A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs

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Abelisaurids are a clade of large, bizarre predatory dinosaurs, most notable for their high, short skulls and extremely reduced forelimbs. They were common in Gondwana during the Cretaceous, but exceedingly rare in the Northern Hemisphere. The oldest definitive abelisaurids so far come from the late Early Cretaceous of South America and Africa, and the early evolutionary history of the clade is still poorly known. Here, we report a new abelisaurid from the Middle Jurassic of Patagonia, Eoabelisaurus mefi gen. et sp. nov., which predates the so far oldest known secure member of this lineage by more than 40 Myr. The almost complete skeleton reveals the earliest evolutionary stages of the distinctive features of abelisaurids, such as the modification of the forelimb, which started with a reduction of the distal elements. The find underlines the explosive radiation of theropod dinosaurs in the Middle Jurassic and indicates an unexpected diversity of ceratosaurids at that time. The apparent endemism of abelisauroids to southern Gondwana during Pangean times might be due to the presence of a large, central Gondwanan desert. This indicates that, apart from continent-scale geography, aspects such as regional geography and climate are important to reconstruct the biogeographical history of Mesozoic vertebrates.

Keywords: Dinosauria; Ceratosauria; Abelisauridae; Middle Jurassic; Argentina; Gondwanan biogeography

1. INTRODUCTION

Abelisaurids are a highly derived lineage of the Ceratosauria, a clade of phylogenetically basal theropod dinosaurs, characterized by a robust, short and high skull, extremely reduced forelimbs, and a highly pneumatized axial skeleton [1]. Abelisaurids were diverse in the Late Cretaceous of Gondwana, where they represent the top predators, but occurrences from the Northern Hemisphere are so far restricted to fragmentary and questionable latest Cretaceous remains from Europe [1]. Although the phylogenetic relationships of the more inclusive abelisauroids indicate that this clade reaches back to the Late Jurassic at least, the oldest secure occurrences of abelisaurids come from the late Early Cretaceous [1–4], and older reports of this clade are based on fragmentary and questionable material that does not provide much information on the early evolution of the group [1,5–7]. Thus, the origin and early history of abelisauroids remains largely unknown.

Here, we report a basal abelisaurid from the early Middle Jurassic of Patagonia, which extends the stratigraphic range of this clade for more than 40 Myr. The discovery of such an early member of this derived clade has important implications for the early evolution of abelisauroids and the origin of their bizarre morphology, as well as for establishing the initial diversification of ceratosaurids in general during Pangean times, which has important biogeographical consequences for understanding the distribution of theropods during the Jurassic.

2. SYSTEMATIC PALAEOONTOLOGY

Dinosauria Owen, 1842
   Theropoda Marsh, 1881
   Ceratosauria Marsh, 1884
   Abelisauridae Bonaparte and Novas, 1985

Eoabelisaurus mefi gen. et sp. nov.

(a) Etymology
From eos, Greek for dawn, for the early occurrence of the new taxon, and Abelisaurus, type genus of the Abelisauridae. The species name refers to the popular abbreviation of the Museo Paleontológico Egidio Feruglio (MEF).

(b) Holotype
Museo Paleontológico Egidio Feruglio (MPEF) PV 3990, an almost complete skeleton, including the posterior half of the skull, five cervical and nine dorsal vertebrae, complete sacrum, 27 caudal vertebrae, left and right scapulocoracoid, left and right humerus, radius and ulna, left and right distal carpals, left and right metacarpals I–IV, five phalanges (including one ungual) of the left and six phalanges (including one ungual) of the right hand, complete pelvic girdle, left and right femur, tibia, fibula, tarsals and metatarsals, and 12 phalanges (including two unguals) of the left and eight phalanges (including one ungual) of the right pes (figure 1).

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**Type locality and horizon**

Jugo Loco locality, close to the village of Cerro Cóndor, Chubut, Argentina. The locality is placed in a series of finely bedded mud-, marl- and limestones of the Canadón Asfalto Formation, early Middle Jurassic (Aalenian-Bajocian; see the electronic supplementary material).

**Diagnosis**

Medium-sized theropod dinosaur (6–6.5 m total length) with the following autapomorphies: quadrate with thickened medial distal articular end and subparallel articular condyles; mid-dorsal vertebrae with double, V-shaped lamina extending from the parapophysis to the prezygoepipophyseal lamina; ulna with hypertrophied olecranon process, accounting for more than 30 per cent of its length; pubic foramen elongate, more than twice as long as high; ambiens process of pubis developed as a large, anterolaterally directed, convex expansion.

3. DESCRIPTION

Whereas the posterior half of the skeleton was found in articulation, the anterior dorsal and cervical vertebrae and forelimbs had been partially disarticulated prior to burial, and the skull was slightly moved from the vertebral column. Furthermore, the skull and anterior presacrals were exposed at the time of discovery and have thus partially been destroyed by erosion.

Of the snout, only a fragment of the right maxilla has been recovered and shows that the interdental plates are fused, but not striated in *Eoabelisaurus*. The posterior part of the skull is high, with an oval orbit and an enlarged infratemporal fenestra (figure 1b,c), as in other ceratosaurs.

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**Figure 1.** Middle Jurassic abelisaurid *Eoabelisaurus mefi*. (a) Skeletal reconstruction, showing preserved parts. Skull in left lateral (b) and posterior (c) views. Middle cervical vertebra in left lateral (d) and dorsal (e) views. (f) Anterior mid-dorsal vertebra in left lateral view. (g) Posterior dorsal vertebra in left lateral view. (h) Anterior caudal vertebra in left lateral view. (i) Right ulna and radius in medial view. (j) Right manus in plantar view. (k) Pelvic girdle in left lateral view. (l) Left femur in lateral view. Pedal ungual in lateral (m) and ventral (n) views. Abbreviations: al, additional lamina; ap, ambiens process; at, antitrochanter; boc, basioccipital condyle; bt, basal tubera; d, depression; dc, distal carpal; di, diapophysis; epi, epipophysis; f, frontal; fm, foramen magnum; g, groove; il, ilium; ios, interorbital septum; is, ischium; j, jugal; l, lacrimal; l, lesser trochanter; Mc, metacarpal; n, notch; ns, neural spine; of, obturator foramen; oI, olecranon process; pa, parietal; pap, paroccipital process; ph, phalanges; pl, pleurocoel; po, postorbital; poz, postzygapophysis; pp, parapophysis; prel, prezygoepipophyseal lamina; ps, paraphenoid; psf, prespinal fossa; pt, pterygoid; ptw, pterygoid wing of the quadrate; pu, pubis; q, quadrate; qj, quadratojugal; r, radius; soc, supraoccipital crest; sq, squamosal; ts, trochanteric shelf; u, ulna; vf, ventral fossa. Scale bars: (a) 500 mm; (b–l) 50 mm; (m,n) 10 mm.
Cervical vertebrae (figure 1d,e) are short and have two pneumatic foramina on either side of the centra. The ante-
riormost preserved cervicals are amphicoelous, whereas middle and posterior cervical vertebrae are flat anteriorly, 
but deeply concave posteriorly and have a low ventral keel. Vertebral centra of middle and posterior cervicals 
are furthermore notably broader than high. Cervical neural arches are strongly pneumatized and have promi-
nent prezygoepipophyseal laminae and large prespinal fossae. Cervical neural spines are anteroposteriorly short 
and very low. The epipophyses are tabular and about as 
high as the neural spine. Only the first two dorsal vertebrae 
have pleurocoels, but the neural arches of all dorsals are 
extensively pneumatized. Mid-dorsal parapophyses are 
set on long lateral stalks and the transverse processes and 
prezygapophyses are connected by a web of bone. The 
sacrum comprises six vertebrae that form a dorsally 
arched structure, with only slight swellings marking the 
border between the fused vertebral centra. Anterior 
caudal vertebrae (figure 1h) have high, massive centra 
without any ventral groove. Neural spines are high and 
anteroposteriorly narrow, and transverse processes are 
long and strongly dorsolaterally and slightly posteriorly 
directed, with a marked posterior expansion at their 
distal end. Hyposphene–hypantrum articulations are pre-
sent in the anterior caudals, but become indistinct at around caudal 10. The length of vertebral centra remains 
constant over the preserved portion of the tail, but 
middle and posterior caudals are considerably lower. 
Mid-caudals have anteroposteriorly short, vertical neural 
spines. Distal caudal prezygapophyses are short. 
The scapula has a broad shaft without distal expansion. 
The coracoid is large and semi-oval. Both humeri are 
poorly preserved, but show remarkably primitive characters. 
The articular head is slightly expanded, but far from 
the globular shape seen in nosaurids [11] and abelisaurids 
[8,12]. The deltopectoral crest is moderately developed 
and the distal end shows two rounded condyles. Radius 
and ulna are short and the ulna has a large olecranon pro-
cess (figure 1i). The manus is strongly foreshortened, 
retains four digits and has a stout, blocky metacarpal II 
(figure 1j). Metacarpal I is about half the length of metacar-
pal II and considerably more slender than the latter; it bears a 
stout phalanx that is slightly longer than the metacarpal. 
Metacarpals II and III have broad extensor grooves with 
raised proximal margins. The non-terminal manual pha-
langes are about as long as wide and lack any constriction 
between the articular ends, and manual unguals are reduced. 
Ilium, pubis and ischium are fused without visible 
sutures (figure 1k). The ilium is low and elongate, with a 
gently arched dorsal margin. The supra-acetabular crest 
is continuous with the lateral brevis shelf and the brevis 
fossa expands posteriorly. The pubis has an elongate 
oburator foramen and a narrow pubic apron that is 
V-shaped in cross section, with the apex pointing anteriorly. 
The distal ends of the pubes lack any anteroposterior 
expansion. A broad, well-developed antitrochanter is pre-
sent in the ischium at the suture with the ilium and the 
ischium has a moderately expanded distal boot. The pub-
ischial plate is extensive, with broad incisions adjacent 
to the shafts of the pubis and ischium. The femur is 
short, only slightly bowed, and shows an anteromedially 
directed head (figure 1l). The lesser trochanter is low, 
but broad, with a well-developed trochanteric shelf. The 
fourth trochanter is developed as a stout, high ridge. As 
in other ceratosaur, the crista tibiofibularis is expanded 
and oriented obliquely in relation to the femoral shaft. 
The tibia has an elevated, rectangular cnemial crest, and 
the fibular crest is proximally placed and well-developed. 
The fibula has a deep, posteriorly facing medial depression 
proximally and the iliofibularis tubercle is developed as a 
stout, oblique ridge. Astragalus and calcaneum are fused 
with each other and the tibia, but not the fibula. The meta-
tarsus is long and slender, with metatarsal III reaching 
almost 50 per cent of the femoral length. As in Ceratosaurus 
[13], the posterior end of the proximal articular surface of 
metatarsal III is expanded transversely. Pedal unguals have 
a broad, triangular depression ventrally (figure 1m), as in 
other abelisaurids [14]. 

4. DISCUSSION
In order to assess the phylogenetic position of Eoabeli-
saurus, we added the codings for this taxon to a 
combined matrix of two recently published phylogenetic 
datasets ([1,15]; see the electronic supplementary material). The analysis places Eoabelisaurus as the most 
basal member of the Abelisauridae (figure 2). Abelisaurid synapomorphies include the laterally covered lacrimal 
antorbital fossa, broad cervical prespinal fossae, anter-
oposteriorly short anterior caudal neural spines, absence 
of a ventral groove in the anterior caudals, presence of 
rudimentary centrodiaepophyseal laminae in the anterior mid-caudals, reduced distal ginglymus in the manual pha-
langes, and the presence of a flexor depression in the 
pedal unguals. Alternative phylogenetic placements of 
Eoabelisaurus are significantly suboptimal, except for a 
slightly more basal position (as a stem-abelisaurid; see the 
electronic supplementary material). 

The so far oldest certain abelisaurids were represented 
by fragmentary remains from the late Early Cretaceous of 
South America [2] and Africa [3,4] and older records of 
abelisaurids in general are fragmentary and questionable 
([1,17]; see also the electronic supplementary material). 
Eoabelisaurus extends the temporal range of this clade 
for more than 40 Myr into the early Middle Jurassic 
(figure 2). The occurrence of a derived ceratosaurs at 
that time indicates a rapid diversification of ceratosaurs 
in the Early to early Middle Jurassic. Indeed, the abeli-
saurid affinities of the new taxon demonstrate that all 
major ceratosaurian lineages (those leading to the clades 
comprising Elaphrosaurus and its closest relatives (‘elaph-
rosaurians’), ceratosaurids, nosaurids, abelisaurids) were 
established by this time. The apparent rarity of cerato-
saur in the Jurassic does most probably not reflect true 
low taxonomic diversity, but is owed to the poor fossil
record of Jurassic theropods in the Southern Hemisphere ([18]; see also the electronic supplementary material). Together with the wide array of basal tetanuran taxa known from the Middle Jurassic [19] and the growing recognition that most, if not all coelurosaurian lineages also reach back to this time [20–23], this underlines the rapid and apparently explosive radiation of theropod dinosaurs in the late Early to early Middle Jurassic. Whereas current research on the origin and success of dinosaurs mainly focuses on the Triassic–Jurassic boundary [24,25], these findings lend support to the hypothesis that the rise of dinosaurs was a two-step process, marked by extinctions of basal archosaurs at the Triassic–Jurassic boundary and of several basal dinosaur lineages in the Pliensbachian–Toarcian, followed by an explosive radiation of ‘modern’ clades [26,27]. New discoveries and more research into this topic are needed to establish the timing and patterns of early diversification of dinosaurs in the Jurassic.

So far, abelisaurid anatomy was almost exclusively known from Late Cretaceous taxa that are highly aberrant in their morphology, especially in their unusual skull structure [8,10] and extreme reduction of the forelimbs [8,28,29]. *Eoabelisaurus* reveals a previously unknown stage in the evolution of abelisaurids, having only some of the cranial modifications and a unique combination of plesiomorphic and apomorphic features in its forelimb. The humerus is plesiomorphic and unreduced, whereas the ulna–radius are shortened, but do not differ significantly from more basal ceratosaurs (e.g. *Ceratosaurus*). The manus of *Eoabelisaurus*, however, has a derived morphology, with short and robust metacarpals, non-terminal phalanges that are as broad as long and lack gynglimoidal distal articulatory surfaces, and reduced manual unguals. Consequently, the modification of the forelimb in the evolution of abelisauroids seems to have occurred in a modular fashion, starting at the distal elements, and only later affected the more proximal elements (figure 3).

*Eoabelisaurus* thus confirms a recently proposed evolutionary scenario for the evolution of abelisaurid limbs based on the incomplete evidence of Cretaceous abelisaurids [29]. The phylogenetic position of the new taxon indicates that modifications similar to those of abelisaurids in the humerus of ‘elaphrosaurs’ [30,31] and noasaurids [11] either arose independently from those in derived abelisaurids, or that these modifications were reversed in *Eoabelisaurus*. Either way, this suggests a surprisingly high level of homoplasy in such an extreme specialization.

With a 40 Myr gap, the fossil record of abelisaurids is certainly still too poor to provide a robust biogeographic
scenario [32]. Based on the previously available fossil record, abelisaurids were thought to have originated after the separation of Gondwana from the continents of the Northern Hemisphere [1,33], and recent discussions have focused on the possible effects (or lack thereof) of Gondwanan fragmentation on abelisaurid biogeography during the Cretaceous [1,3,4,33–35]. The discovery of *Eoabelisaurus* demonstrates that there was ample time for a dispersal of abelisaurids over the Gondwanan continents prior to their separation in the course of the ‘middle’ to Late Cretaceous, as it has been argued recently on the basis of geological palaeogeographic evidence [33].

However, the finding of an abelisaurid some 10–15 Myr before the effective separation of the continents of the Northern and Southern Hemispheres begs the question why no abelisaurid remains have been recorded from the Jurassic of Laurasia (a recent record of an abelisaurid from the Middle Jurassic of England [17] cannot be substantiated; see the electronic supplementary material). In contrast, other theropod lineages, which arose at approximately the same time, such as ‘elaphrosaurs’ [31], ceratosaurs [7,9,36] and basal tetanurans [19], achieved a Pangean distribution during this time (see the electronic supplementary material). Interestingly, a similar biogeographic pattern has recently been inferred for other groups of Mesozoic vertebrates, such as basal eusauropods [37], heterodontosaurid ornithischians [38] and mammals [39,40], in which some clades were restricted to southern Gondwana during the Jurassic, whereas other clades had a global distribution. The congruent pattern of restricted distribution for multiple vertebrate clades during Pangean times may be related to a common biogeographic cause. There is growing evidence from climate modelling and geological data for a large, central Gondwanan desert during the Middle and Late Jurassic [41–43], which might provide a possible explanation, acting as a filter for certain groups. However, further work on Jurassic palaeogeography and palaeoclimatology is needed. Nevertheless, this biogeographic pattern present in the above-mentioned clades of vertebrates during the Jurassic indicates that regional geographical and climatic conditions, and differential dispersal capabilities, may be as important to explain the biogeographic history of a group as continental fragmentation.

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