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ARTICLE

Reassessment of *Aeolosaurus maximus*, a titanosaur dinosaur from the Late Cretaceous of Southeastern Brazil

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ABSTRACT

Aeolosaurus is a late Cretaceous Titanosaur genus with two species discovered in Argentina and one in Brazil. Although the allocation of the Argentinean *Aeolosaurus* seems unequivocal, that is not the case for the Brazilian species *Aeolosaurus maximus* since several authors questioned its positioning into this genus, based on both anatomical and phylogenetic data. The revision of the diagnosis of *Ae. maximus*, with the proposition of a new autapomorphy, corroborates the anatomical uniqueness and our phylogenetic analysis stresses that the relation of *Ae. maximus* to the Argentinean *Aeolosaurus* is uncertain. Based upon that, we propose a new genus, *Arrudatitan*, to accommodate the Brazilian taxon.

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Introduction

Even though *Titanosauria* is the most diverse clade within Sauropoda, with several Cretaceous species described worldwide, the group is composed mainly of monospecific genera (Mannion and Calvo 2011; De Jesus Faria et al. 2015). One of the few exceptions is *Aeolosaurus*, erected by Powell (1986, 1987), which has three nominated species being two from Argentina and one from Brazil. The type species, *Ae. rionegrinus*, was proposed to include a partial skeleton (holotype MJG-R 01) discovered in the Late Cretaceous Angostura Colorada Formation, Casa de Piedra locality, Estancia Maquinchao, Río Negro, Argentina (Powell 1986, 1987). Powell (1987, p. 148) also described a sequence of 15 caudal vertebrae from the Campanian-Maastrichtian Los Alamitos Formation of Argentina as possibly referred to *Ae. rionegrinus*, but that assignment was questioned by Salgado and Coria (1993) and Salgado et al. (1997). Later, other remains discovered in northern Patagonia were ascribed to *Aeolosaurus* sp. (Salgado and Coria 1993; Salgado et al. 1997; Garcia and Salgado, 2013), coming from the roughly coeval Los Alamitos and Allen formations.

Casal et al. (2007) described a second *Aeolosaurus* species, *Ae. colhuehuapensis*, unearthed from the Campanian-Maastrichtian Bajo Barreal Formation, central Patagonia. Furthermore, in the last 20 years or so, there were several reports of *Aeolosaurus* sp. in the Upper Late Cretaceous rocks of southeastern and central Brazil, usually based upon incomplete and poorly preserved material (e.g., Bertini et al. 1999a; Bertini et al. 1999b, 2000; Candeiro 2006, 2010; Candeiro et al. 2006; Lopes and Buchmann 2008; Santucci and Bertini 2017). The referral of these specimens to *Aeolosaurus* was questioned by Martinelli et al. (2011), who instead considered them all as indeterminate *Aeolosaurini*.

In particular, one of the materials referred as *Aeolosaurus* sp. from the state of São Paulo consists of various axial and appendicular bones of a single individual (Bertini, 1999a) that was included in the review of the Brazilian material done by Martinelli et al. (2011; it was labelled at the time as MPMA/without number). Those authors concluded that this specimen lacks several diagnostic features of the genus and should be regarded as an indeterminate *Aeolosaurini*. In the same year, that specimen (then numbered as MPMA 12–0001/97) was designated as the holotype of a new species, *Aelosaurus maximus* Santucci and Arruda-Campos, 2011. The phylogenetic analysis that accompanied that proposal positioned *Ae. maximus* as the sister-taxon to *Ae. rionegrinus* plus *Ae. colhuehuapensis*, with the Brazilian *Gondwanatitan faustoi* as the sister taxon of that clade. However, more recent phylogenetic analyses placed *Ae. maximus* in disparate alternative positions (e.g., Bandeira et al. 2016; Filippi et al. 2019; Silva Junior et al. 2019; Hechenleitner et al. 2020). In this contribution, we revise the diagnosis and affinities of *Ae. maximus*, proposing a new genus to accommodate the species.

Institutional abbreviations: **CPPLIP**, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; **CRILAR**, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Argentina; **IANIGLA-PV**, Instituto Argentino de Nivología, Glaciología y Ciencas Ambientales, Colección Paleovertebrados, Mendoza, Argentina; **MAU-Pv**, Paleontología de Vertebrados, Museo Municipal 'Argentino Urquiza', Rincón de los Sauces, Neuquén, Argentina; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil; **MJG-R**, Museo Jorge Gerold, Ingeniero Jacobacci, Río Negro, Argentina; **MPM**, Museu

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de Paleontologia de Marília, Marília, Brazil; **MPM-PV**, Museo Regional Provincial ‘Padre Jesus Molina’, Rio Gallegos, Santa Cruz, Argentina; **MPMA**, Museu de Paleontologia Antônio Celso de Arruda Campos, Monte Alto, Brazil; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; **ZPAL**, Instytut of Paleobiologii, Polish Academy of Sciences, Warsaw, Poland.

Observations: Following article 6, recommendation 6.1A, from PhyloCode (Cantino and De Queiroz 2020), all clades established under this code are italicised.

Geological settings

The Bauru Basin (Figure 1) is a cratonic depression developed in the southeastern portion of the South American Plate during the Late Cretaceous (Fernandes and Ribeiro 2015). Sedimentation within the basin occurred under semi-arid to arid conditions, but the age of the deposits is a matter of intense debate (e.g., Batezelli and Ladeira 2016; Menegazzo et al. 2016). In particular, the Adamantina Formation had a complex nomenclatural history, being subdivided into different schemes in the literature (e.g., Soares et al. 1980; Fernandes and Coimbra 2000; Paula E Silva et al. 2005; Batezelli and Ladeira 2016; Menegazzo et al. 2016). As for its age, the most recent review suggested a Campanian assignment (Castro et al. 2018), but ages ranging from Cenomanian to Maastrichtian have been proposed (Gobbo-Rodrigues et al. 1999; Dias-Brito et al. 2001; Menegazzo et al. 2016), and different sites, with distinctive faunal components, may actually have different ages (Martinelli and Teixeira 2015; Martinelli et al. 2018).

The Monte Alto region is an important source of vertebrate fossils within the eastern border of the Bauru Basin, with dozens of catalogued digging sites referred to both the Adamantina and Marília formations, which yielded several species of turtles, crocodyliforms, and dinosaurs (e.g., Bertini et al. 2001; Carvalho et al. 2007; Andrade and Bertini 2008; Pinheiro et al. 2008; Santucci and Arruda-Campos 2011; Iori and Carvalho 2011; Iori and Garcia 2012; Méndez et al. 2014; Ferreira et al. 2018; Iori et al. 2018).

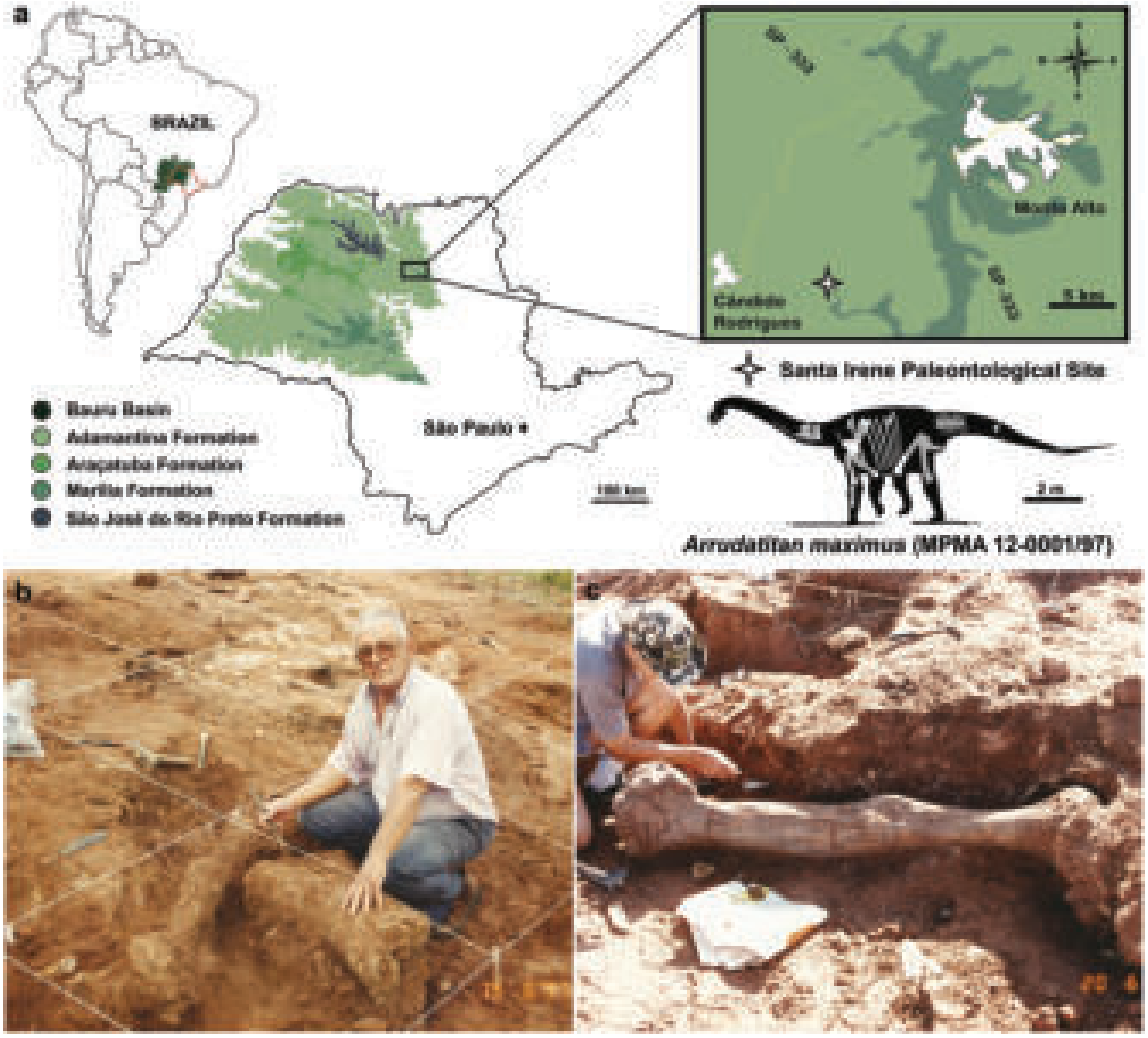

Figure 1. **A**, Bauru Group in São Paulo state map, highlighting the digging site of MPMA 12–0001/97 within the Adamantina Formation. Silhouette modified from Santucci and Arruda-Campos (2011). **B**, The late Prof. Antonio de Celso Arruda Campos during the excavation of MPMA 12–0001/97 (taken in 19 June 1997). **C**, One of the authors (FVI) during the excavation of the femur MPMA 12–0001/97 (taken in 20 June 1997). Photographs of B and C from the MPMA collection, used with permission.

The type-locality and holotype (MPMA 12–0001/97) of *Ae. maximus* were discovered during 1997 by Ademir Frare and Luiz Augusto dos Santos Frare in the 'Santa Irene' farm, a property located near the limits between Monte Alto and Cândido Rodrigues municipalities (Iori 2019; GPS = S21°19′44.3″/W 48°34′ 54.6″). Santucci and Arruda-Campos (2011) mentioned that the site is located about 12 km southwest of Monte Alto, but its position in their map (Santucci and Arruda-Campos 2011: Figure 1) is not correct. In fact, the outcrop is located further 9 km to northwest of the point marked at that map, within Cândido Rodrigues municipality. The specimen was unearthed during two excavation campaigns in 1997 and 1998, when most of the partially articulated skeleton was collected (see Santucci and Arruda-Campos 2011) associated with numerous isolated theropod and crocodyliform teeth (Tavares et al. 2011, 2014). The remains were removed from a massive, reddish sandstone layer, with local carbonatic cementation. According to Santucci and Arruda-Campos (2011), the skeleton has undergone little transport, and small theropod dinosaurs and crocodyliforms have fed on the carcase.

Taxonomy and affinities of *Aeolosaurus maximus*

Historical background

Along with the description of *Ae. rionegrinus*, Powell (1987) proposed several autapomorphies for the species, some of which were later suggested to represent synapomorphies of *Aeolosaurini* by Franco-Rosas et al. (2004). In the description of *Ae. colhuehuapensis*, Casal et al. (2007) proposed to diagnose the genus based on the presence of mid-caudal vertebrae with postzygapophyses located anterior to the anterior articular facet of the centrum and proximally opened haemal arches, with articular facets arranged on two planes. Later on, Santucci and Arruda-Campos (2011) employed two putative synapomorphies of *Aeolosaurus* to place MPMA 12–0001-97 in that genus: (1) well-developed posterior protuberance below the articular area on the anterior and middle haemal arches and (2) lateral bulge on the distal portion of the articular process of the mid-posterior haemal arches.

Based on the direct comparison between MPMA 12–0001-97 and the two Argentinean species of *Aeolosaurus*, Martinelli et al. (2011), stated that due to the absence of the synapomorphies proposed for the genus by Casal et al. (2007), MPMA 12–0001-97 could only be considered as an indeterminate *Aeolosaurini* as it bears a number of characteristics of this clade (i.e., antero-dorsal margin of caudal centrum anteriorly tilted, neural arch placed on the anterior half of the centrum, and neural spine anteriorly inclined and large prezygapophysis). In particular, the postzygapophyses of the caudal vertebrae of MPMA 12–0001-97 are not positioned anterior to the level of the anterior edge of the centrum. Notably, this trait is only seen in the Patagonian species of *Aeolosaurus* (Casal et al. 2007) and was never reported in other titanosaurs.

In the description of *Ae. maximus*, Santucci and Arruda-Campos (2011; see also França et al. 2016) used a modified version of the dataset of Wilson (2002) to evaluate its phylogenetic position. The taxon was recovered within *Aeolosaurini*, as sister taxon to the clade, including both Argentinean species of *Aeolosaurus*. Later, Bandeira et al. (2016) found *Ae. maximus* closer to *Rinconsauria* than to *Aeolosaurini*, whereas the analysis of a modified version of that matrix (Silva Junior et al. 2019) recovered *Ae. maximus* again as an *Aeolosaurini*, but not particularly close to the Argentinean *Aeolosaurus*. More recently, Carballido et al. (2017) and Filippi et al. (2019) recovered *Ae. maximus* as sister to *Overosaurus*, within *Rincosauria*, but these datasets did not include the Argentinean *Aeolosaurus*, nor *Gondwanatitan*. Lastly, a comprehensive phylogeny by Hechenleitner et al. (2020) obtained *Ae. maximus* as sister taxon of a clade including the Argentinean *Punatitan* and *Aeolosaurus*.

Uniqueness of Aeolosaurus maximus

Santucci and Arruda-Campos (2011) identified a set of unique traits of MPMA 12–0001-97. Some of these features are related to the peculiar laminae configurations seen in its vertebrae, which can be distinguished from those of all other titanosaurs. Firstly, according to Santucci and Arruda-Campos (2011), the posterior centrodiapophyseal lamina (pcdl) is at least 50% thicker (expanded both dorsoventrally and mediolaterally) than the postzygodiapophyseal lamina (podl) in the posterior cervical vertebrae. This condition differs from that of other titanosaurs, where pcdl and podl have similar dimensions, as is the case of *Overosaurus* (Coria et al. 2013; MAU-Pv-CO-439, Figure 2A) and some Bauru Group taxa, such as *Trigonosaurus* (Campos et al. 2005; MCT 1488-R, Figure 2) and *Brasilotitan* (Machado et al. 2013; MPM 125 R, Figure 5A). Santucci and Arruda-Campos (2011) identified the presence of intrapostzygapophyseal laminae (tpol) in the posterior trunk vertebrae of MPMA 12–0001-97 as autapomorphic. This condition is uncommon among titanosaurs, which normally have this lamina only in anterior and/or mid-trunk vertebrae as seen in *Petrobasaurus* (Filippi et al. 2011; MAU-Pv-PH-449/18, Figure 4G), *Mendozasaurus* (González Riga et al. 2018; IANIGLA-PV 066, Figure 6 C), and *Uberabatitan* (Silva Junior et al. 2019; CPPLIP-

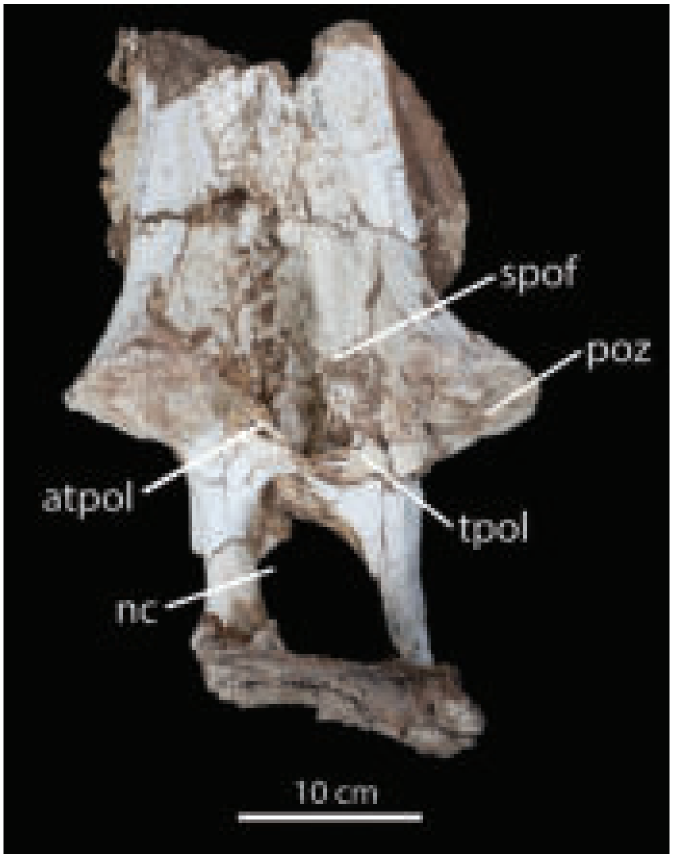

Figure 2. MPMA 12–0001-97. Posterior trunk vertebra in posterior view. Abbreviations: **atpol**: accessory intrapostzygapophyseal lamina; **nc**: neuralcanal; **poz**: postzygapophysis; **spof**: spinopostzygapophyseal fossa; **tpol**:intrapostzygapophyseal lamina.

1077, Figure 7A). Yet, given that this character is shared with other titanosaurs, such as *Narambuenatitan* (Filippi et al. 2011; MAU–Pv–N – 425, Figure 7B), *Dreadnoughtus* (Voegele et al. 2017; MPM-PV 1156–11, Figure 3G), and *Bravasaurus* (Hechenleitner et al. 2020; CRILAR-Pv 612, Figure 3F), it cannot be considered as unique to MPMA 12–0001-97.

As also mentioned by Santucci and Arruda-Campos (2011), MPMA 12–0001-97 has posterior trunk vertebrae with an oblique anterior centropostzygapophyseal lamina (acpol), which bifurcates from the proximal portion of the centropostzygapophyseal lamina (cpol). This pattern is indeed unknown in any other titanosaur, in which a single lamina (cpol) is responsible to connect the posterior portion of the neural arch to the postzygapophysis as seen in *Opisthocoelicaudia* (Borsuk-Białynicka 1977; ZPAL MgDI/48, Figure 3C), *Punatitan* (Hechenleitner et al. 2020; CRILAR-Pv 614, Figure 2D), and *Saltasaurus* (Powell 2003; PVL 4017–136, Figure 28). Although not discussed by Santucci and Arruda-Campos (2011), our comparative review shows that the posterior trunk vertebrae of *Ae. maximus* possess an accessory intrapostzygapophyseal lamina (atpol), creating two small lateral camerae on the

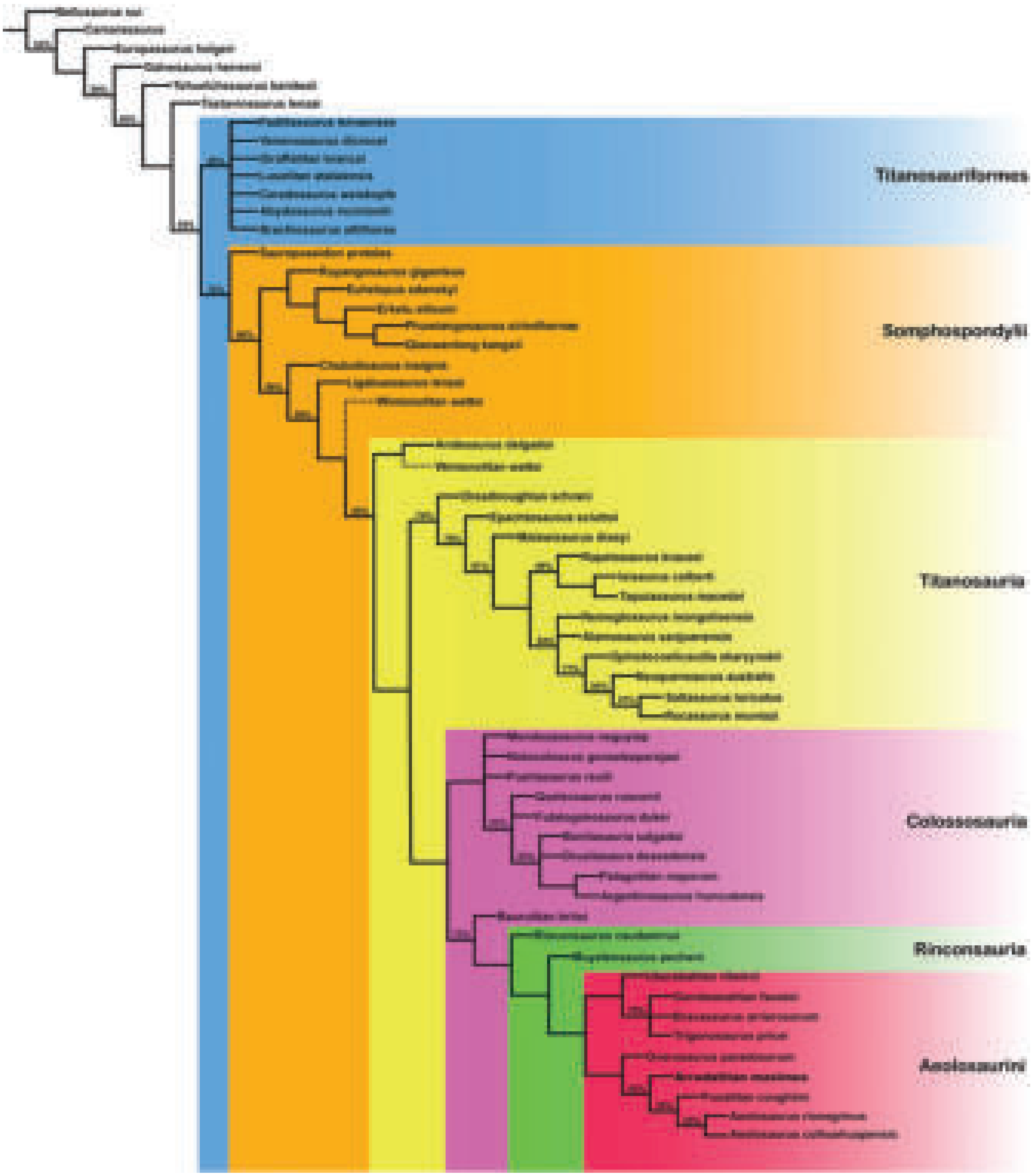

Figure 3. Simplified 50% majority-rule consensus of 3,680 MPTs based on Hechenleitner et al. (2020) plus modifications (see text).

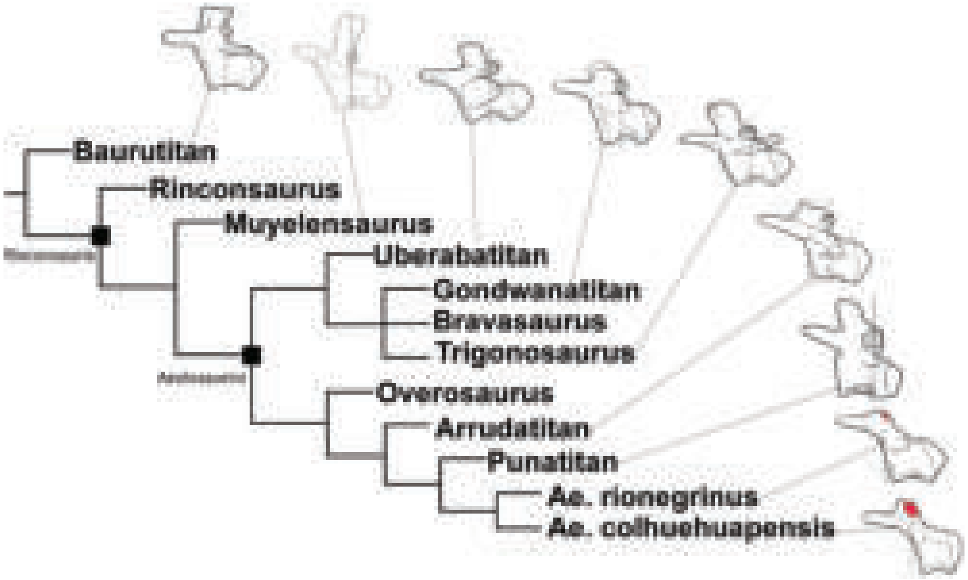

Figure 4. Comparison of the position of the postzygapophysis of posteriormost anterior to middle caudal vertebrae of *Aeolosaurini* and closely related taxa. Indicated only for taxa with those vertebrae preserved.

spinopostzygapophyseal fossa (Figure 2). Although the presence of accessory laminae is common in posterior trunk vertebrae of titanosaurs as seen in *Trigonosaurus* (Campos et al. 2005; MCT 1488-R, Figure 19) and *Dreadnoughtus* (Voegele et al. 2017; MPM-PV 1156–11, Figure 1E), they differ from the pattern found in *Ae. maximus* because in the later taxa the accessory laminae are associated with the diapophyseal lamination. Finally, titanosaurs usually possess plank-like shape trunk ribs (Wilson 2002), although this condition may vary as seen in *Uberabatitan* (Silva Junior et al. 2019; CPPLIP-923, Figure 13O), the rib shafts of which are concave on their medial portions. A different pattern was noted by Santucci and Arruda-Campos (2011) in *Ae. maximus*, in which the mid trunk ribs have well-developed anterior and posterior crests, creating a D-shaped cross section, as unique among titanosaurs.

The characters discussed above are indeed unique to *Ae. maximus* when compared with titanosaurs in general, including some *Aeolosaurini* as defined below (i.e., *Bravasaurus, Punatitan, Overosaurus, Trigonosaurus*, and *Uberabatitan*). Yet, the corresponding anatomical parts are not preserved in other *Aeolosaurini* such as *Ae. rionegrinus, Ae. colhuehuapensis*, and *Gondwanatitan*. Hence, as stated by Santucci and Arruda-Campos (2011), depending on further specimen recovered for these taxa and on the chosen phylogenetic arrangement, these characters may reveal to be synapomorphies of a given subset of *Aeolosaurini*, instead of autapomorphies of *Ae. maximus*.

Affinities of Aeolosaurus maximus *and its bearing on stratigraphic correlation*

In order to infer the relationships of *Ae. maximus*, we employed a modified version of the dataset of Hechenleitner et al. (2020), which was based on that provided by Carballido et al. (2020) and represents the most complete and up-to-date phylogenetic study of South American titanosaurs. Four characters (423–426) were added to the dataset (see supplementary material), which, respectively, correspond to characters 235, 238, 239, and 240 of Santucci and Arruda-Campos (2011). Furthermore, *Ae. colhuehuapensis* was added as a terminal unit and scored based on Casal et al. (2007). Summarising, the dataset analysed here (see Suppl. mater.) has 426 characters scored for 97 sauropodomorph terminals. The analysis was conducted in TNT 1.5 (Goloboff et al. 2016) with tree bisection and reconnection (TBR) as the branch swapping algorithm, hold established as 50, 5,000 replicates, and random seed as ‘0’.

The analysis resulted in 3,680 Most Parsimonious Trees (MPTs) of 1,496 steps. The strict consensus shows *Ae. maximus* forming a polytomy with *Overosaurus, Punatitan, Ae. rionegrinus*, and *Ae. colhuehuapensis*. In the 50% majority-rule consensus tree (Figure 2), *Ae. maximus* represents the sister taxon of the clade formed by *Punatitan* and *Ae. rionegrinus* + *Ae. colhuehuapensis*. The clade congregating these four taxa is supported by two synapomorphies: (1) posteriormost anterior and middle caudal vertebrae with neural spines directed anteriorly (Ch. 257), shared by *Ae. maximus* and *Punatitan*, and (2) middle caudal vertebrae with prezygapophysis longer than 50% of the centrum (Ch. 420), shared by all four taxa.

The clade composed by *Punatitan* and both Argentinean *Aeolosaurus* is supported by two synapomorphies: (1) groove in the ventral surface of anterior and middle caudal centra (Ch. 251), shared by *Punatitan* and *Ae. rionegrinus* – *Ae. maximus* lacks this grove –, and (2) prezygapophyses of middle caudal vertebrae oriented anterodorsally (Ch. 413), shared by all three taxa – whereas *Ae. maximus* presents prezygapophysis anteriorly oriented. *Ae. rionegrinus* and *Ae. colhuehuapensis* form a clade based on a single synapomorphy: postzygapophyses of posteriormost anterior and middle caudal vertebrae located anteriorly or at the level of the anterior border of the centrum (Ch. 424). As discussed above, this condition is unique to the Argentinean *Aeolosaurus* (Figure 4; Casal et al. 2007) and lacking in *Ae. maximus*, the anterior and middle caudal vertebrae of which have the postzygapophysis located at the level of the anterior half of the centrum.

The phylogenetic analyses presented here show that *Ae. maximus*, although related to *Aeolosaurini*, is not the sister-taxon to the clade formed by the Argentinean species of *Aeolosaurus*. This is not sufficient reason, according to the principles of Phylogenetic Nomenclature (Cantino and De Queiroz 2020), to replace the generic epithet of *Ae. maximus*. Yet, we believe this is the best option (see Systematic Palaeontology below) because the taxic approach in Palaeontology has been widely employed for stratigraphic correlation based on fossils. Such an approach may lead to erroneous assumptions if a given generic epithet is applied to species that do not form a clade but is otherwise interpreted as such. In the particular case of *Aeolosaurus*, the putative presence of that genus in the Bauru Basin, including *Ae. maximus*, has been used to propose a Campanian-Maastrichtian age for its bearing deposits (e.g., Bertin et al. 1999a; Bertini et al. 2000; Santucci and Bertini 2017) because such an age has been established for the *Aeolosaurus* records of Argentina (Powell 1987; Salgado and Coria 1993; Casal et al. 2007).

As defined here (Table 1), apart from *Ae. rionegrinus* and *Ae. colhuehuapensis, Aeolosaurini* includes Brazilian taxa from the Serra da Galga Formation, such as *Uberabatitan* and *Trigonosaurus*, which is almost consensually accepted as of Campanian-Maastrichtian age (see Soares et al. 2021), along with taxa from the more uncertainly dated Adamantina Formation, such as *Gondwanatitan* and *Ae. maximus*. As for the Argentinean taxa, *Overosaurus* was unearthed from the Bajo de la Carpa Formation (Filippi 2015), dated as Santonian (Hugo and Leanza 2001), whereas *Punantitan* and *Bravasaurus* come from the Cíenaga del Rio Huaco Formation, dated as Campaninan-Maastrichtian (Ciccioli et al. 2005; see also Hechenleitner et al. 2020: suppl. info.). Hence, all well-dated *Aeolosaurini* come from Santonian-Maastrichtian (i.e., a span of 20.3 million years) deposits. Therefore, even if *Ae. maximus* is not assigned to *Aeolosaurus*, its affinity to *Aeolosaurini* suggests a Santonian-Maastrichtian age for the Adamantina Formation.

Systematic palaeontology

Titanosauriformes Salgado et al. 1997
Somphospondyli Wilson and Sereno 1998
Titanosauria Bonaparte and Coria 1993
Colossosauria González Riga, Lamanna, Otero, Ortiz David, Kellner and Ibiricu, 2019
Rinconsauria Calvo et al. 2007
Aeolosaurini Franco-Rosas et al. 2004
Arrudatitan gen. nov.

Type-species: *Arrudatitan maximus* (Santucci and Arruda-Campos 2011)

Diagnosis: same as for the only known species.

Etymology: In honour of the late Prof. Antonio de Celso Arruda Campos, fossil collector, populariser of science, and first curator of the MPMA in Monte Alto.

Arrudatitan maximus (Santucci and Arruda-Campos 2011)
1999a *Aeolosaurus* sp. Bertini et al.
1999b *Aeolosaurus* sp. Bertini et al.
2001 *Aeolosaurus* sp. Santucci and Bertini
2011 *Aeolosaurini* indet. Martinelli et al.
2011 *Aeolosaurus maximus* Santucci and Arruda-Campos
2016 *Aeolosaurus maximus* Bandeira et al.
2016 *Aeolosaurus maximus* França et al.
2017 *Aeolosaurus maximus* Carballido et al.
2019 *Aeolosaurus maximus* Silva Junior et al.
2019 *Aeolosaurus maximus* Filippi et al.
2020 '*Aeolosaurus*' *maximus* Hechenleitner et al.

Holotype: MPMA 12–0001-97, two incomplete posterior cervical vertebrae, seven incomplete cervical ribs, a fragmentary anterior trunk centrum, a probable fragment of a middle trunk vertebra, a fragmentary posterior trunk vertebrae, several incomplete diapophysis of trunk vertebrae, 12 incomplete trunk rib, six articulated anterior caudal vertebrae, a mid-caudal centrum, two posterior caudal vertebrae, six anterior, one mid, and one posterior haemal arches, a probable fragmentary scapula, an incomplete right humerus, a probably fragmentary left humerus, a probably incomplete radius, incomplete right femur, left femur, left ischium, and several unidentified fragments.

Remarks: The above set of materials was assigned to the holotype of *Ar. maximus* based on topotypic principles (they were all found associated in the type-locality) and agreeing morphology. In order to further test if the elements could belong to more than one individual, we correlated two continuous variables using a linear regression on R environment (Development Core Team 2013): (1) the estimated total body lengths of four exceptionally well-preserved titanosaurs, *Rapetosaurus krausei* (Rogers and Forster 2001), *Alamosaurus sanjuanensis* (Tykoski and Fiorillo 2017), *Dreadnoughtus schrani* (Lacovara et al. 2014), and *Overosaurus paradasorum* (Coria et al. 2013) and, (2) the absolute size of a left femur and six anterior caudal vertebrae of *Ar. maximus* (the only elements complete enough to be measured), based on measurement of the same element in those titanosaurs. The vertebrae were measured based on the anteroposterior length of their centra and the femur on its proximodistal length. The estimates based on all elements indicate specimens measuring from 19 to 22 metres, within a confidence interval that intuitively suggests that they should belong to a single individual.

Diagnosis: Large-sized titanosaur sauropod with the following autapomorphies – new autapomorphy indicated with an asterisk (*); the others were proposed by Santucci and Arruda-Campos (2011): posterior cervical vertebrae with posterior centrodiapophyseal lamina (pcdl) at least 50% thicker than the postzygodiapophyseal lamina (podl); posterior trunk vertebrae with oblique anterior centropostzygapophyseal lamina (acpol) that bifurcates from the proximal portion of the centropostzygapophyseal lamina (acpol); accessory intrapostzygapophyseal lamina on the posterior trunk vertebrae, creating two small lateral camarae on the spinopostzygapophyseal fossa*; mid-trunk ribs with well-developed anterior and posterior crests with a D-shaped cross section.

Phylogenetic definitions

The hierarchical patterns expressed in the 'Systematic Palaeontology' of *Ar. maximus* as inferred from its position in the phylogeny of Figure 3, invites the proposal of phylogenetic definitions under the renewed aftermath of the PhyloCode (Cantino and De Queiroz 2020) and Phylonyms (De Queiroz et al. 2020). Accordingly, for future systematised use, Table 1 provides definitions for the successively more inclusive clades that include *Ar. maximus: Aeolosaurini, Rinconsauria, Colossosauria, Titanosauria, Somphospondyli*, and *Titanosauriformes*. In the particular case of *Titanosauria*, a polytomy encompassing *Andesaurus, Wintonotitan*, and a large clade including *Colossosauria* and Lognkosauria, hampers the precise identification of the name-bearing clade. This problem was graphically avoided in Figure 3 by pruning *Wintonotitan* from the original consensus tree and indicating the two possible positions it takes in the whole set of MPTs.

Conclusions

A revised diagnosis, with the proposition of a new autapomorphy, strengthens the validity of *Ae. maximus*. A phylogenetic analysis

Table 1. Phylogenetic definitions of clade names used in this study.

Clade name and registration	Phylogenetic definition, reference phylogeny, and composition
Titanosauriformes **L. Salgado, R. Coria and J. Calvo, 1997** [this work], converted clade name **Registration Number**: 438	**Phylogenetic definition**: The least inclusive clade containing *Giraffatitan* (originally *Brachiosaurus*) *brancai* Janensch 1914, and *Saltasaurus loricatus* Bonaparte and Powell 1980. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Titanosauriformes* includes Brachiosauridae and *Somphospondylii*.
Somphospondylii **J. Wilson & P.** Sereno 1998 [this work], converted clade name **Registration Number**: 436	**Phylogenetic definition**: The largest clade containing *Saltasaurus loricatus* Bonaparte and Powell 1980, but not *Giraffatitan* (originally *Brachiosaurus*) *brancai* Janensch 1914. This is a maximum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Somphospondylii* includes *Titanosauria, Chubutisaurus insignis, Ligabuesaurus lenzai, Wintonotitan wattsi*, and a clade including *Erketu ellisoni, Phuwiangosaurus sirindhornae, Qiaowanglong kangxii*, and *Tastavinsaurus sanzi*.
Titanosauria **J. F. Bonaparte and R. Coria, 1993** [this work], converted clade name **Registration Number**: 435	**Phylogenetic definition**: The least inclusive clade containing *Andesaurus delgadoi* Calvo and Bonaparte 1991, and *Saltasaurus loricatus* Bonaparte and Powell 1980. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Titanosauria* includes *Andesaurus delgadoi, Colossosauria¸ Dreadnoughtus schrani, Epachtosaurus sciuttoi* and Lithostrotia.
Colossosauria **González Riga, Lamanna, Otero, Ortiz David, Kellner and Ibiricu, 2019** [this work], converted clade name **Registration number**: 551	**Phylogenetic definition**: The largest clade containing *Mendozarasaurus neguyelap* González Riga, 2003, but not *Saltasaurus loricatus* Bonaparte and Powell 1980 or *Epachthosaurus sciuttoi* Powell 1990. This is a maximum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Colossosauria* includes Lognkosauria, *Baurutitan britoi*, and *Rinconsauria*.
Rinconsauria **J. Calvo, B. González-Riga and J. Porfiri, 2007** [this work], converted clade name **Registration Number**: 434.	**Phylogenetic definition**: The least inclusive clade containing *Rinconsaurus caudamirus* Calvo & González-Riga, 2003, and *Muyelensaurus pecheni* Calvo, González-Riga & Porfiri, 2007. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Rinconsauria* includes *Aeolosaurini, Muyelensaurus pecheni*, and *Rinconsaurus caudamirus*.
Aeolosaurini **A. Franco-Rosas, L. Salgado and I. Carvalho, 2004** [this work], converted clade name **Registration Number**: 433.	**Phylogenetic definition**: The least inclusive clade containing *Aeolosaurus rionegrinus* Powell 1987, and *Gondwanatitan faustoi* Kellner and Azevedo 1999. This is a minimum clade definition. **Reference phylogeny**: Phylogenetic hypothesis depicted in Figure 2 of this work. **Composition**: based on the reference phylogeny, *Aeolosaurini* includes *Aeolosaurus rionegrinus, Aeolosaurus colhuehuapensis, Arrudatitan maximus, Bravasaurus arrierosorum, Gondwanatitan faustoi, Punantitan coughlini, Overososaurus paradasorum, Trigonosaurus pricei*, and *Uberabatitan ribeiroi*.

stresses that, although related to *Aeolosaurini*, its sister taxon relationship to the Argentinean *Aeolosaurus* is uncertain, and perhaps even the less probable option, given that this position is occupied by *Punatitan* in the majority rule consensus tree. As such, we opted to establish a new genus, *Arrudatitan*, to accommodate *Ae. maximus* as *Ar. maximus*. Otherwise, keeping *Ar. maximus* in *Aeolosaurus* could lead taxic-approach-based macroevolutionary studies to erroneous conclusions. The postzygapophyses placed anteriorly or just at the level of the anterior border of the centrum in posteriormost anterior and middle caudal vertebrae remains as a feature only recovered in the two Argentinean species, *Ae. rionegrinus* and *Ae. colhuehuapensis*, not seen in any other related taxa (e.g., *Arrudatitan, Punatitan, Overosaurus, Trigonosaurus*), that is useful to bolster previous proposals to diagnose the genus *Aeolosaurus* (Casal et al. 2007; Martinelli et al. 2011) and thus to exclude other related *Aeolosaurini* form of the genus.

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No potential conflict of interest was reported by the authors.

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