Reply to
Rauhut et al. 2020: The oldest record of the genus *Torvosaurus* (Theropoda: Megalosauridae) from the Callovian Ornatenton Formation of north-western Germany.
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Rauhut et al. (2020, p.41), in their description of *Torvosaurus* remains from the Middle Jurassic of Germany, made some references to our (Soto et al. 2020a) referral to isolated teeth from Uruguay and Tanzania to the genus *Torvosaurus*.

We will address some of their statements below.

a) "Hendrickx et al. (2019) pointed out that isolated teeth of theropods are rarely diagnostic on genus level, and this also applies to the teeth of *Torvosaurus*."

Hendrickx et al. (2019) also listed several genera that are indeed diagnostic, such as *Majungasaurus*, *Piatnitzkysaurus*, *Afrovenator*, *Acrocanthosaurus*, *Tyrannosaurus*, *Saurornitholestes* and *Troodon*. We would add to this list *Torvosaurus* and *Ceratosaurus* (see Soto et al. 2020a, 2020b). Soto et al. (2020a) clearly demonstrated that the teeth from Uruguay belong to a megalosaurid theropod, and particularly to a megalosaurine distinct from *Duriavenator* or *Megalosaurus*. Only *Torvosaurus* and the lesser known *Wiehenvenator* are likely candidates on morphological grounds. The Middle Jurassic age of *Wiehenvenator* favour the assignment to *Torvosaurus*, given that the Tacuarembó Formation has been independently dated as Late Jurassic based on conchostracans (Shen et al. 2004) and the presence of taxa not recorded in the Middle Jurassic such as the shark *Priohybodus* (Perea et al. 2001), the theropod *Ceratosaurus* (Soto et al. 2020b) and a *Gnathosaurus*-like pterosaur (Soto et al. 2021). The radiometric dating of the Gaspar Formation basalts (165 Ma) which underlies the Itacumbú Formation (de Santa Ana & Veroslavsky 2004), which in turn underlies the Tacuarembó Formation, should be taken into account.

b) "Even accounting for the unusual large size of these teeth, similarly large teeth are also found in *Wiehenvenator*, ceratosaurids and carcharodontosaurids" (references omitted for clarity).

Soto et al. (2020a) did not base their referral just on crown height. The study covered all aspects of dental anatomy, such as cross-sectional shape, carinae development and placement, denticle size (the largest among theropods) and morphology, enamel texture, enamel undulations, interdenticular sulci, etc. were taken into account. *Torvosaurus* and ceratosaurid lateral teeth differ morphometrically: *Torvosaurus* teeth are larger (e.g., maximum crown height 152.8 mm, compared with 75.0 mm in *Ceratosaurus*; see supplementary information in Young et al. 2019) and

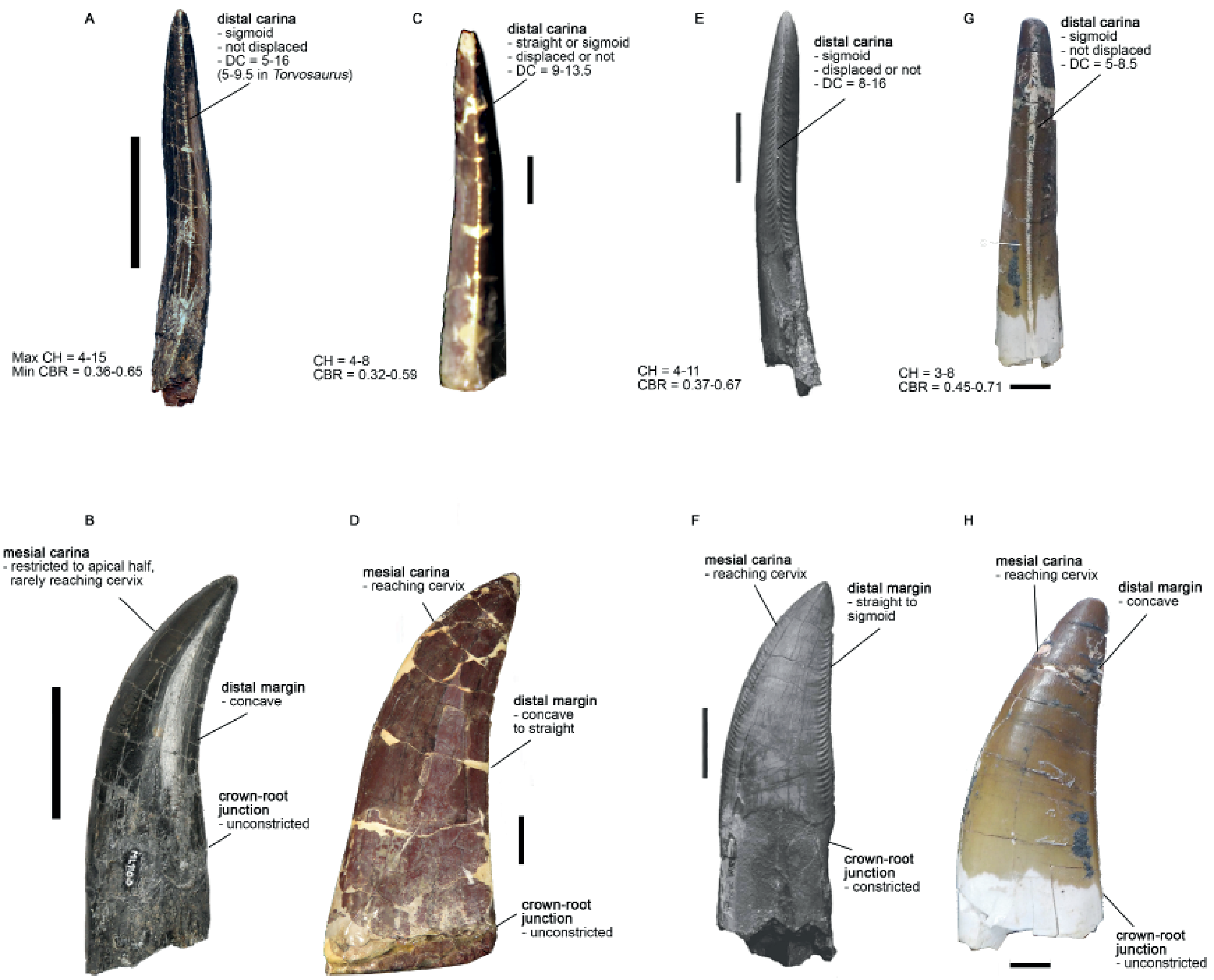

Fig. 1: Comparison of lateral teeth of **A, B** *Torvosaurus gurneyi* (Hendrickx & Mateus, 2014), **C, D** *Ceratosaurus* sp. (photographs kindly provided by C. Hendrickx), **E, F** *Carcharodontosaurus saharicus* (Brusatte et al., 2007) and **G, H** the Uruguayan megalosaurid (Soto et al., 2020a) in distal (A, C, E, G) and labial/lingual views (B, D, F, H). Characters that do not vary among these taxa (mesial carina straight, braided enamel texture, transverse undulations, marginal undulations (although more conspicuous and consistently present in *Carcharodontosaurus saharicus* than in most megalosaurid and ceratosaurid teeth), well-developed interdenticular sulci) are not depicted. Measurements taken from supplementary information in Young et al. (2019), considering the ranges of the families. Scales: 1 cm (C, D, G, H), 3 cm (E, F) and 5 cm (A, B). Photos courtesy of C. Hendrickx and S. Brusatte.

have coarser denticles (distocentral density of 5–10 in *Torvosaurus* versus 8–13 in *Ceratosaurus*; see supplementary information in Young et al. 2019). Moreover, they also differ morphologically, to mention a few characters: *Torvosaurus* bears subsymmetrical lateral teeth, with mesial carinae restricted to the apical portion of the tooth in most cases and distal carinae not labially displaced, whereas *Ceratosaurus* has asymmetrical lateral teeth (the labial face being flat; Hendrickx et al. 2019), with mesial carinae reaching the cervix, and a labially displaced distal carinae (Fig. 1). The mesial teeth (both of which have been found in Uruguay) are even more different (Fig. 2), with *Ceratosaurus* having a conspicuously fluted lingual face and strongly labially displaced and bowed distal carina, versus non-fluted lingual face and centrally positioned and straight distal carina in *Torvosaurus* (Fig. 2), besides the already mention differences in denticle density. Although in both genera the mesial carina is restricted to the apical portion of the crown in mesial teeth, in *Ceratosaurus* it can be either straight or lingually twisted (C. Hendrickx, pers. comm., 2021) whereas it is always straight in *Torvosaurus*. Differences between *Torvosaurus* and carcharodontosaurids are addressed below.

c) "Furthermore, both in respect to morphometric data, as well as qualitative characters, the teeth of *Torvosaurus* are similar to carcharodontosaurid teeth, a group that has also been reported from the Tendaguru Formation" (references omitted for clarity).

Although we agree that there are some similarities, such as the crown base ratio range, and presence of braided enamel texture, transverse and/or marginal undulations and long interdenticular sulci in some taxa, many differences do exist. Both maximum crown height and denticle size in *Torvosaurus* (see

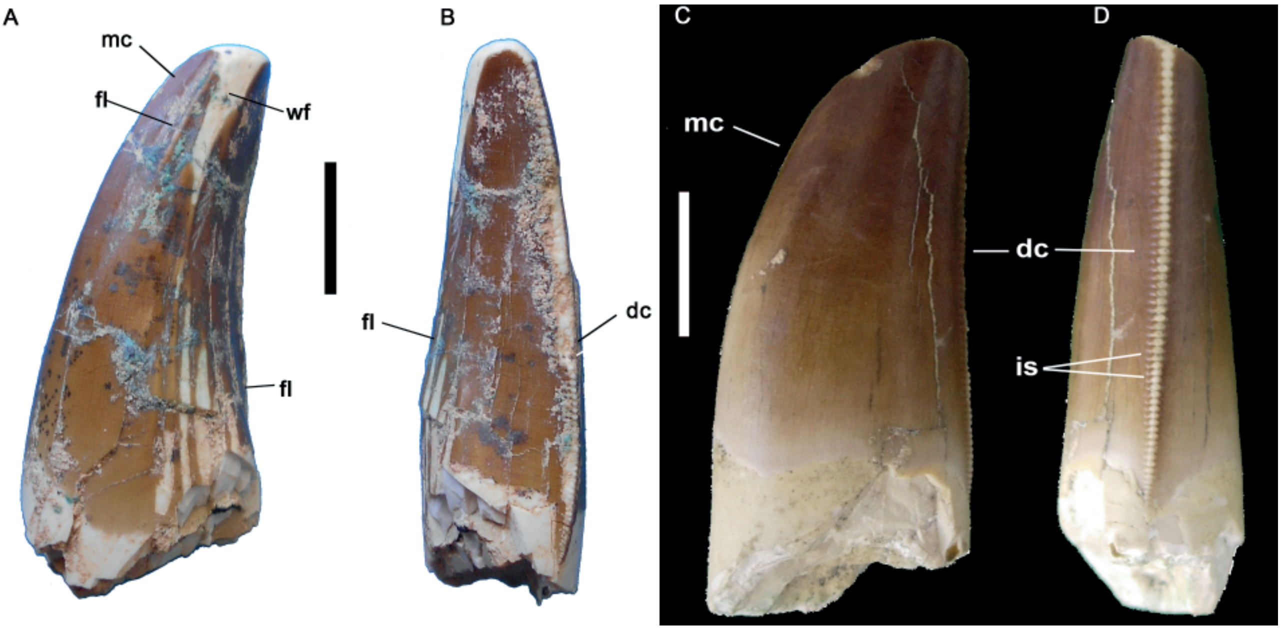

Fig. 2: Mesial teeth of *Ceratosaurus* in lingual (A) and distal (B) view. Distal teeth of *Torvosaurus* in lingual (C) and distal (D) views. Taken from Soto et al. (2020a, 2020b). Abbreviations: dc, distal carina; fl, flutes; is, interdenticular sulci; mc, mesial carina; wf, wear facet. Scales: 1 cm. Taken from Journal of South American Earth Sciences, 98, M. Soto, P. Toriño & D. Perea, "A large sized megalosaurid (Theropoda, Tetanurae) from the late Jurassic of Uruguay and Tanzania", Copyright Elsevier and Journal of South American Earth Sciences ,103, M. Soto, P. Toriño & D. Perea, "*Ceratosaurus* (Theropoda, Ceratosauria) teeth from the Tacuarembó Formation (Late Jurassic, Uruguay)", Copyright Elsevier.

above) are significantly larger than in carcharodontosaurids (102.6 mm and 7–17.5 distocentral denticle density; see supplementary information in Young et al. 2019). Morphologically (Fig. 1), the distal profile is concave in *Torvosaurus* whereas it is straight, convex or even sigmoid in carcharodontosaurids (Hendrickx et al. 2019). In addition, the distal carina is labially displaced in some carcharodontosaurid teeth whereas there is no displacement in *Torvosaurus* (Hone & Rauhut 2009). Finally, a weak constriction between crown and root can be seen in some carcharodontosaurids whereas no crowns are constricted in *Torvosaurus* (Hendrickx et al. 2019).

It should be noted that the Uruguayan and Tanzanian teeth fell into the *Torvosaurus* morphospace in both principal component and discriminant analyses (Fig. 3) performed by Soto et al. (2020a). They were also retrieved among *Torvosaurus* teeth in two diffe-

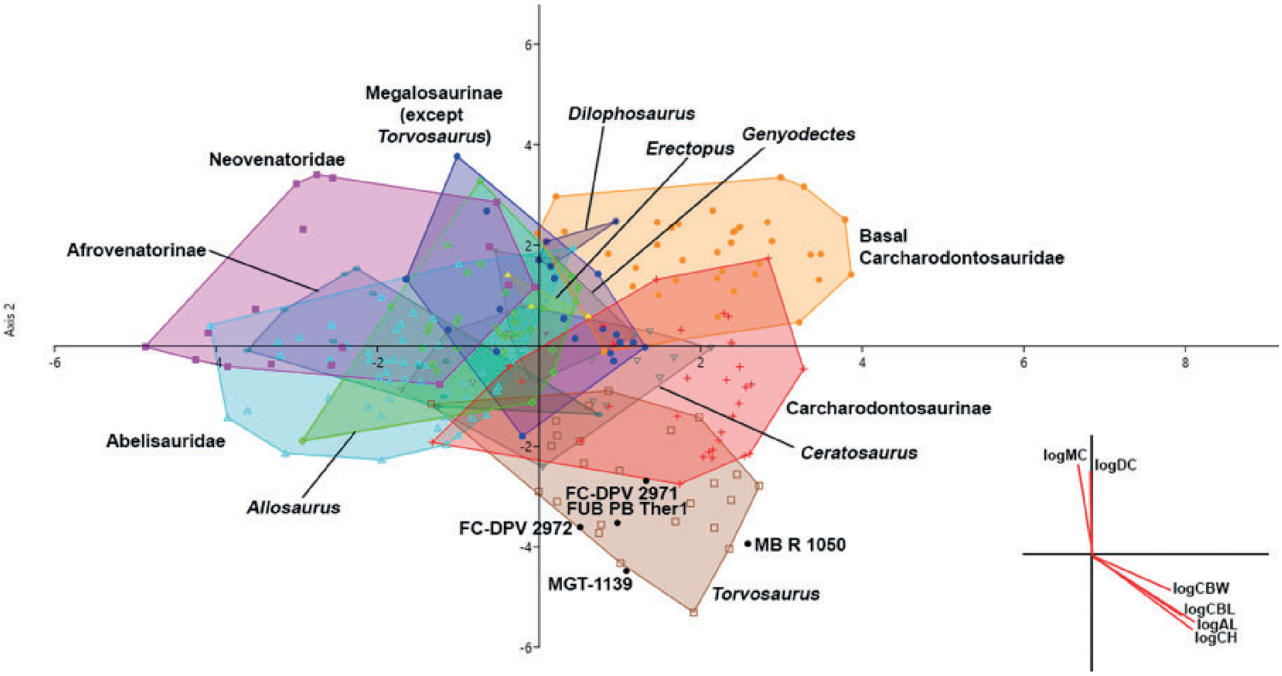

Fig. 3: Results of the discriminant analysis on the first dataset of Soto et al. (2020a). Taken from Journal of South American Earth Sciences, 98, M. Soto, P. Toriño & D. Perea, "A large sized megalosaurid (Theropoda, Tetanurae) from the late Jurassic of Uruguay and Tanzania", Copyright Elsevier.

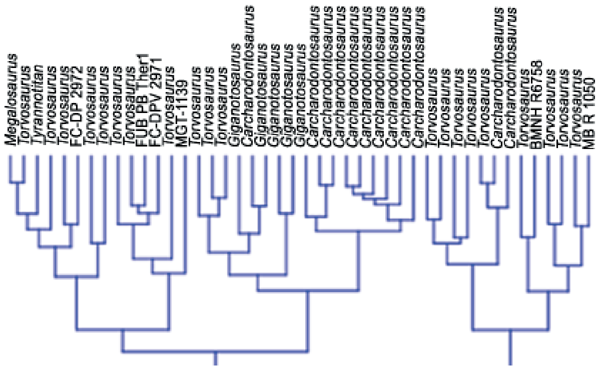

Fig. 4: Results of a cluster analysis (detail) on the first dataset of Soto et al. (2020a). Teeth from Uruguay: FC-DPV 2971, FC-DPV 2972, MGT-1139. Teeth from Tanzania: BMNH R 6758, MB R 1050. Tooth from Portugal: FUB PB Ther1. Taken from Journal of South American Earth Sciences, 98, M. Soto, P. Toriño & D. Perea, "A large sized megalosaurid (Theropoda, Tetanurae) from the late Jurassic of Uruguay and Tanzania", Copyright Elsevier.

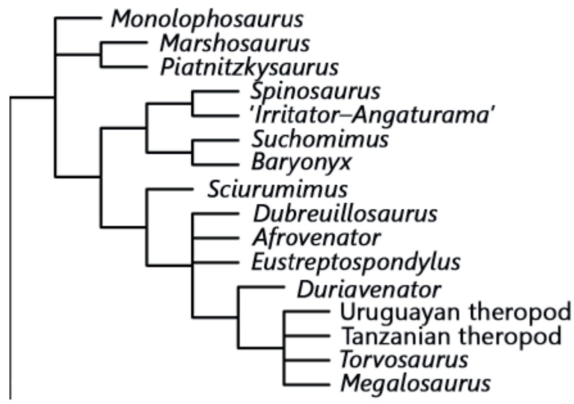

Fig. 5: Results of the phylogenetic analysis with emphasis on megalosauroids. Based on data from Soto et al. (2020a).

rent cluster analyses (although some carcharodontosaurid teeth are included, they do not form part of the small clusters; Fig. 4), and in a polytomy with *Torvosaurus* and *Megalosaurus* in the phylogenetic analysis (Fig. 5). Forcing these teeth to be related with ceratosaurids or carcharodontosaurids in the latter analysis would require 13 steps in the former case and between 9 and 13 steps in the latter. Finally, and perhaps more importantly, a large, robust megalosauroid was also represented in the Tendaguru Formation by skeletal material (Rauhut 2011). Nevertheless, having not examined the teeth from Tendaguru at first hand and given that a carcharodontosaurid is represented by skeletal material (Rauhut 2011), we cannot discard the fact that carcharodontosaurid teeth are also present among the material Janensch (1920, 1925) originally referred to '*Megalosaurus*' *ingens*.

In conclusion, we agree with Rauhut et al. (2020) that caution should be used when studying isolated theropod teeth. However, the morphology of some particularly well preserved and particularly diagnostic teeth enables confident taxonomic referrals, especially when this identification is further supported by multivariate (Figs. 3, 4) and phylogenetic (Fig. 5) analyses. As stated by Soto et al. (2020a), the large size of both teeth (lateral crown height > 70 mm, fragments of larger teeth do exist) and denticles (less than 7 denticles per 5 mm at mid-crown), the well-visible braided enamel texture, the centrally placed and apically restricted mesial carina in mesial teeth, and general shape of the teeth strongly resembles those of *Torvosaurus*.

Theropod teeth offer a wealth of information, and are often phylogenetically informative despite homoplasy, as recent work by Hendrickx et al. (2019) shows clearly. We emphasize that a megalosaurine theropod different from *Duriavenator* and *Megalosaurus* was present in the Late Jurassic of Gondwana, which is biogeographically and biostratigraphically relevant.

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