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Note on the paleobiogeography of Compsognathidae (Dinosauria: Theropoda) and its paleoecological implications

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ABSTRACT

The paleobiogeography of the theropod clade Compsognathidae is here reassessed in order to test the hypothesis of this taxon being adapted specifically to inhabit semi-arid environments. Data about localities where these fossils were collected and their paleoenvironments were gathered from the literature. Compsognathids seem to be found especially in sedimentary deposits known as *Fossil Lagerstätten*, which were formed under a set of specific conditions that allowed the preservation of the fragile bone remains of these animals. This bias limits an accurate analysis of the historical and/or ecological paleobiogeography of this taxon. Actually, it is possible that compsognathids had an almost worldwide distribution during the Mesozoic Era. Their occurrence in Lower Cretaceous rocks of China suggests that they also inhabited environments with moist conditions instead of being restricted to semi-arid to arid environments.

Key words: Compsognathidae, *Fossil Lagerstätten*, fossil record, paleobiogeography, paleoecology, Theropoda.

INTRODUCTION

Compsognathidae is a group of small theropods that has been positioned among basal coelurosaurs in recent phylogenies (Holtz Jr 1998, Sereno 1999, Senter 2007). In recent years, compsognathids have taken an important role in discussions about the origin of feathers and their color patterns (Xu 2006, Zhang et al. 2006, 2010). However, few considerations on their paleoecology and paleobiogeography were made so far. One attempt is from Naish et al. (2004), who considered these theropods as “specifically adapted to inhabit semi-

arid environments” once they were found in the Solnhofen Plattenkalk and Santana Formation.

When Naish et al. (2004) proposed this scenario they recognized only four species as members of Compsognathidae: which were the Laurasian *Compsognathus longipes*, *Aristosuchus pusillus*, and *Sinosauropteryx prima* and the Gondwanan *Mirischia asymmetrica*. Therefore, it is necessary to review the distribution of this taxon and its paleoecological implications given that four other species described after Naish et al. (2004) are now also considered as compsognathids (Peyer 2006, Ji et al. 2007, dal Sasso and Maganuco 2011) and that they did not take into account the paleoenvironment

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of the Early Cretaceous Jehol Biota, where *S. prima* inhabited. Hence the aim of this work is to reanalyze the paleobiogeography of Compsognathidae *sensu* Peyer (2006) and its implications, especially if it can (or cannot) support the paleoecological inference aforementioned. In order to do this, data about localities where compsognathids were found and the paleoenvironments where they inhabited were compiled and reviewed.

COMPSOGNATHIDS THROUGH SPACE AND TIME

Compsognathidae comprise a set of species with unclear relationships among them and with other theropods, so sometimes it appears as a non-monophyletic group. Testing the monophyly of this taxon will require further phylogenetic studies, including especially more basal coelurosaurs (Chiappe and Göhlich 2010). In order to define the range of taxa that is considered here to be a compsognathid, the diagnostic features proposed by Peyer (2006) are adopted: (i) fan-shaped mid to posterior dorsal neural spines; (ii) metacarpal I very stout, approximately as broad as long; (iii) proximal width of phalanx I-1 more than minimal shaft diameter of radius; (iv) lack of an external mandibular fenestra; (v) lack of pleurocoels in dorsal vertebrae; (vi) short, wide and only slightly inclined dorsal transverse processes; (vii) hook-shaped ligament attachments on dorsal neural spines. This combination of features is not the same as those employed by other authors (eg. Chen et al. 1998, Hwang et al. 2004, Naish et al. 2004, Göhlich and Chiappe 2006), but circumscribe all the species assigned by them to Compsognathidae. These species are presented below in temporal order.

The first compsognathid described was *Compsognathus longipes* Wagner 1861, firstly found in Solnhofen Lithographic Limestones, also known as the Solnhofen Plattenkalk, in Germany (Ostrom 1978). More recently it was also recovered from Canjuers limestones in France (Peyer 2006) and, possibly, in Portugal (Antunes and Mateus 2003, Mateus et al. 2006). All these records are Late

Jurassic in age (Fig. 1a). *Juravenator starki* Göhlich and Chiappe 2006 is also from Germany, but it was found in the Schamhaupten plattenkalk, which is at least five million years older than Solnhofen (Göhlich and Chiappe 2006, Chiappe and Göhlich 2010). In this way the two species were not coeval. However, there is some disagreement concerning the compsognathid identity of *J. starki* (Xu 2006, Butler and Upchurch 2007).

The Early Cretaceous compsognathid fossil record includes taxa recovered from Europe, Asia and South America (Fig. 1b). *Scipionyx samniticus* dal Sasso and Signore 1998, from the Pietrarroia Plattenkalk, in Italy, and *Aristosuchus pusillus* Owen 1876, from the Wessex Formation, in Great Britain, are the European species (Seeley 1887, dal Sasso and Signore 1998). Their allocation in Compsognathidae is sustained by some authors (Naish 2002, Naish et al. 2004, Peyer 2006, Naish and Martill 2007, dal Sasso and Maganuco 2011).

All the Asiatic compsognathid species come from the Yixian Formation, in China. Despite some disputes, an Early Cretaceous age is usually assumed for this stratigraphic unit (Zhou et al. 2003, Tan and Ren 2006, Liu et al. 2012). The first Chinese taxon described was *Sinosauropteryx prima* Ji and Ji 1996 (Chen et al. 1998) and the second *Huaxiagnathus orientalis* Hwang et al. 2004 (Hwang et al. 2004). The third species, named *Sinocalliopteryx gigas* Ji et al. 2007 (Ji et al. 2007), was described after the work of Peyer (2006).

Lastly, *Mirischia asymmetrica* Naish et al. 2004, from the Santana Formation (Early Cretaceous, Brazil; Naish et al. 2004), is the only compsognathid discovered hitherto in Gondwana (Naish et al. 2004, Bittencourt and Langer 2011, but see dal Sasso and Maganuco 2011).

DISCUSSION

The presence of an organism is promptly confirmed when body fossils or ichnofossils securely assigned to it are found in a determined area. However, the

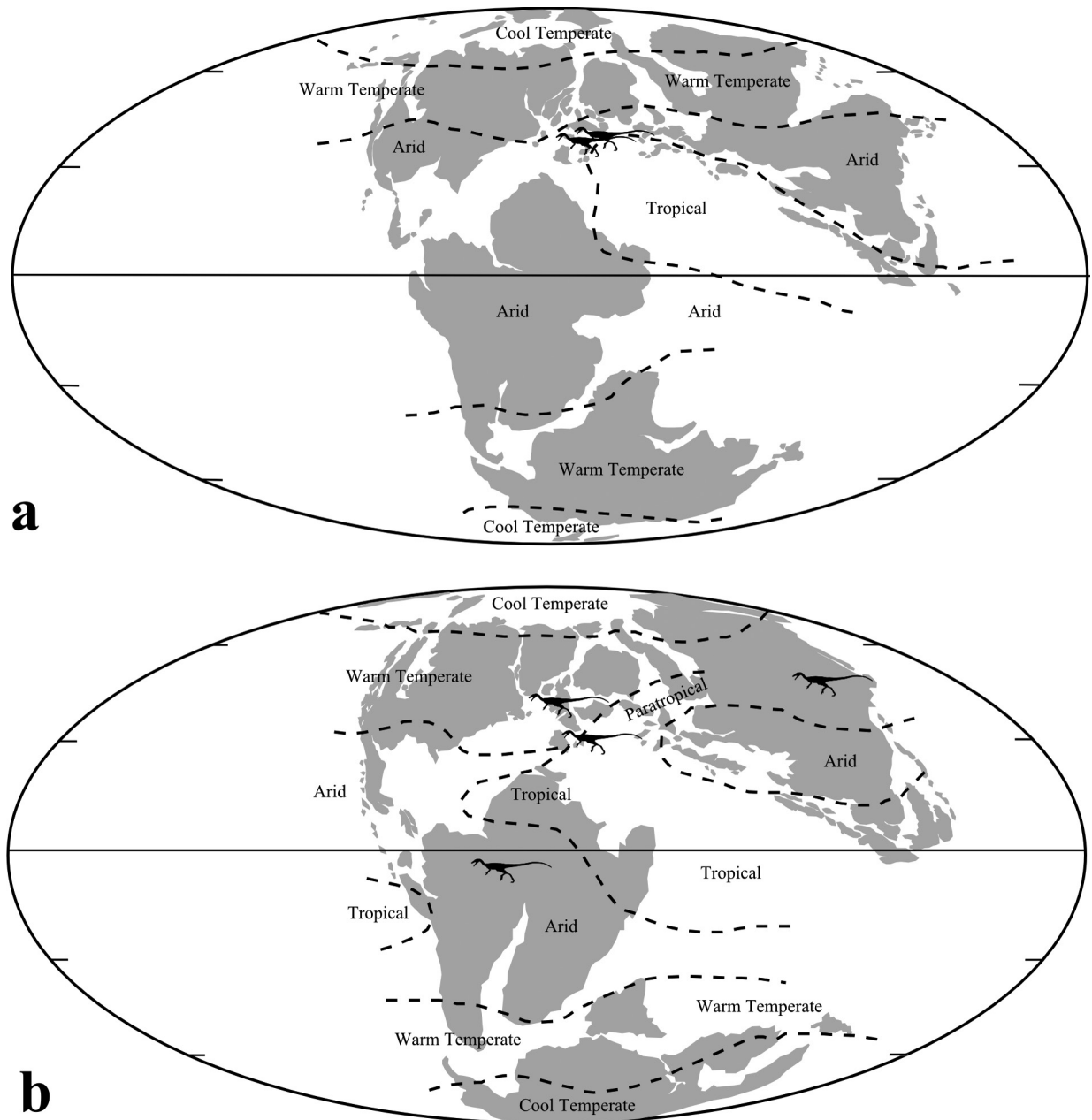


Fig. 1 - Paleogeographic maps of **(a)** Late Jurassic and **(b)** Early Cretaceous times showing the geographical distribution of compsognathids. The areas of occurrence are signalized with compsognathid body icons. Because of the proximity, the occurrences within the same country were indicated with only one body icon. Body icons were modified from Naish et al. (2004), while the maps from Blakey (2006) are after Scotese (2002).

absence of an organism is more difficult to prove as it might be due to three main reasons (Upchurch et al. 2002): (i) it never inhabited that area; (ii) it inhabited there but then became extinct; and (iii) it inhabited that region but its fossils have not been preserved or discovered yet.

Before analyzing the paleobiogeographic distribution of Compsognathidae, it is fundamental to highlight that most of the species came from *Fossil Lagerstätten*, sedimentary deposits with exquisite fossil records. Solnhofen and Santana Formations have been known because of their

exceptional fossils, which are listed in compendia dedicated exclusively to each sedimentary deposit (eg. Maisey 1991, Frickhinger 1994). In fact, Martill (1990) considered these two deposits among the ten principal *Fossil Lagerstätten* of the world. The Yixian Formation, along with other formations of the Jehol Group, has contributed with many excellently preserved fossils to the discussions about the origin and/or radiation of important taxa, like angiosperms and mammals (Lucas 2001, Zhou et al. 2003, Zhou 2006, Liu et al. 2012). The Pietraroia Plattenkalk and Schamhaupten Plattenkalk also have well-preserved fossil specimens and can be considered among the main *Fossil Lagerstätten* (dal Sasso and Signore 1998, dal Sasso 2003, Chiappe and Göhlich 2010).

This could mean that these small-bodied animals, with skeletons constituted by relatively fragile elements, would require some special conditions for their preservation as fossils. Indeed, most specimens are in excellent state of preservation and some of them also have soft tissues, feathers and/or gut contents preserved (Ostrom 1978, Norman 1990, Chen et al. 1998, dal Sasso and Signore 1998, Naish et al. 2004, Göhlich and Chiappe 2006, Ji et al. 2007, Chiappe and Göhlich 2010). If this hypothesis is correct two implications are plausible (see below).

The first one is that the distribution of this taxon during Mesozoic times could have been larger than that suggested by the fossil record. In fact, compsognathids were small carnivores whose diet included small vertebrates (Ostrom 1978, Norman 1990, Chen et al. 1998, Ji et al. 2007). Actually this trophic niche should have been present in almost all types of ecosystems during Late Jurassic and Early Cretaceous, from forests to deserts (Zhou 2006, Leonardi et al. 2007). So it seems that there were no major trophic restrictions to the presence of compsognathids in other areas of the world, although possible competition with other theropods and terrestrial taxa should be also taken into account when speculating that.

The second aspect concerns the absence of this clade in Africa. Once this group was found in Europe, Asia and South America, it would be expected that it was also present in the African continent, the main land connection between Laurasia and South America until the end of the Early Cretaceous (Naish et al. 2004, Sereno et al. 2004). Russell and Paesler (2003) commented that the taphonomy of Early Cretaceous African fluvial deposits favored the preservation of robust bony elements, so that the presence of small and delicate taxa would be negatively biased. Accordingly, it is also likely that the diversity of small dinosaurs has not been well sampled (Russell and Paesler 2003). Therefore, it is plausible that the unfavorable fossilization conditions prevented the fossil record of Compsognathidae in Africa, what does not exclude the possibility that these theropods may be found there in the future (Upchurch et al. 2002).

A similar inference may explain the Jurassic compsognathid fossil record. According to Xu (2006) and Chiappe and Göhlich (2010), complete skeletons of small theropods of this period are rare. Notably, *Juravenator starki* and *Compsognathus longipes*, the only two Jurassic compsognathid species, were respectively found in Schamhaupten and Solnhofen. Alternatively, one could suggest that these species represent the beginning of the compsognathid radiation, a hypothesis that the poor Jurassic theropod fossil record cannot rule out. However, some cladograms show *C. longipes* in a more derived position within Compsognathidae (Naish et al. 2004, Hwang et al. 2004, dal Sasso and Maganuco 2011), which could mean that the radiation had begun before the Late Jurassic times and not necessarily in Europe. Actually, this is an issue that requires further investigations based on new specimens.

Luo (1999) and, then, Zhou et al. (2003) suggested that Asia, especially the Chinese region, had acted as a refuge for many “typically” Jurassic taxa due to the geographic isolation between that

land mass and the rest of Laurasia during Middle Jurassic to Early Cretaceous. Among these taxa were the compsognathid *Sinosauropteryx prima*, considered the sister-group of *C. longipes*, and the anurognathid pterosaurs. However, the *status* of “typically Jurassic” assigned to Compsognathidae does not seem to be appropriate nowadays, as only two out of eight species are from Jurassic sedimentary deposits. Furthermore, Naish et al. (2004), based on the similarity of the pelvic girdle, considered *Compsognathus longipes* more similar to *Mirischia asymmetrica* than to *S. prima*. In fact, Manabe et al. (2000) suggested that the presence of ‘Late Jurassic’ taxa in Eastern Asia might be the result of a more gradual Jurassic-Cretaceous faunal transition.

Actually, once the paleobiogeographic distribution of compsognathids may have been biased by taphonomic factors, any analysis aiming to determine historical aspects and to identify dispersion events and/or vicariant evolution is not possible or secure enough to be performed. Moreover, if the distribution of these small theropods during Jurassic and Cretaceous was wider than that suggested by the fossil record, the presence of this taxon in Asia could be a consequence of a pangeic distribution. Accordingly, these animals might have arrived in Asia before the geographic isolation that began during the Jurassic as the result of the formation of the Turgai epicontinental sea (Upchurch et al. 2002), as proposed for spinosaurs (E. Buffetaut, unpublished data).

Paleobiogeography can be a tool to make paleoecological inferences, mainly when it is not possible to recognize anatomical adaptations to paleoecological conditions like the weather (Russell and Paesler 2003). However, keeping in mind the possibility of the compsognathid paleobiogeography being almost all restricted to *Fossil Lagerstätten*, any paleoecological generalization based on paleobiogeographic data does not seem to be very consistent for this taxon.

Another important fact is that, despite recognizing *Sinosauropteryx prima*, as the only Chinese species found until then, and *Aristosuchus pusillus* as members of Compsognathidae, Naish et al. (2004) did not mention these species in their inference about these theropods being exclusively adapted to inhabit semi-arid to arid environments. The Yixian Formation, where the three Chinese compsognathids were discovered, seems to have been deposited in an environmental setting that alternated between mesic and semi-arid conditions (Zhou et al. 2003). However, a warm and moist climate is also proposed for this stratigraphic unit, what fits better with the flourishing forest that presumably existed there, supporting many arboreal and herbivorous vertebrate taxa, including the gliding lizard *Xianglong zhaoi* and the arboreal theropod genus *Microraptor* (Xu et al. 2000, Zhou et al. 2003, Zhou 2006 and the references therein, Li et al. 2007). The presence of maculae in some cockroaches wings from this formation is also proposed to be related to a warm and moist climate (Tan and Ren 2006, Wang et al. 2007).

Plant taxa adapted to more mesic conditions also inhabited the Araripe Basin when the Crato Formation was deposited (Bernardes-de-Oliveira et al. 2007). Thus, mesic conditions should have been also present in some regions within the Crato Formation paleoenvironment (M.E.C. Bernardes-de-Oliveira et al., unpublished data) and the same is plausible to Santana Formation, which overlies the former formation and shares with it many generic and supra-generic taxa. Furthermore, Frickhinger (1994) considered the absence of true ferns in the Solnhofen plattenkalk as an evidence of the absence of both abundant moisture and more or less shady habitats. However, these plants are found in Yixian and Crato Formations (Zhou et al. 2003, Martill et al. 2007, Bernardes-de-Oliveira et al. 2007). Therefore, the paleoenvironment of Yixian and, possibly, Santana Formation should have been relatively less arid than that of Solnhofen.

FINAL CONSIDERATIONS

Although paleobiogeography may be useful for making paleoecological inferences by suggesting the main paleoecological factors present in the habitat during the lifespan of a taxon, including type of vegetation and climate (eg. Garcia 2007, Butler and Barrett 2008, Carvalho et al. 2010), a geographic distribution pattern biased by taphonomic factors can limit considerably the possibility of this approach being applied. This seems to be the case of compsognathids, for which it is unsafe nowadays to perform any detailed paleobiogeographic analysis. Actually, this situation is aggravated by the fact that there is not an accurate phylogeny for this taxon as a whole, being not possible to recognize phylogenetic relationships among the eight species that could bring some insights for this question.

For this study's purposes it was possible at least to test and reject the proposition of Naish et al. (2004), which was not totally in accordance with the fossil record. Compsognathids also inhabited areas considerably moister than Solnhofen paleoenvironment, including forests. Finally the present work emphasizes the need of a critical analysis of the fossil record and its limitations before any further study.

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RESUMO

A paleogeografia do clado de terópodes Compsognathidae é aqui reavaliada a fim de testar a hipótese de

este táxon ser exclusivamente adaptado a ambientes semiáridos. Os dados sobre as localidades onde esses fósseis foram coletados e seu paleoambiente foram levantados a partir da literatura. Compsognatídeos parecem ser encontrados especialmente em depósitos sedimentares conhecidos como *Fossil Lagerstätten*, os quais se formaram sob um conjunto de condições que possibilitaram a preservação dos frágeis elementos ósseos desses animais. Esse tendenciamento impede qualquer análise acurada da paleobiogeografia histórica ou ecológica deste táxon. Na realidade, é possível que compsognatídeos tenham tido uma distribuição por quase todo o planeta durante a Era Mesozoica. Sua ocorrência nas rochas do Cretáceo Inferior na China sugere que também ocupavam ambientes com condições húmidas em vez de estarem restritos a ambientes semiáridos e áridos.

Palavras-chave: Compsognathidae, *Fossil Lagerstätten*, registro fóssil, paleobiogeografia, paleoecologia, Theropoda.

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