *Patagosaurus*. *Volkheimeria* was recovered as a basal sauropod in a previous analysis (Pol *et al*., 2011) however, in the 2011 analysis it was recovered as more derived than *Shunosaurus*, and more basal than *Lapparentosaurus*, *Barapasaurus*, *Omeisaurus*, and *Patagosaurus*.

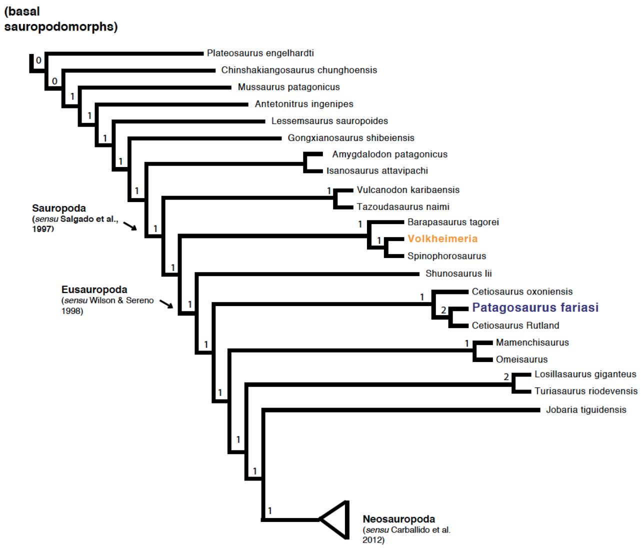

Figure 1. Consensus tree with Bremer support, *Patagosaurus* highlighted in blue and *Volkheimeria* highlighted in yellow.

Table 1. List of synapomorphies for *Patagosaurus* and other nodes.

Node	Synapomorphies
Spinophorosaurus + Volkheimeria	155: weakly developed hyposphene-hypanthrum complex on posterior dorsals
Barapasaurus + eusauropods	108: presence of longitudinal grooves on teeth 175: height of pedicels of middle and posterior dorsal postzygapophyses subequal or higher than centrum
Patagosaurus + Rutland Cetiosaurus	123: Complex pleurocoel on cervical centra 134: laterally expanded neural spine on posterior cervicals 157: single tpol supporting hyposphene from below 179: medial spol on posterior dorsals
Cetiosaurus + Patagosaurus + Rutland Cetiosaurus	164: pcpl absent on middle and posterior dorsals 165: slightly dorsoventrally compressed dorsal centrum 175: height of pedicels of middle and posterior dorsal postzygapophyses subequal or higher than centrum 217: presence of ventral longitudinal hollow on anterior and middle caudals
Mamenchisaurus + eusauropods	115: presence of pleurocoels within cervical centra 137: 12 or more dorsal vertebrae 138: pleurocoels in dorsal centra 148: single neural spines on dorsal vertebrae 174: dorsal contact of spdl + lspol 192: dorsoventral length sacral ribs 238: size scapular acromion process

Table 2. number of steps required to move key taxa to other nodes or positions.

Taxon	Moved to position/node	n.o. extra steps required
Barapasaurus	*Cetiosaurus oxoniensis*	12
Barapasaurus	*Patagosaurus* + Rutland *Cetiosaurus*	15
Barapasaurus	Sister taxon to *Patagosaurus*	14
Barapasaurus	Spinophorosaurus + Volkheimeria	8
Patagosaurus	Sister taxon to *Cetiosaurus oxoniensis*	5
Spinophorosaurus	*Cetiosaurus oxoniensis*	2
Spinophorosaurus	Sister taxon to *Patagosaurus*	3
Spinophorosaurus	Sister taxon to Rutland *Cetiosaurus*	5
Volkheimeria	*Patagosaurus* + Rutland *Cetiosaurus*	11
Volkheimeria	Sister taxon to *Patagosaurus*	14

4. DISCUSSION

Even though the phylogenetic position of *Patagosaurus* with respect to most non-neosauropod sauropods does not differ much in this analysis from previous analyses, the nesting of *Patagosaurus* within *Cetiosaurus* is an interesting new outcome of this phylogeny. This position does confirm the original assessment of Bonaparte (1986a), in that *Patagosaurus* and *Cetiosaurus* share a close phylogenetic affinity. Both are from roughly the same age; *Patagosaurus* from the early Middle Jurassic (likely Aalenian–Bajocian), *Cetiosaurus oxoniensis* from the Bathonian, and the Rutland *Cetiosaurus* being Bajocian in age (Cox *et al*., 1992; Upchurch & Martin, 2002, 2003; Liston, 2004a, 2004b; Barrett, 2006; Noè, *et al*., 2010; Cúneo *et al*., 2013; Hauser *et al*., 2017). Further research, especially on the Rutland *Cetiosaurus*, might give more information on the precise relationships between these taxa and whether or not the 'cetiosaurs' as a group are in need of revision.

The separation of *Patagosaurus* and *Barapasaurus* by several steps is another new outcome of this analysis. The break-up of the *Barapasaurus*+*Patagosaurus* grouping has interesting biogeographical implications. Remes *et al*. (2009) suggested the Central Gondwanan Desert may be a biogegraphical barrier that isolated southern Gondwana and cited the sister-group relationship of *Barapasaurus*+*Patagosaurus* as lending support to this hypothesis. The new phylogenetic results do not support such a scenario and, furthermore, it also shows few extra steps are necessary to group *Patagosaurus* with the North African taxon *Spinophorosaurus*. More osteological information on *Spinophorosaurus* may resolve this in the future.

The high diversity of sauropods in the Cañadón Asfalto Formation, shown here by *Patagosaurus* as a derived non-neosauropod eusauropod and *Volkheimeria* as a more basal sauropod, whilst both originating from the same bonebed, is compatible with a rapid regional diversification in the early Middle Jurassic, a pattern also noted for Jurassic theropods from Patagonia (Pol & Rauhut, 2012). Finally, the presence of a derived eusauropod in the Aalenian–Bajocian suggests an earlier sauropod diversification, which might be pushed back into the Early Jurassic or even to the Late Triassic. However, in order to investigate whether the early Middle Jurassic strata of Patagonia were a sauropod biodiversity 'hotspot', other sauropods from Gondwana require revision, such as *Barapasaurus*, *Lapparentosaurus*, *Bothriospondylus* and even *Volkheimeria*.

5. CONCLUSIONS

With this new analysis, *Patagosaurus fariasi* is retrieved as a derived non-neosauropodan eusauropod, more derived than most non-neosauropodan sauropods, and basal to (*Mamenchisaurus*+*Omeisaurus*, turiasaurians). It is retrieved as sister taxon to the Rutland *Cetiosaurus*, and as nested within *Cetiosaurus.* The analysis shows a high sauropod taxonomic and evolutionary diversity, which in turn points to a rapid regional diversification in the early Middle Jurassic of Patagonia, making South Gondwana an important site for sauropod evolution and radiation.

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