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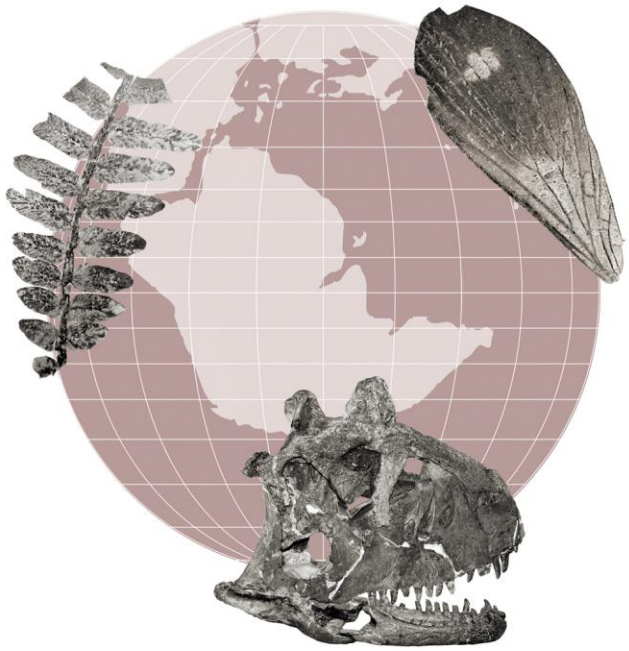

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ISOLATED ABELISAURID TEETH FROM GONDWANA AND DENTAL EVOLUTION IN ABELISAURIDAE

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Short Description: We here describe several isolated abelisaurid teeth of stratigraphic and historic importance using cladistic and machine learning analyses. We also explore dental evolution in Abelisauridae.

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Abstract. Abelisauridae were medium to large-bodied carnivorous dinosaurs with short ornamented skulls, poorly recurved ziphodont teeth, and reduced forelimbs. They were the dominant terrestrial carnivores in many Gondwanan ecosystems during the Cretaceous and the apex predators in South America, Africa, India, and Europe in the latest part of the Cretaceous. Their Jurassic origin, primarily based on the putative abelisaurid *Eoabelisaurus* from the Early Jurassic of Patagonia, remains debated, with many authors considering Abelisauridae as a strictly Cretaceous theropod radiation. Here we describe several historically and stratigraphically important isolated theropod teeth from Gondwana identified as belonging to abelisaurids using new cladistic and machine learning methods. Dental evolution in Abelisauridae was additionally explored using an updated version of a dentition-based data matrix focused on ceratosaurs. Results of this study shows that the evolution of the dentition in abelisaurids was marked by a decrease in size of the mesialmost dentary teeth and the displacement of the tallest crowns towards the middle part of the maxilla. Two isolated abelisaurid teeth from the Late Cretaceous of India and Patagonia were also identified as the earliest published record of a non-avian theropod in Asia and an abelisaurid in Argentina, respectively. More importantly, isolated theropod teeth confidently referred to Abelisauridae from the Middle Jurassic of Madagascar provide additional support for the emergence of this clade in Gondwana before the Late Jurassic and reveal that the acquisition of abelisaurid dental traits occurred early in the evolutionary history of one of the most successful radiations of non-avian theropods from Europe and the Southern Hemisphere.

Keywords. Theropoda. Ceratosauria. Crown. Dentition. Southern Hemisphere.

Resumen. Los abelisáuridos eran dinosaurios carnívoros de tamaño mediano a grande con cráneos cortos y ornamentados, dientes zifodontos poco recurvados y extremidades delanteras reducidas. Fueron los carnívoros terrestres dominantes en muchos ecosistemas de Gondwana durante el Cretácico y los superdepredadores en Sudamérica, África, India y Europa en los

pisos superiores del Cretácico. Su origen jurásico, basado principalmente en el supuesto abelisáurido *Eoabelisaurus* del Jurásico temprano de la Patagonia, sigue siendo objeto de debate, ya que muchos autores consideran que los Abelisauridae son una radiación de terópodos estrictamente cretácica. Aquí describimos varios dientes de terópodos aislados de Gondwana, importantes desde el punto de vista histórico y estratigráfico, que se han identificado como pertenecientes a abelisáuridos mediante nuevos métodos cladísticos y de aprendizaje automático. La evolución dental en los abelisáuridos se exploró adicionalmente utilizando una versión actualizada de una matriz de datos basada en la dentición centrada en los ceratosaurios. Los resultados de este estudio muestran que la evolución de la dentición en los abelisáuridos se caracterizó por una disminución del tamaño de los dientes dentarios más mesiales y el desplazamiento de las coronas más altas hacia la parte media del maxilar. También se identificaron dos dientes aislados de abelisáuridos del Cretácico Superior de la India y la Patagonia como el registro más antiguo publicado de un terópodo no aviano en Asia y un abelisáurido en Argentina, respectivamente. Más importante aún, slos dientes aislados de terópodos que se atribuyen con certeza a los Abelisauridae del Jurásico Medio de Madagascar proporcionan un respaldo adicional a la aparición de este clado en Gondwana antes del Jurásico Tardío y revelan que la adquisición de los rasgos dentales de los abelisáuridos se produjo en una etapa temprana de la historia evolutiva de una de las radiaciones más exitosas de terópodos no aviares de Europa y el hemisferio sur.

Palabras clave. Terópodos. Ceratosauria. Corona. Dentición. Hemisferio Sur.

FOR NEARLY 135 MILLION YEARS, throughout the Jurassic and Cretaceous, the role of apex predators in terrestrial ecosystems was essentially played by two groups of theropod dinosaurs, non-neocoelurosaur averostrans (e.g., dilophosaurids, ceratosaurs, megalosauroids, allosauroids, and tyrannosauroids) and, to a lesser extent, dromaeosaurids (e.g., unenlagiines and dromaeosaurines). In the Late Cretaceous, while this trophic guild was mainly dominated (if not monopolized) by the eponymous tyrannosaurids and their closest relatives in Asiamerica (Holtz, 2021), several medium to large-bodied theropods (>5m in body length), namely abelisaurids, spinosaurids, carcharodontosaurids, megaraptors, and unenlagiine dromaeosaurids, were often competing at the top of the food chain in Gondwana (Novas *et al.*, 2013; Ezcurra and Novas, 2016; Ibrahim *et al.*, 2020; Holtz, 2021). The extinction of spinosaurids and carcharodontosaurids, the largest land predators from the Southern Hemisphere, in the Cenomanian and Turonian, respectively (Novas *et al.*, 2005; Candeiro *et al.*, 2017; Delcourt and Grillo, 2018; Delcourt *et al.*, 2020; Meso *et al.*, 2021b; Canale *et al.*, 2022; n.b., spinosaurids may have nonetheless persisted in western South America up to the end of the Cretaceous; Olmedo-Romaña *et al.*, 2025), gave abelisaurids the opportunity to fully dominate this trophic niche in Europe, Africa (including Madagascar), and India during the remaining of the Cretaceous (Wilson *et al.*, 2003; Novas *et al.*, 2004; Rogers *et al.*, 2007; Tortosa *et al.*, 2014; Longrich *et al.*, 2017; Buffetaut, 2024), while also competing with various large-sized megaraptors and unenlagiines in South America (n.b., apex theropods from Antarctica and Australia remain largely unknown in the latest Cretaceous and, to date, no abelisaurid fossils have been recovered from these continents; Novas *et al.*, 2013; Holtz, 2021; Baiano *et al.*, 2022; Pol *et al.*, 2024).

Abelisauridae were medium to large-bodied carnivorous ceratosaurs (5–9 m) with deep ornamented skulls, short rounded snouts, and reduced forelimbs (Pol and Rauhut, 2012; Hendrickx *et al.*, 2015a; Grillo and Delcourt, 2017; Delcourt, 2018; Cerroni *et al.*, 2022a).

Their stratigraphic origin remains controversial owing to the disputed phylogenetic position of *Eoabelisaurus* from the Toarcian (Early Jurassic) of Patagonia, either as an early branching abelisaurid (Pol and Rauhut, 2012; Baiano *et al.*, 2023; Pol *et al.*, 2024), pushing the origin of Abelisauridae to the Early Jurassic; or an early branching non-abelisaurid neoceratosaur/abelisauroid, restricting Abelisauridae to the Cretaceous or the Late Jurassic and Cretaceous (Tortosa *et al.*, 2014; Wang *et al.*, 2017; Agnolín *et al.*, 2022). Nonetheless, abelisaurids were a key component of many dinosaur biota in Europe and Gondwana during the Cretaceous as their remains have been abundantly recovered from Cretaceous deposits of southwestern Europe (Buffetaut *et al.*, 1988; Tortosa *et al.*, 2014; Buffetaut, 2025a), Africa (Sereno *et al.*, 2004; Mahler, 2005; Sereno and Brusatte, 2008; Longrich *et al.*, 2017), Madagascar (Sampson *et al.*, 1998; Ratsimbaholison *et al.*, 2016), India (Wilson *et al.*, 2003; Novas *et al.*, 2004), and South America, where they were particularly abundant and diversified (e.g., Canale *et al.*, 2009; Novas *et al.*, 2013; Ezcurra and Novas, 2016; Zaher *et al.*, 2020; Pol *et al.*, 2024).

Even though the dentition of abelisaurids exhibits the classic ziphodont morphology characteristic of most carnivorous theropods, abelisaurid teeth are particularly diagnostic, displaying several apomorphic dental features (Smith, 2007; Hendrickx and Mateus, 2014; Hendrickx *et al.*, 2020a). Abelisaurid dentition is typically characterized by subrectangular alveoli in an “en echelon disposition” in the maxilla, biconvex mesialmost crowns with a salinon-cross section outline created by two concave surfaces adjacent to the carinae, and poorly curved lateral crowns with a straight to convex distal profile. In most abelisaurids, the crowns also have mesial and distal carinae reaching the cervix and centrally positioned mesial and distal carinae on their respective mesial and distal margins. Abelisaurid crowns also often show apically hooked denticles, well-developed interdenticular sulci, marginal and/or transverse undulations, and an irregular surface texture of the enamel (Smith, 2007;

Hendrickx *et al.*, 2020a). Such a combination of diagnostic abelisaurid dental features have helped many authors to recognize their presence in many Mesozoic ecosystems such as the Late Jurassic of Uruguay (Soto *et al.*, 2023), Portugal (Hendrickx and Mateus, 2014) and possibly Brazil (Ribeiro *et al.*, 2025), the Early Cretaceous of Brazil (de Carvalho and Santucci, 2018; Sales *et al.*, 2018; Ribeiro *et al.*, 2022, 2023, 2024b) and Libya (Smith and Dalla Vecchia, 2006), and the Late Cretaceous of Africa (Smith and Lamanna, 2006; Fanti and Therrien, 2007; Ibrahim *et al.*, 2020; Hendrickx *et al.*, 2023), India (Prasad *et al.*, 2016), South America (e.g., Meso *et al.*, 2021a, 2024; Juarez *et al.*, 2023; Candeiro *et al.*, 2024; Delcourt *et al.*, 2024; Ribeiro *et al.*, 2024a, 2024b), and Europe (Isasmendi *et al.*, 2022, 2024; Malafaia *et al.*, 2025).

This contribution aims to: i) describe and identify stratigraphically and historically important isolated theropod teeth from Gondwana, either tentatively referred to Abelisauridae or having abelisaurid dental traits, from Middle Jurassic, Late Jurassic, and Late Cretaceous deposits (Figs. 1-2); ii) examine the dental evolution of abelisaurids throughout the Cretaceous based on an updated version of a dentition-based data matrix focused on ceratosaurs; and iii) implement a more robust and improved machine learning approach with new algorithms and pipeline.

Institutional abbreviations. FC-DPV, Colección de Vertebrados Fósiles, Facultad de Ciencias, Universidad de la República, Uruguay; **FSL,** Faculté des Sciences de Lyon, Lyon, France; **MACN,** Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MSNM,** Museo Civico di Storia Naturale di Milano, Milan, Italy; **NHMUK,** The Natural History Museum, Palaeontology Vertebrates, London, UK; **PVL,** Fundación ‘Miguel Lillo,’ San Miguel de Tucumán, Argentina.

Other abbreviations. AL, apical length; **CBL,** crown base length; **CBR**, crown base ratio; **CBW,** crown base width; **CH,** crown height; **CHR,** crown height ratio; **DA,** distoapical

152 denticle density; **DB,** distobasal denticle density; **DC,** distocentral denticle density; **DCR,**
153 denticle crown ratio; **DDL,** distal denticle length; **de/5 mm,** number of denticles per five
154 millimeters; **DSDI,** denticle size density index; **LAF**, number of labial flutes; **LIF**, number of
155 lingual flutes; **MA,** mesioapical denticle density; **MB,** mesio-basal denticle density; **MC,**
156 mesiocentral denticle density; **MCL,** mid-crown length; **MCR,** mid-crown ratio; **MCW,** mid-
157 crown width; **MDE,** mesiobasal denticle extent; **MDL,** mesial denticle length .

158 # MATERIAL AND METHODS

159 **Comparative methodology and terminology**

160 The dental material from the Mesozoic of Gondwana (Figs. 1-2), represented by 20 isolated
161 shed tooth crowns (one from India, two from Uruguay, eight from Madagascar, and nine from
162 Argentina), was examined first-hand and photographed with a digital camera by one of the co-
163 authors (CH for the Argentine and Indian specimens; MSN for the Uruguayan dental material,
164 and SM for the Malagasy teeth). Information on the paleogeographic and stratigraphic
165 distribution is provided for each specimen in the Systematic Paleontology section (See also
166 supplementary information). The denticles and enamel surface texture of the teeth from the
167 NHMUK, MACN and PVL collections were additionally examined with the help of a
168 portable DinoLite microscope. The isolated theropod teeth were described and annotated
169 using the *modus operandi*, terminology, and annotations proposed by Hendrickx *et al.*
170 (2015b). The latter is mainly based on the terminology provided by Smith and Dodson (2003)
171 for the positional nomenclature, and Smith *et al.* (2005) for the anatomical and morphometric
172 nomenclatures. Morphometric measurements on the crowns provided in Table 1 were taken
173 using the methodology summarized by Hendrickx *et al.* (2015b) and further detailed by
174 Hendrickx *et al.* (2020b, appendix A4). A new variable quantifying the size of the denticles in
175 relation to the height of crown, here called the “denticle crown ratio” (DCR), was introduced
176 in this study. DCR corresponds to the quotient of the largest distal denticle height (DDL;

typically at mid-crown) by the crown height (CH) multiplied by a hundred (DCR=DDL/CH*100; DCR=[5/DC]/CH*100). Teeth with minute denticles such as those of baryonychines have a DCR lower than 0.5 whereas teeth with particularly large denticles such as those of *Troodon* and *Saurornithoides* have a DCR higher than 10. The teeth were compared with those from a large sample of non-avian theropods, which includes 11 abelisaurid taxa deposited in the collection of nine institutions from France, Argentina, and the USA (see supplementary data). We finally followed the phylogenetic definitions given by Hendrickx *et al.* (2024) for each ceratosaur clade and either corrected or provided an updated version of the definitions for Berthasauridae, Elaphrosaurinae, and Noasaurinae in Table 2.

Cladistic analysis

The identification of the dental material was assisted with the help of a cladistic analysis performed on a revised version of Hendrickx *et al.*'s (2024) data matrix focused on the dentition of non-avian theropods. The dataset includes 148 non-ordered and similarly weighted discrete dental characters scored in 127 saurischians (i.e., 125 non-avian theropods and five early branching saurischians), to which we added six new dental characters and the abelisaurids *Rahiolisaurus gujaratensis* (Novas *et al.*, 2010) and *Llukalkan aliocranianus* (Gianechini *et al.*, 2021) (see supplementary information). Unlike previous authors who used cladistic analysis as a way to identify isolated theropod teeth (e.g., Hendrickx *et al.*, 2023; Candeiro *et al.*, 2024; Isasmendi *et al.*, 2024; Meso *et al.*, 2024; Chowchuvech *et al.*, 2025; Malafaia *et al.*, 2025), only operational taxonomic units (OTUs) for which more than 50% of crown-based characters (i.e., characters on the mesial and lateral dentition) could be scored were kept in the analysis. Likewise, we excluded all edentulous taxa as well as the dental characters related to the premaxillary, maxillary, and dentary dentition. We additionally divided the dataset into mesial and lateral dentitions so that only mesial and lateral-based characters were kept in the datamatrices. The isolated teeth from Madagascar and the Salta

Province were scored by morphotypes whereas those from Uruguay, Patagonia, and India were scored as separate specimens. Specimens and morphotypes were preliminary identified as belonging to the mesial or the lateral dentition and scored in the mesial or lateral-crown based datamatrices accordingly. As done by Hendrickx *et al.* (2020a, 2023), the cladistic analysis was performed on TNT 1.5 (Goloboff and Catalano, 2016) using a constrained topological tree of non-avian theropod relationships and the dental material (i.e., morphotypes or separated specimens) as floating taxa. However, unlike previous authors, we additionally performed the cladistic analyses using two constrained trees representing alternative hypotheses of theropod relationships. The first topology hypothesizes herrerasaurids as early branching saurischians, elaphrosaurines as early branching coelurosaurs, allosauroids among avetheropods, megaraptors within tyrannosauroids, and scansoriopterygids among oviraptorosaurs. It is based on the results of Moro *et al.* (2024) for non-theropod saurischians, Ezcurra *et al.* (2023) for non-averostran theropods, Hendrickx *et al.* (2024; first analysis) for Ceratosauria, Kellermann *et al.*'s (2025; split dataset) for non-maniraptoriform tetanurans, Zheng *et al.* (2024) for derived Tyrannosauroidea, Cuesta et al. (2022) for Ornithomimosauria, Kubo *et al.* (2023) for Alvarezsauria, Kobayashi *et al.* (2025) for Therizinosauria, Hao *et al.* (2025) for non-scansoriopterygid oviraptorosaurs, Brum *et al.* (2021) for non-eudromaeosaur Dromaeosauridae, Czepiński (2023) for Eudromaeosauria, and Kubota *et al.* (2024) for Troodontidae. Conversely, the second tree topology postulates a phylogenetic position of elaphrosaurines within noasaurids, megalosauroids among carnosaurians, megaraptorans within allosauroids, compsognathids as earliest branching coelurosaurs, therizinosaurs and alvarezsaurs as sister taxa, and *Ornitholestes* as the earliest branching oviraptorosaur. This topology is mainly based on the results of the cladistic analyses performed by Pol *et al.* (2024) for Ceratosauria, Pradelli *et al.* (2025) for Carnosauria, Zheng *et al.* (2024) for non-tyrannosaurid Tyrannosauroidea, Dalman *et al.*

(2024) for Tyrannosauridae, and Chapelle *et al.* (2021) for *Ornitholestes* (the rest of the neocoelurosaur classification being the same as in the first topology). In both topologies, the data matrix was phylogenetically bracketed between the early branching dinosaur *Daemonosaurus chauliodus* (Sues *et al.*, 2011) as recovered by Cau (2024), and the avialan theropod *Archaeopteryx lithographica* (Meyer, 1861), whose dentitions are well-known (e.g., Howgate, 1984; Rauhut *et al.*, 2018; Nesbitt and Sues, 2020). 3,000 trees were used as the maximum number of trees to be stored. We also used a combination of the tree-search algorithms Wagner trees, TBR branch swapping, sectorial searches, Ratchet (perturbation phase stopped after 20 substitutions), and Tree Fusing (5 rounds), until 100 hits of the same minimum tree length were achieved, and finally subjected the best trees to a final round of TBR branch swapping. The resulting command in TNT was "xmult = hits 100 rss fuse 5 ratchet 20" followed by "bb". The slack for sectors was increased to 50 using the command "sect:slack 50" in case the message "out of memory re-packing data for sectorial searches" appeared during the analysis. The Excel and Mesquite files with the datamatrices and the TNT files used in the cladistic analysis are available in the supplementary information.

Machine learning analysis

A machine learning analysis performed on a dataset of crown-based measurement variables compiled by Hendrickx *et al.* (2023) for non-avian theropods further helped identify the most complete shed tooth crowns, i.e., those for which sufficient measurements could be taken on the crown. We compiled a composite dataset that merged the morphometric matrices of Hendrickx *et al.* (2023) yielding 1334 theropod tooth specimens, which correspond to previously published, taxonomically resolved teeth and were treated as the training block, while the remaining rows served as an independent prediction block for which two response variables were considered: "Clade" and "Clade + Tooth-type", however, we focused our analyses for the "Clade" predictions. While we attempted to run "Taxon + Tooth type" as a

response variable too, there are not enough specimens per category to accurately predict and train the models. All analyses were run in R 4.4.0 within RStudio 2024.04.1.

Every morphometric column whose entries were numeric strings, were log-transformed (log x + 1) to reduce skew, and then centered and scaled with caret (Kuhn, 2008). Standardizing the data by first centering each measurement to zero mean and then scaling it to unit variance, ensures that no single high-variance morphometric variable can overwhelm the learning algorithm, while simultaneously improving numerical stability and convergence speed in gradient-boosted trees and neural networks. Crucially, we perform this transformation after the missForest imputation, so the scaling parameters are drawn from the full, balanced dataset rather than the reduced subset used by Barker *et al.* (2024), thereby preserving information that would otherwise be discarded. Together, these choices yield models that learn from a richer signal and generalize more reliably. Furthermore, we implemented missing values (ignored or list-wise deleted by Barker *et al.*, 2024) with missForest (Stekhoven and Bühlmann, 2012), preserving more than 98% of the original observations and improving class balance in minority groups. Feature selection was performed separately for each response using the Boruta wrapper algorithm (Boruta; Kursa and Rudnicki, 2010). The Boruta wrapper shields the pipeline from noise and subjective bias by exhaustively testing every variable against "shadow features" and keeping only those that show a statistically significant, data-driven contribution to clade separation. This automatic winnowing both lifts predictive accuracy and focuses the measurements that are relevant, insights that a fixed, hand-picked variable list could easily miss. The Boruta wrapper was performed for one hundred iterations with the random-forest Z-score importance metric retained, on average, 15 variables (mean ± SD = 14.6 ± 3.2) per fold (n.b., the Boruta wrapper considered 21 variables: Taxa (Genus), Source, Taxon + Tooth type, Clade, Clade + Tooth type, CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MSL, LAF+1, LIF+1, MDL, DDL, MDL*, and DDL* and only retained

277 the following eight to nine morphometric variables: CBL, CBW, CH, AL, CBR, CHR, MCL,
278 MCW, MDL, and sometimes DDL). Folds are the non-overlapping slices of the training data
279 used in cross-validation; for each fold, one slice is held back for validation while the
280 remainder drive the learning pipeline, so Boruta reruns on a different specimen set every time,
281 keeps only the variables that matter, and logs how many survive. Averaging these counts
282 across folds (~15 ± 3 variables) reveals the stability of feature choice and prevents over fitting
283 to a single partition; this is an adaptive safeguard absent from Barker *et al.* (2024), who relied
284 on one fixed six-variable list throughout. Model training followed a fully nested resampling
285 design: an outer stratified k-fold cross-validation (k = 2–5, depending on sample size)
286 provided an unbiased generalization estimate (Varma and Simon, 2006), while an inner 2–5-
287 fold grid search tuned five candidate algorithms: random forest (Liaw and Wiener, 2002),
288 C5.0 decision tree (Quinlan, 1993), mixture discriminant analysis (Hastie *et al.*, 1994),
289 gradient-boosted trees (i.e., XGBoost; Chen and Guestrin, 2016), and a weight-decayed
290 single-layer neural network (Bergmeir and Benítez, 2012). The algorithm with the highest
291 mean outer-fold macro-accuracy was refit to the full training block under a ten-fold cross-
292 validation with class probabilities enabled. For each unseen specimen the final model
293 produced posterior probabilities that were sorted to yield the three most likely classes, their
294 probabilities, the name given to the selected algorithm, and single-algorithm predictions from
295 all remaining models; these outputs were written to a *.csv file, while fitted models and fold-
296 wise performance metrics were archived separately. Probability-ranked predictions provide
297 explicit uncertainty estimates lacking in Barker *et al.*'s pipeline and facilitate downstream
298 ensemble. Relative to Barker *et al.* (2024) and previous studies using machine learning
299 algorithms, the present workflow retains incomplete records via imputation, broadens the
300 algorithmic search (adding XGBoost and MLP), replaces a single 80/20 split with nested
301 cross-validation, and selects features data-driven rather than a fixed set of variables simply

because the researcher decrees it (without letting the data demonstrate their relevance), collectively delivering a gain in macro-accuracy during outer folds and a far richer characterization of predictive uncertainty. All the files used in the machine learning and the Excel files with the results of this analysis are available in the supplementary information.

Dental evolution analysis

The evolution of the dentition in abelisaurid ceratosaurs was examined using our updated version of Hendrickx *et al.*'s (2024) dataset that we restricted to ceratosaur taxa. This data matrix includes a total of 22 ceratosaurs and 13 abelisaurid taxa, and the non-ceratosaur averostran *Dilophosaurus wetherilli* (Welles, 1970; Marsh and Rowe, 2020) was used to root the tree. Dental evolution in Abelisauridae was explored by mapping apomorphic dental features on three topological trees representing alternative phylogenetic hypotheses of ceratosaur evolution. The first topology is based on the results of the cladistic analysis performed by Hendrickx *et al.* (2024) using an update version of Agnolín *et al.*'s (2022) dataset, which places *Berberosaurus* closer to abelisauroids than ceratosaurids and the toothless ceratosaurs *Limusaurus* and *Berthasaura* at the base of the ceratosaur and abelisauroid clades, respectively. The placement of the Moroccan abelisaurid *Chenanisaurus* in this topology follows that of Longrich *et al.* (2017). The second topology follows the classification obtained by Pol *et al.* (2024), which recovers *Berberosaurus* as the earliest branching ceratosaur and *Limusaurus* as a noasaurid abelisauroid. The last topology is based on the reduced strict consensus tree recovered by Cau and Paterna (2025), which classifies the edentulous *Berthasaura* and *Limusaurus* among berthasaurids (*sensu* Hendrickx *et al.*, 2024), *Berberosaurus* as an early branching abelisauroid, and *Ceratosaurus* as a particularly basal ceratosaur. Character distributions for dental features were visualized on each tree using TNT 1.5 (Goloboff and Catalano, 2016) and WinClada 1.00.08 (Nixon, 2002) based on the Nexus

file created with Mesquite 3.2. All the Mesquite files used in the dental evolution analysis and the pdf files with the results of this analysis are available in the supplementary information.

Morphological disparity and phylogenetic generalized least square analyses

To explore morphological disparity throughout the evolutionary history of abelisaurids, we conducted separate analyses based on two discrete character–dental matrices: one comprising data from lateral teeth, and the other from mesial teeth. Both matrices were processed using the R package Claddis v.0.6.3 (Lloyd, 2016), which allowed us to compute distance matrices employing the maximum observable rescaled distance (MORD). This method is particularly suitable for datasets with a moderate to high proportion of missing data, thereby minimizing the biases associated with generalized Euclidean distance (GED) methods (Ezcurra and Butler, 2018; Flannery Sutherland *et al.*, 2019; Lehmann *et al.*, 2019). Principal coordinates analyses (PCo) were then performed on each matrix, incorporating the Lingoes correction to address negative eigenvalues. For the lateral tooth matrix, the first 14 PCo axes were retained, accounting for 100% of the total variance, whereas in the case of the mesial tooth matrix, the first 9 axes were selected, explaining 100% of the total variance. These axes were used to reconstruct and visualize the morphospace occupied by the sampled taxa. Morphological disparity was subsequently quantified using the weighted mean pairwise dissimilarity (WMPD) metric, calculated before ordination. Disparity values were compared within two temporal bins: the “Early Cretaceous” and the “Late Cretaceous”. While an initial three-bin temporal structure was considered, this was ultimately simplified to avoid potential biases resulting from underpopulated intervals, which could compromise statistical robustness.

To examine the potential effect of body length on variation in dental morphology, we carried out two phylogenetic generalized least squares (pGLS) regressions. These analyses were based on a reduced consensus phylogeny derived from the topology proposed by Hendrickx *et al.* (2024). To obtain a fully bifurcating tree suitable for comparative analysis, polytomies

were randomly resolved using the multi2di() function in R. The resulting topology was then time-calibrated using the minimum branch length ("mbl") approach (Laurin, 2004; Brusatte *et al.*, 2008), implemented via the timePaleoPhy() function from the paleotree package.

First, we performed phylogenetic generalized least squares (pGLS) regressions between the log-transformed estimates of body length (see Pereyra *et al.*, 2025) and the first principal coordinate axis (PCo1) for each of the two matrices independently. For the lateral tooth dataset, PCo1 accounted for 52.72% of the total morphological variance, whereas for the mesial tooth dataset, PCo1 explained 57.10%. These axes, capturing the primary axis of variation in each dataset, were regressed individually against log-transformed body length to evaluate potential correlations between overall size and morphospace occupation. All pGLS regressions were carried out using the gls() function from the nlme package v.3.1 in R (Pinheiro-Silva *et al.*, 2020), with phylogenetic correlation structures modelled under a Brownian motion framework. Statistical significance was assessed at the conventional threshold of $P < 0.05$. The phylogenetic signal in morphospace was visualized using the phylomorphospace() function from the phytools package (Revell, 2012). All the files used in this analysis are available in the supplementary data.

RESULTS

Cladistic analysis

The cladistic analysis performed on the dentition-based data matrix restricted to mesial-related dental characters using the first constrained tree topology yielded eight most parsimonious trees (MPTs) whose strict consensus tree recovered all floating dental OTUs (Mada I and II, Salta I and II) among abelisaurid ceratosaurs (Fig. 3.1). The two dental morphotypes from the Salta Province were classified in the same clade whereas the Malagasy Morphotype I and II were classified as the sister taxon of *Chenanisaurus* and Abelisaurinae, respectively (Fig. 3.1). Performing the same analysis using the second tree topology yielded

24 MPTs whose strict consensus tree classified Mada II in Abelisauridae and the rest of the floating dental morphotypes in a polytomy at the base of Abelisauridae (Fig. 3.2). Conducting the cladistic analysis on the data matrix of lateral-based dental characters using the first tree topology resulted in 2519 MPTs where all Gondwanan specimens were recovered in a large polytomy at the base of Averostra in the strict consensus tree and within Abelisauroidea in the 95% majority rule consensus tree (Fig. 3.3). Excluding specimens PVL 3672 and MACN 18.172 from the analysis, however, classified the rest of the dental material in a large polytomy within Abelisauridae (Fig. 3.4). Using the second tree topology as a backbone tree gave relatively similar results where the strict consensus tree of 1712 MPTs classified the dental material in a fully unresolved Abelisauroidea and Abelisauridae when PVL 3672 and MACN 18.172 are excluded from the analysis.

Machine learning analysis

The accuracy of classifying the most complete theropod teeth here studied using purely morphometric methods is largely independent of both the composition of the training dataset and the specific machine-learning algorithm chosen. Instead, classification success depends primarily on how closely each tooth matches the stereotypical Abelisauridae tooth morphology. To assess this, we used three progressively "cleaner" training sets that trace out a stepwise improvement in how confidently the teeth are recognized as Abelisauridae, i.e., (i) the full published dataset, (ii) that same dataset pared down to large-bodied theropods, and (iii) the author's own (personal) dataset with an optional large-only filter. For the full published dataset (small + large teeth) with the entire reference sample in play, shape variation linked to body size overwhelms the abelisaurid signal (Fig. 4). Only MSNM V 5779, NHMUK R 4190, and PVL 4062-1 emerge with ≥ 0.60 probability of being abelisaurid, and the overall mean probability is only about 0.40. The remaining ten teeth disperse their

likelihoods among tyrannosauroids, neovenatorids or dromaeosaurids, showing how "small-taxon noise" can mask true affinity. Removing small-bodied taxa helps but does not produce a blanket fix. Exactly six specimens (MSNM V 5778, MSNM V 5779, MSNM V 5809, NHMUK R 4190, PVL 4062-1, and PVL 4062-2) now take Abelisauridae as their single highest-probability clade, usually in the 0.50–0.70 range (Fig. 4). Seven other teeth remain equivocal: MSNM V 5781, MSNM V 5814, MSNM V 5818, MSNM V 5789, MGT-1161, and MACN 18172 still share the lead with one or more other clades, while PVL 4173 sits far back at 0.136 for Abelisauridae. The grand mean lifts to a little above 0.50, showing that size-filtering removes much of the noise but cannot rescue every specimen on morphometrics alone. Switching to the author's personal measurements yields the most significant gain of predicted probability. With no size filter, four teeth (MSNM V 5779, NHMUK R 4190, PVL 4062-1, PVL 4062-2) clear the 0.75 mark for Abelisauridae, while MSNM V 5778 (≈ 0.43) and PVL 4173 (≈ 0.2) do not exceed the 0.50 mark (Fig. 4). Similar results are obtained when restricting the dataset to large-bodied specimens, with 8 out of 13 specimens correctly identified with Abelisauridae appearing among the top three predicted clades. Irrespective of the dataset the models usually recover Abelisauridae as among the top hits (7 out of 13 teeth); refining the dataset mainly boosts the associated probability. The trade-off is that the same refinement can also amplify the probability assigned to the wrong answer, which means our apparent confidence in those rare misidentifications (i.e., the Type II error rate) rises as well. In further studies, it is crucial to include other sources of information that complement morphometric data. In what concerns, Random-Forest, C5.0, mixture discriminant analysis and XGBoost turn out to be largely interchangeable; for any given training subset they return nearly identical average probabilities. The decisive factor is not architecture nor whether the comparative sample is size-matched and ideally measured in a consistent fashion, instead, how closely the tooth in question matches the typical clade gestalt. All lines of quantitative

evidence still converge on Abelisauridae as the best referral for these teeth (Fig. 4), but the correctness of that referral hinges to a certain degree on training-set curation (42% of correct identifications if the whole dataset is used versus 46% of correct identifications if the personal dataset with large teeth is used). Leaving small theropods in the mix little influences the abelisaurid signature for most of the sample; restricting the reference set to large taxa lifts five specimens into a clear abelisaurid slot (i.e., >0.5). PVL 4173 and even to a greater extent MSNM V5818, MSNM V5789, MGT-1161, and MACN 18172 (Fig. 4), remain morphometrically ambiguous even under the best scenario, underscoring why qualitative dental characters and a tightly controlled comparative framework are essential companions to morphometric classification when identifying isolated theropod teeth.

Dental evolution analysis

Mapping dental characters on three topological trees representing alternative hypothesis of the ceratosaur classification reveals that the clade Abelisauridae is diagnosed by a minimum of two non-homoplastic dental characters (Fig. 5): the presence of mesialmost dentary teeth significantly smaller than mid- and distal dentary teeth (char. 30:2); and the tallest crowns in the middle portion of the maxilla (char. 42:1). Four and five apomorphic dental features constrain the abelisaurid clade when it forms the sister clade of Noasauridae (which excludes Elaphrosaurinae) among Abelisauroidea (Hendrickx's topology; Fig. 5.1) and the sister taxon of *Masiakasaurus* (Cau's topology; Fig. 5.3), respectively. Abelisauridae is, however, diagnosed by two to three dental synapomorphies when sister to a noasaurid clade gathering the edentulous *Berthasaura* and/or Elaphrosaurinae (Pol's topology; Fig. 5.2). In this configuration, Abelisauroidea is constrained by a particularly large number of dental apomorphies (11 to 12; Fig. 5.2) whereas zero to one dentition-based character diagnose Abelisauroidea when the toothless taxa are classified outside Noasauridae (Fig. 5.1, 5.3).

Within Abelisauridae, few clades are constrained by unambiguous dental characters whose position changes with the tree topology. Nonetheless, in Cau and Hendrickx's topological trees, abelisaurids more derived than *Spectrovenator* are diagnosed by apically inclined distal denticles in lateral teeth (char. 107:1) whereas those more derived than *Rugops* are diagnosed by the presence of mesialmost and mid-maxillary teeth subequal is size (char. 21:0; Fig. 5.1, C). Likewise, a single apomorphic dental character (either char. 105 or 116) diagnoses the most inclusive clade gathering *Abelisaurus* in all trees. *Chenanisaurus* is the abelisaurid taxon with the highest number of dental apomorphies (10; n.b., this taxon is only included in the first topology), followed by *Spectrovenator* (four to eight autapomorphies) and/or *Arcovenator* (six) (Fig. 5).

Morphological variation and phylogenetic generalized least squares regressions

Results of the WMPD indicate that the mesial dentition of ceratosaurs already exhibited a high degree of morphological differentiation during the Early Cretaceous, with a mean of 0.47 and a confidence interval of 0.36–0.55 (Fig. 6.1). However, a decline is evident in the Late Cretaceous, where the mean drops to 0.39 and the interval narrows to 0.31–0.48, suggesting a reduction in morphological variability in ceratosaurs and a trend towards greater homogeneity in mesial tooth morphology (Fig. 6.1). As for the lateral dentition, WMPD values reveal greater disparity in the Early Cretaceous, with a mean value of 0.4 and a moderately wide confidence interval (0.26–0.66; Fig. 6.2). This suggests that these small to medium-sized predators had already developed from the early stages of their evolutionary history lateral dental traits that enabled them to exploit a broader range of ecological niches. Such disparity likely reflects an adaptive radiation occurring during this interval. In contrast, the lower mean value observed in the Late Cretaceous (0.28) and the narrower confidence interval (0.25–0.30; Fig. 6.2) indicate a more homogeneous lateral dental morphology, possibly indicating

morphological specialization or more uniform selective pressures acting upon this group during that time. Morphological disparity analyses based on mesial dentition were visualized using PCo1 (57.10% of the explained variance) against PCo2 (32.61%), as well as PCo1 versus PCo3 (9.23%). In the PCo1 vs. PCo2 plot, the overall distribution pattern broadly resembles that of the lateral dentition, albeit with some noteworthy differences. For instance, brachyrostrans and majungasaurines cluster closely together, with the notable exception of *Skorpiovenator*, which is separated from this group, suggesting a distinctive mesial dental morphology for this taxon (Fig. 7.1). Morphological disparity analyses based on lateral dentition were visualized using PCo1 (accounting for 52.72% of the explained variance) against PCo2 (26.99%), as well as PCo1 versus PCo3 (19.92%). In the PCo1 vs. PCo2 plot, which retains the highest proportion of variance, Early Cretaceous forms are restricted to the third and fourth quadrants, exhibiting a limited distribution within the morphospace. In contrast, Late Cretaceous ceratosaur taxa occupy all four quadrants, reflecting a substantially greater degree of morphological disparity (Fig. 7.2). Noasaurid taxa cluster in the lower regions of the third and fourth quadrants, markedly distant from the rest of Abelisauroidea. Among non-brachyrostran abelisaurids, *Spectrovenator*, *Rugops*, and *Kryptops* are closely positioned within the fourth quadrant. Conversely, brachyrostrans and majungasaurines show partial overlap but remain relatively distinct, with *Chenanisaurus* and *Arcovenator* standing out by plotting far from Gondwanan abelisaurids, near the upper boundary of the morphospace in the second quadrant in the former and the bottom left quadrant in the latter (Fig. 7.2). Phylogenetically informed linear regressions (pGLS) revealed no significant relationship between body length and the main axis of dental morphological variation (PCo1) for either mesial (Fig. 8.1) or lateral dentition (Fig. 8.2). For mesial teeth, the model yielded a non-significant negative correlation (PCo1 coefficient = –0.1713; p = 0.7435; AIC = 12.02; Fig. 8.1), while the model for lateral teeth similarly showed no significant association(PCo1

coefficient = –0.2044; p = 0.5977; AIC = 6.37; Fig. 8.2). These results indicate that morphological variation in abelisaurid dentition is not primarily determined by body size.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

AVEROSTRA Paul, 2002

cf. ABELISAURIDAE Bonaparte and Novas, 1985

Gen. and sp. indet.

Material. MSNM V5814, V5818; MGT-1161; MACN 18.172.

CERATOSAURIA Marsh, 1884

ABELISAUROIDEA Bonaparte, 1991

ABELISAURIDAE Bonaparte and Novas, 1985

Gen. and sp. indet.

Material. MSNM V5778, V5779, V5781, V5789, V5799, V5809; FC-DPV 3531; PVL 3672, 4062-1 to 4062-4, 4173, 4174, 4175; NHMUK R4190.

Middle Jurassic of Madagascar

Material. MSNM V5778, V5779, V5781, V5789, V5799, V5809, V5814, V5818, eight isolated shed teeth (Fig. 9; Table 1).

Locality and Horizon. Near Ambondromamy, Borizini (= Port-Bergé), and Tsinjorano (see Maganuco *et al.*, 2005 for more precise location of the specimens), Mahajanga Province, northeastern Madagascar; Sakaraha Formation (=Isalo IIIb "faciès mixte – dinosauriens"), Bathonian, Middle Jurassic (Maganuco *et al.*, 2005) (Fig. 1.1-1.2).

Importance. Some of the isolated theropod teeth classified into Morphotype 1 to 4 by Maganuco *et al.* (2005) represent the oldest abelisaurid record from Africa. They might additionally be the oldest abelisaurid remains worldwide if the putative abelisaurid

Eoabelisaurus mefi from the Middle-Late Toarcian (Lower Jurassic) Cañadón Asfalto Formation of Southern Patagonia (Pol and Rauhut, 2012) is a non-abelisaurid ceratosaur, as recovered in the cladistic analyses of various authors using several independent datamatrices (e.g., Dal Sasso *et al.*, 2018; Delcourt, 2018; Salem *et al.*, 2022; Hendrickx *et al.*, 2024). Maganuco *et al.* (2005) assigned all theropod specimens from Madagascar as "Theropoda gen. and sp. indet." and tentatively referred the isolated theropod teeth from Morphotypes 1 to 4 (29 teeth) to Abelisauridae, a classification supported by Soto *et al.* (2023).

Description. Photos of the dental material belonging to morphotypes 1 to 4 reveal that many shed teeth have particularly distinct morphologies, suggesting that they may belong to distantly related ziphodont theropod clades. This is especially the case of the three mesial teeth grouped into Morphotype 1, whose morphologies suggest that they belong to distinct groups. Most of these isolated teeth (e.g., MSNM V5780, V5782, V5783, V5784, V5790, V5794, V5806, V5817, V5821, V5957, V5962) are also too incomplete to evaluate their taxonomic affinities with confidence. Eight of them are, however, particularly complete, well-preserved, and exhibit abelisaurid traits so that their phylogenetic affinity was assessed in this study. These shed tooth crowns are grouped into five morphotypes related to their position along the jaw and their ontogenetic stage (Table 1). All, however, share a ziphodont morphology with denticulated mesial and distal carinae, centrally positioned distal carina reaching the cervix, mesial and distal denticles decreasing in size basally, and an irregular enamel surface texture.

The first morphotype (Mada Morpho I), represented by MSNM V5778 (Fig. 9.1-9.8), includes a shed tooth identified by Maganuco *et al.* (2005) as a mesial crown and grouped into their Morphotype 1. This shed tooth crown is characterized by having convex mesial and distal profiles, a weak constriction at the base crown, and mesial and distal carinae centrally positioned on their respective margins and extending to the cervix. It also exhibits two

concave surfaces adjacent to the carinae on the lingual side, resulting in a salinon-cross sectional outline of the base crown in basal view where the labial profile is significantly more convex than the lingual one (Fig. 9.7). The crown is poorly compressed (CBR of 0.7), particularly elongated (CHR of 2.4), and has a low denticle crown ratio (DCR=1.53; Table 1). Both mesial and distal carinae share 13 denticles per 5 mm (here abbreviated de/5 mm) at mid-crown (DSDI=1) and a higher density (17 de/5 mm) in the apical part of the crown. The size of the denticles also decreases basally so that the basalmost denticles are particularly small. Both mesial and distal denticles are subquadrangular and have symmetrically convex external margins and well-developed interdenticular sulci curving basally on the lingual side of the crown (Fig. 9.5-9.6).

MSNM V5809, which represents the second morphotype (Mada Morpho II; Appendix 1, Fig. A1.1-1.3), was identified by Maganuco *et al.* (2005, p. 182) as "undoubtedly occupying a lateral position in the jaw" and classified among Morphotype 3. The tooth shares with the previous morphotype a salinon-cross section at the crown base resulting from the two concavities present next to the carinae on the lingual side of the crown (the cross section should, however, be described as parlinon for its stronger labiolingual compression; Hendrickx *et al.*, 2015b). It is also relatively poorly compressed (CBR of 0.57), has both mesial and distal carinae extending to the cervix, and similar mesial and distal denticle density (13 de/5 mm) at mid-crown. However, it differs from Morphotype I in having a straight distal profile, distal denticles that project apically from the distal profile, a much higher DCR (2.22), and shorter interdenticular sulci restricted to the distal denticles. MSNM V5779 representing the third morphotype (Mada Morpho III; Fig. 9.9-9.15) was also classified within Morphotype 3 by Maganuco *et al.* (2005). This tooth shares a very similar morphology than MSNM V5809: it is weakly elongated (CHR of 1.88; Table 1), has both mesial and distal carinae extending to the cervix, similar mesial and distal denticle density (Table 1), lingual

concavities adjacent to the carinae, and a salinon-cross sectional outline at the base crown (Fig. 9.15). It is nonetheless distinct from Morphotype II in having a much stronger labiolingual compression (CBR of 0.41) and larger mesial and distal denticles (MC and DC with 10 de/mm). Morphotypes I, II and III all have relatively tall crowns (CH>2 cm).

The fourth morphotype (Mada Morpho IV), which includes MSNM V5781, V5789 and V5799 (Fig. 9.16-9.22), classified among morphotypes 2 and 4 by Maganuco *et al.* (2005), is similar to Morphotype III in being significantly compressed (CBR between 0.41 to 0.51) and having a high DCR (from 2 to 2.74), as well as mesial and distal carinae extending to the root. The distal denticles are also apically inclined, hooked apically, and exhibit short interdenticular sulci (Fig. 9.20). Morphotype IV, however, differs from the third one in its shorter crown height (CH>1.2 cm), slightly to significantly smaller mesial and distal denticles (14 to 25 de/5 mm), and, more importantly, a strong discrepancy between mesial and distal denticles, with the distal ones being larger than the mesial denticles (DSDI>1.2; Fig. 9.20-9.21). The crown cross-section outline is also more lanceolate to lenticular in outline, with symmetrically convex lingual and labial profiles in basal views, and a few poorly defined transverse undulations are visible basally on the crown. If mesial and distal carinae are centrally positioned on the crown in most of these teeth, we note that MSNM V5781 has a strongly labially deflected distal carina.

MSNM V5814 and V5818, classified in Morphotype 2 by Maganuco *et al.* (2005), represent the last morphotype (Mada Morpho V; Appendix 1, Fig. A1.4-1.10). Unlike all the previous teeth grouped into morphotypes I to IV, the mesial carina does not reach the cervix and extends a certain distance above the root (Appendix 1, Fig. A1.4, 1.8). The crowns, however, share all the dental features present in Morphotype IV such as a short crown height (CH<1.7 cm; Table 1), strong discrepancy between mesial and distal denticles (DSDI>1.2), relatively high denticle density (DC>16 de/5mm), apically hooked distal denticles, well-

developed interdenticular sulci, and a few poorly defined transverse undulations. MSNM V5814, however, shows a combination of irregular and braided enamel surface texture not seen in all previous teeth (Appendix 1, Fig. A1.6, 1.10).

Identification. The combination of dental features seen in morphotypes I to III strongly points towards an abelisaurid affinity whereas the latter is less straightforward for morphotypes IV and V. Results of the cladistic analysis, however, classifies all morphotypes as abelisaurid teeth (Fig. 3). Conversely, the machine learning analysis only identifies morphotypes I-III as abelisaurid teeth, the two other morphotypes (IV and V) being classified as Dromaeosauridae, non-megalosaurian Megalosauroidea, Neovenatoridae, and non-tyrannosaurid Tyrannosauroidea (Fig. 4).

We agree with Maganuco *et al.* (2005) that Morphotype I represents the mesialmost type (pm1 to 2) based on the salinon-shape outline of the crown with two lingual concavities adjacent to the carinae, low crown compression (CBR of 0.7; Table 1), a weak constriction at the cervix, convex mesial and distal profiles, well-developed interdenticular sulci, and a labial side of the crown significantly more convex than the lingual side in basal view (Smith, 2007; Hendrickx *et al.*, 2020a). Such a combination of dental features is, to our knowledge, restricted to mesialmost abelisaurid teeth such as those of *Majungasaurus*, also unearthed in the Mahajanga basin (Fanti and Therrien, 2007; Smith, 2007), as well as *Spectrovenator* (MZSP-PV 833). A salinon-shape is also present in mesialmost teeth of early branching allosauroids like *Allosaurus* and *Sinraptor*; however, none exhibits the constriction at the base crown present in some abelisaurids. In addition, the CBR of mesialmost teeth in early branching allosauroids is closer to or higher than 1 while DCR is lower than 2 (C.H. pers. obs.). Conversely, mesialmost abelisaurid teeth with deep lingual concavities have a CBR ranging from 0.7 to 0.9 (Hendrickx *et al.*, 2019, 2020b) and some taxa such as *Majungasaurus* have DCR higher than 2.

With a parlinon-shape cross-section with two lingual concavities adjacent to the carinae, a relatively high CBR (0.57), mesial and distal carinae extending to the root, apically hooked distal denticles, and an irregular enamel surface texture, Morphotype II most certainly represents transitional abelisaurid teeth.

Finally, with a CBR close to or lower than 0.5, a lenticular cross-section outline with or without shallow concavities adjacent to the carinae, symmetrically convex labial and lingual margins, mesial and distal carinae centrally positioned on their respective surface and extending to the root, apically hooked distal denticles with interdenticular sulci, and an irregular enamel surface texture, Morphotype III to IV most probably represent lateral abelisaurid teeth (Hendrickx and Mateus, 2014; Hendrickx *et al.*, 2020a). With mesial and distal denticles of similar size at mid-crown and a crown height higher than 2 cm, teeth grouped into Morphotype III most likely pertain to adult abelisaurids. Conversely, a strong discrepancy between mesial and distal denticles (DSDI > 1.2) and shorter crown height (CH < 2 cm) suggest that teeth of Morphotype IV and V probably belong to juvenile abelisaurid individuals. Indeed, teeth belonging to juvenile abelisaurids such as *Majungasaurus* (Fanti and Therrien, 2007) and *Spectrovenator* (see Discussion) and other ziphodont theropods (e.g., tyrannosaurids; (Carr and Williamson, 2004; Hendrickx *et al.*, 2019) have been shown to have a DSDI > 1.2 whereas those of adults have mesial and distal denticles of similar size (n.b., Ribeiro *et al.*, 2024, however, described an isolated abelisaurid tooth possibly belonging to a juvenile with a reversed condition).

With a mesial carina restricted to some part of the crown, teeth belonging to Morphotype V are the most distinct from traditional abelisaurid teeth. Nevertheless, they still exhibit a combination of dental features typical of abelisaurids such as apically hooked distal denticles, mesial and distal carinae centrally positioned on their respective surface, a subsymmetrical convex surface of the labial and lingual surface, and an irregular (but also

braided) enamel surface texture. Results of the cladistic analysis suggests that they represent abelisaurid lateral teeth and they are, consequently, tentatively referred to Abelisauridae. A mesial carina not extending along the whole crown height is here interpreted as a possible plesiomorphic dental feature seen in more early branching abelisauroids and retained in early branching abelisaurids from the Middle Jurassic (n.b., it should be noted that the European abelisaurid *Arcovenator* also has a mesial carina not reaching the root; see discussion below; Hendrickx *et al.*, 2020a). Our identification of morphotypes IV and V as abelisaurid teeth should, however, be seen as tentative as we do not reject the possibility that they belong to other ziphodont theropod groups such as non-megalosaurian megalosauroid or a dromaeosaurid, as suggested by the machine learning analysis (Fig. 4).

Late Jurassic of Uruguay

Material. FC-DPV 3531 and MGT-1161 (Fig. 10), a complete and partially complete lateral shed tooth crowns, respectively.

Locality and Horizon. Bidegain Quarry, Tacuarembó city, Tacuarembó Province, Northeastern Uruguay; Tacuarembó Formation, Kimmeridgian–Tithonian, Upper Jurassic (Soto *et al.*, 2020a, 2020b) (Fig. 1.3-1.4).

Importance. Although scarce, the abelisaurid dental material from Uruguay represent one of the oldest abelisaurid record from western Gondwana, along with the possible abelisaurid postcranial remains from the Oxfordian–Kimmeridgian Cañadón Calcáreo Formation of Chubut Province, Argentina (Rauhut and Pol, 2021) and the Kimmeridgian–Tithonian Tendaguru Formation of Tanzania (Rauhut, 2011). The abelisaurid teeth from Uruguay additionally expand the theropod diversity of the Tacuarembó Formation, already represented by megalosaurid and ceratosaurid theropods (Soto *et al.*, 2020a, 2020b).

Description. FC-DPV 3531, a lateral ziphodont crown missing the apex, was comprehensively described by Soto *et al.* (2023) so that the description will not be repeated here. The second specimen, MGT-1611, is an almost complete ziphodont lateral tooth only lacking the apex due to pre-mortem apical abrasion (Fig. 10). The crown is medium-sized (CH around 2 to 2.5 cm), moderately compressed (CBR and MCR of ~0.49), and most likely moderately elongated (CHR around 2 to 2.5) when complete. It exhibits a centrally positioned mesial carina, which, unlike FC-DPV 3531, does not reach the base of the crown and slightly twist towards the lingual side of the crown basally (Fig. 10.3), possibly due to its more mesial position within the lateral dentition. The distal carina is centrally positioned, straight (Fig. 10.4) and extends to the root. In basal view, the cross-section outline of the crown-base is lanceolate, with symmetrically convex lingual and labial margins (Fig. 10.5). The latter also shows a flat to almost concave surface at mid-crown width (Fig. 10.5). There are 20 distal de/5 mm at the base of the crown and 15 at mid-crown height. Distal denticles are mesiodistally rectangular, apically hooked (i.e., the narrow shaft distally expands into an apically pointing tip), and with moderate spacing between them (Fig. 10.7). Distobasal denticles do not have the narrowing of the shaft and appear to be more closely spaced than the distocentral denticles. This, coupled with the reduction of absolute size, explains the fact that the distobasal denticle density is higher than the distocentral one. Most mesial denticles are not discernible due to wear (Fig. 10.3) and only the bases of the basalmost denticles can be seen. There were approximately 20 to 25 de/5mm at the base of the mesial carina. Interdenticular sulci are present between distal denticles but differ from MGT-3531 in being short and less inclined towards the base of the crown (Fig. 10.2). Tooth enamel is irregular (i.e., non-oriented) and shows numerous, closely packed transverse undulations visible under oblique light (Fig. 10.8). No marginal undulations, flutes, basal striations, longitudinal ridges or grooves are, however, visible on the crown.

Identification. A cladistic analysis performed by Soto *et al.* (2023) retrieved FC-DPV 3531 nested among abelisaurid theropods, supporting this identification. A combination of features such as the apically hooked denticles, well-developed interdenticular sulci, irregular enamel surface texture, and lanceolate cross-sectional shape indeed warrants its referral to Abelisauridae (Hendrickx *et al.*, 2020a). Specimen MGT-1161 similarly shows a combination of dental traits typical of abelisaurid lateral teeth such as an irregular enamel surface texture, hooked distal denticles with interdenticular sulci, poorly defined transverse undulation, a centrally positioned distal carina, and a lenticular cross-section outline with symmetrically convex labial and lingual (Hendrickx *et al.*, 2020a). One dental feature uncommon in abelisaurid lateral teeth but observed in some of them (e.g., *Arcovenator*) is the presence of a mesial carina slightly twisting lingually and restricted to the apical half of the crown (Fig. 10).

Results of the cladistic analysis recovered this specimen as an abelisaurid tooth (Fig. 3.3-3.4) whereas machine learning identifies it as a non-megalosaurian megalosauroid (e.g., piatnitzkysaurid) or a neovenatorid (which here includes megaraptors; Fig. 4). We note that MGT-1161 shares many dental features with *Piatnitzkysaurus* (PVL 4073) such as hooked distal denticles, interdenticular sulci between distal denticles, a mesial carina restricted to the apical portion of the crown, weakly developed transverse undulations, and an irregular enamel surface texture (C.H. pers. obs.). The main difference between MGT-1161 and *Piatnitzkysaurus* is the strong labial displacement of the distal carina in most lateral crowns of the latter; however, this is not the case in all of them (C.H. pers. obs.). One way to separate abelisaurid from piatnitzkysaurid lateral teeth would be to compare the size of mesial and distal denticles. DSDI is indeed typically close to one in Abelisauridae and close to or higher than 1.2 in Piatnitzkysauridae (Hendrickx *et al.*, 2019, 2020a). Unfortunately, the mesial denticles are worn out in MGT-1161, preventing us from knowing if an important size difference between mesial and distal denticles occurred in this specimen. Importantly, the

lateral tooth FC-DPV 3531 described by Soto *et al.* (2023) has a mesial denticulated carina extending to the cervix and similar mesial and distal denticle density at mid-crown, comparing better to abelisaurid teeth than piatnitzkysaurid ones.

Because an abelisaurid tooth (FC-DPV 3531) was already reported in the Tacuarembó Formation by Soto *et al.* (2023), we follow the identification given by the cladistic analysis for MGT-1161 over that from the machine learning analysis, which is restricted to crown-based measurements. MGT-1161 is, however, tentatively referred to Abelisauridae as we do not reject the possibility that this specimen belongs to a non-abelisaurid such as a piatnitzkysaurid. This latter clade was also present during the Late Jurassic although its geographic distribution is currently restricted to North America (Madsen, 1976; Carrano *et al.*, 2012).

Late Cretaceous of Chubut, Argentina

Material. MACN 18.172, a fairly complete but badly preserved lateral shed tooth crown (Fig. 11).

Locality and Horizon. 43°30’S, 68°20’W, Department Paso de Indios, Chubut Province, Argentina; Bayo Overo Member, Cerro Barcino Formation, Chubut Group, Cenomanian, Upper Cretaceous (del Corro, 1966; Carrano *et al.*, 2012; Ezcurra and Novas, 2016) (Fig. 2.3).

Importance. One of the five theropod teeth reported by del Corro (1966) represents, to our knowledge, the earliest published record of an abelisaurid theropod from Argentina. It may also represents the second earliest published record of an Abelisauridae from the New World six years after the description of two isolated carnosaur teeth from the Cretaceous Alter do Chão Formation of Amazonas Basin by Brazilian paleontologist Llewellyn Ivor Price (1960), one of which was referred to Abelisauridae by Ribeiro *et al.* (2024a). The isolated teeth reported by del Corro (1966) were found associated with the holotypic skeleton of the

somphospondylian sauropod *Chubutisaurus insignis* in February 1966 (del Corro, 1966, 1975) and referred by del Corro (1966) to the new *Megalosaurus* species '*Megalosaurus inexpectatus*', an hypodigm considered by Ezcurra and Novas (2016) as a *nomen vanum*. Four of these teeth, among which two appear to be lost (Ezcurra and Novas, 2016), were in a good state and used by del Corro (1966) as the type material of the new *Megalosaurus* species. The isolated teeth were compared to those of carcharodontosaurids and abelisaurids by Carrano *et al.* (2012) and Ezcurra and Novas (2016), respectively, but never received a proper description nor identification.

Description. One of the several ziphodont theropod teeth under the collection number MACN 18.172 shows typical abelisaurid traits (Fig. 11). The tooth is fairly complete but poorly preserved, with the denticles and most of the enamel surface missing. The preserved crown is ziphodont in shape, moderately tall (CH of 2.7 cm), relatively compressed (CBR of 0.47), and elongated (CHR of 2.23; Fig. 11.1). The mid-crown (CBR 0.45) is only slightly more compressed than the base crown. In lateral view, the mesial profile is weakly convex whereas the distal profile is straight so that the crown apex lies at the same level as the distal margin of the crown. The crown bears straight and centrally positioned mesial and distal carinae extending all along the crown height (Fig. 11.3-11.4). In basal view, the cross-sectional outline of the base crown is symmetrically lenticular with both labial and lingual profiles having the same convexity. A flat surface is, however, visible adjacent to the distal carina on the labial side of the crown (Fig. 11.5). If both carinae were denticulated all along their length, none of the denticles are completely preserved to provide information on the size, elongation, denticle density, and shape of the external margin (Fig. 11.7-11.8). The crown is also too badly preserved to rule out the presence of crown ornamentations such as marginal and transverse undulations. It at least does not bear flutes, longitudinal ridges or grooves,

774 basal striations, nor labial/lingual depressions. The enamel from the best-preserved part of the
775 crown also exhibits an irregular surface texture (Fig. 11.9).
776 **Identification.** Although poorly preserved, MACN 18.172 bears all dental features present in
777 abelisaurid lateral teeth such as a straight distal profile, mesial and distal carinae centrally
778 positioned on their respective surface and extending to the root, and a lenticular profile with
779 symmetrically convex lingual and labial profiles. The tooth differs from two of the teeth
780 illustrated by del Corro (1966) in the absence of well-defined and apicobasally wide
781 transverse undulations typically present in carcharodontosaurid teeth. Transverse undulations
782 are also common in abelisaurid teeth (Hendrickx *et al.*, 2019, 2020a) but they do not form
783 such thick and well-marked bands transversally crossing the whole crown like those visible in
784 del Corro's (1966) figures 1 and 2 (C.H. pers. obs.). The specimen further differs from that
785 figured by del Corro (1966: fig. 2) in the absence of an apical convexity forming the apical
786 third of the distal margin of the crown, a dental feature seen in carcharodontosaurid teeth
787 (Hendrickx *et al.*, 2019).
788 The cladistic analysis identifies this specimen as a tooth of an abelisauroid (Fig. 3.3).
789 A noasaurid affinity can, however, be excluded based on the large size of the crown (CH>25
790 mm). Indeed, all noasaurids bear crowns of less than 2 cm (Carrano *et al.*, 2002; Hendrickx *et*
791 *al.*, 2019, 2024). Although the denticles are badly preserved and almost missing entirely, the
792 tooth also does not seem to have a strong size discrepancy between mesial and distal
793 denticles, a dental feature typical of noasaurid teeth (Hendrickx *et al.*, 2019, 2024). Results of
794 the machine learning analysis conversely classifies this tooth as belonging to a
795 dromaeosaurid, and to a lesser extent, a megalosaurid, a tyrannosaurid, and a non-spinosaurid
796 megalosauroid (Fig. 4). None of these clades other than Dromaeosauridae were present in
797 Patagonia during the middle of the Cretaceous and we, therefore, confidently disregard a non-
798 spinosaurid megalosauroid or a tyrannosaurid affinity for this tooth. In South America during

the mid-Cretaceous, Dromaeosauridae are only represented by the unenlagiine *Buitreraptor*, whose lateral teeth strongly differ from MACN 18.172 in being non-denticulated, strongly labiolingually compressed, apically pointed, and showing a labial depression and often longitudinal ridges on the labial surface (Gianechini *et al.*, 2011). Unenlagiines, which are the only dromaeosaurids present in South America, bear non-denticulated (ziphodont or conidont) teeth devoid of carinae so that we confidently reject the possibility that MACN 18.172 belongs to a dromaeosaurid. Even though we disregard a noasaurid, dromaeosaurid, megalosaurian, or tyrannosaurid affinity for this tooth, we remain cautious with the identification of this poorly preserved specimen, which is tentatively referred to Abelisauridae. However, based on the result of the cladistic analysis and the abundance of abelisaurid remains in Cenomanian deposits of Patagonia (e.g., *Ilokelesia*, *Xenotarsosaurus*, *Ekrixinatosaurus*, *Skorpiovenator*; Coria and Salgado, 1998; Calvo *et al.*, 2004; Canale *et al.*, 2009; Ibiricu *et al.*, 2021; Cerroni *et al.*, 2022b), this shed crown most likely represents an abelisaurid tooth.

Late Cretaceous of Salta, Argentina

Material. PVL 3672, 4062-1 to 4062-4, 4173, 4174, 4175, eight incomplete to almost complete mesial and lateral teeth (Figs. 12-14).

Locality and Horizon. All the specimens come from the Department of Candelaria, Southern Salta Province, northeastern Argentina (Fig. 2.4), and were unearthed in deposits from the upper part of the Salta Group of Campanian–Maastrichtian in age. More precise information on the locality and horizon of the specimens here follows: PVL 4173 to 4175: Finca Sanchez, near El Ceibal, Los Blanquitos Formation, Pirgua Subgroup, upper Campanian or lower Maastrichtian (Marquillas *et al.*, 2005); PVL 4062: 2.6 km south of the El Brete Estancia, Lecho Formation, Balbuena Subgroup, lower or mid-Maastrichtian (Hendrickx *et al.*, 2024)

(Fig. 2.4); PVL 3672: 5 km North of the Arroyo Morterito fossil site, Sierra La Candelaria, El Ceibal; Yacoraite Formation, Balbuena Subgroup; upper Maastrichtian (Powell, 1979).

Importance. PVL 3672 (Fig. 14) represents the earliest published record of a non-avian theropod from northern Argentina (Bonaparte and Bossi, 1967) and one of the youngest abelisaurid records from South America (Ezcurra and Novas, 2016). It is also the second abelisaurid remain from Argentina to be reported in the literature after "*Megalosaurus inexpectatus*" described by del Corro (1966; see above). The isolated tooth was briefly described by Powell (1979) who referred it to an indeterminate carnosaur. The four carnosaur teeth from El Brete (PVL 4062; Fig. 13) are, with the noasaurid theropod *Noasaurus*, the second non-avian theropod record from northern Argentina (Bonaparte *et al.*, 1977) and the isolated teeth represent the only evidence of a large bodied theropod from the famous site that yielded the saltasaurine titanosaur *Saltasaurus* and the first enantiornithine material ever described (Bonaparte and Powell, 1980; Walker, 1981; Powell, 1992, 2003; Hendrickx *et al.*, 2024). These four teeth were only briefly described by Bonaparte and Powell (1980) and assigned to an indeterminate carnosaur, whereas specimens PVL 4173 to 4175 (Fig. 12) were never reported in the literature.

Description. The eight shed tooth crowns exhibit variable state of preservation, ranging from fairly complete and missing only small portions of the crown (PVL 4072-1 and -2) to particularly incomplete (PVL 4174; Fig. 12.7-12.10). The largest crown (PVL 4173; Fig. 12.1-12.4) has many mesiodistally oriented fractures, especially in its basal part. This tooth lacks large portions of the distal part of the crown and some mesially (Fig. 12.1-12.2). PVL 4174 is the most incomplete, missing most of the distal profile of the crown (Fig. 12.7-12.10).

If three morphotypes can be distinguished in the PVL sample (see below), the eight teeth all share a ziphodont morphology and a convex mesial profile. Likewise, if the distal profile is either straight or weakly convex, the crown apex always lies at the same level as the

849 distal limit of the crown. All teeth additionally have straight to weakly bowed but always
850 centrally positioned mesial and distal carinae on the mesial and distal surfaces, respectively.
851 The mesial denticles are subquadrangular and project perpendicular to the mesial profile
852 whereas the distal denticles have asymmetrically convex to apically hooked external margins
853 and project either perpendicular to or slightly apically from the distal profile. Although the
854 number of denticles per 5 mm varies in different teeth, all have similarly sized mesial and
855 distal denticles (i.e., DSDI~1) and a decrease in denticle size basally in both mesial and distal
856 carinae. All teeth also share an irregular enamel surface texture, and those with the best-
857 preserved denticles have medium to well-developed interdenticular sulci between the distal
858 denticles. Finally, none bear flutes, lingual/labial depressions, longitudinal grooves/ridges, or
859 basal striations.
860 Among the three morphotypes, the mesial one (Salta Morpho I), represented by PVL
861 4062-5, is weakly labiolingually compressed (CBR~0.65), moderately elongated (CHR~2)
862 and has a particularly convex mesial profile and a slightly lingually displaced crown apex
863 (Fig. 13.18-13.25). In basal view, it has a strongly asymmetrical parlinon-shape cross-
864 sectional outline at the base crown where both carinae are lingually deflected and the labial
865 profile is strongly convex, whereas the lingual side shows a weaker convexity and two
866 concave surface adjacent to the mesial and distal carinae (Fig. 13.24). PVL 4062-5
867 additionally differs from the other teeth by having well-developed interdenticular sulci
868 between mesial denticles (Fig. 13.23), pronounced marginal undulations adjacent to the distal
869 carina on the lingual side, and a particularly low denticle density, with 8 and 8.5 de/5 mm on
870 the mesial and distal carina at mid-crown, respectively.
871 The transitional type (Salta Morpho II) includes PVL 4062-4 and 4175 (Figs. 12.11-
872 12.16, 13.13-13.17) and differs from the previous one in being slightly more labiolingually
873 compressed (CBR from 0.55 to 0.63) and having a more symmetrical lenticular cross-section

874 at the base crown, with only weakly concave surfaces adjacent to the carinae on the lingual
875 surface (at least in PVL 4175; Fig. 12.16). However, it shares with the previous morphotype a
876 convex distal profile, a lingually displaced crown apex, a moderately elongated crown
877 (CHR~1.5; n.b. this was estimated based on the crown profiles), particularly large mesial and
878 distal denticles compared to the crown height, and marginal undulations adjacent to the distal
879 carina (n.b., unlike the first morphotype, these undulations are faint and on the labial side of
880 the crown), a combination of dental features absent in the lateral morphotype. The mesial and
881 distal denticle densities in the crowns belonging to the second morphotype fluctuate between
882 12.5 to 15 de/5 mm at mid-crown.
883 The third morphotype (Salta Morpho III; PVL 3672, 4062-1, 4062-2, 4173, 4174;
884 Figs. 12.1-12.10, 13.1-13.14, 14) includes moderately compressed crowns (CBR from 0.47 to
885 0.54) with a straight to weakly convex distal profile, a symmetrically lenticular cross-
886 sectional outline with no concave surfaces adjacent to the carinae, and a crown apex
887 exhibiting no lingual displacement. It should be noted that teeth from this morphotype
888 strongly vary in height (CH between 18 to 46 mm), elongation (CHR of ~1.44 to 2.43),
889 denticle crown index (~0.93 to 2.08), denticle densities (MC between 9 to 12.5; DC between
890 8.75 to 13.3), and the presence or absence of transverse and marginal undulations on the
891 crown surface.
892 **Identification.** The dental material from the Campanian-Maastrichtian of Salta Province
893 shows a combination of dental features restricted to Abelisauridae (Hendrickx *et al.*, 2020a).
894 Indeed, like abelisaurid teeth, all shed tooth crowns bear mesial and distal denticulated carinae
895 extending to the cervix, interdenticular sulci between distal and sometimes mesial denticles,
896 and an irregular enamel surface texture. Like abelisaurid mesial teeth, the first morphotype
897 has two strongly convex mesial and distal profiles of the crown, and the basal crown cross
898 section outline is parlinon with two concave surfaces adjacent to the carinae on the lingual

side, and a strongly convex labial surface. Conversely, the lateral type shows centrally positioned mesial and distal carinae on their respective surface, a distal profile either straight or slightly convex, resulting in a crown apex lying at the same level as the distal margin if the crown, as well as a lenticular cross-section outline with symmetrically convex lingual and labial surfaces.

All Salta morphotypes are recovered among Abelisauridae by the cladistic analysis (Fig. 3) whereas two of the three most complete PVL crowns are classified as abelisaurid teeth by the machine learning analysis, the third (PVL 4173), being identified as a non-abelisauroid ceratosaur (Fig. 4). We agree with the machine learning analysis that the size, proportion, and general morphology displayed by PVL 4173 are reminiscent of those seen in Ceratosauridae; the latter clade is, however, restricted to the Late Jurassic and Early Cretaceous (Rauhut, 2004). The largest terrestrial predators from the Late Cretaceous of northern Argentina are currently limited to abelisaurids (*Guemesia*; Agnolín *et al.*, 2022) and a large-bodied maniraptoran (*Unquillosaurus*) whose dentition and precise taxonomic affinities among Paraves are currently unknown (Powell, 1979; Novas and Agnolin, 2004; Novas, 2009). We, however, note that the dentition of the unique large-bodied paravian from the Late Cretaceous of South America, *Austroraptor*, bear ziphodont to conidont crowns with non-denticulated mesial and distal carinae, labial depressions, and numerous flutes (or longitudinal grooves; Motta and Novas, 2025). Consequently, based on the results of the phylogenetic and machine learning analyses combined with the paleogeographic and stratigraphic distributions of the isolated theropod teeth from the Late Cretaceous of Salta, PVL teeth are confidently referred to an indeterminate Abelisauridae, probably related to (and for PVL 4173 to 4175, possibly from) *Guemesia ochoai* from the Los Blanquitos Formation of central Salta (Agnolín *et al.*, 2022).

924 **Late Cretaceous of India**

925 **Material.** NHMUK R4190, an isolated lateral tooth crown (Fig. 15).

926 **Locality and Horizon.** Takli, Nagpur area, Maharashtra State, western India; Lameta
927 Formation (also referred to the Takli Formation), upper Maastrichtian, Upper Cretaceous
928 (Carrano *et al.*, 2012) (Fig. 2.2).

929 **Importance.** This specimen likely represents the earliest historical record of a non-avian
930 theropod in Asia (Carrano *et al.*, 2010; Hendrickx *et al.*, 2015a) and possibly the first
931 theropod remains to be reported from this continent (Hendrickx and Carrano, 2016). This
932 tooth is also among the youngest abelisaurid records from Asia. NHMUK R4190 is part of
933 several theropod teeth reported by Reverend Stephen Hislop (1861, 1864) and appears to be
934 the only surviving specimen from this collection. The specimen was found between 1858 and
935 1861 by Mr. Rawes in the locality of Takli (Nagpur area, Maharashtra State) and sent to the
936 Geological Society's Museum of London (which is now part of the Natural History Museum)
937 where it was studied and illustrated by English naturalist Richard Lydekker (Lydekker, 1879,
938 1885, 1890). The latter recognized the theropod affinity of the tooth and assigned it to
939 a new species of *Massospondylus*, *M. rawesi* (Lydekker, 1890), owing to its resemblance with
940 the teeth of this early branching sauropodomorph thought at the time to be a theropod. The
941 tooth was later referred to *Megalosaurus* by Vianey-Liaud *et al.* (1988) and to an
942 indeterminate theropod by Carrano *et al.* (2010, 2012) who, nevertheless, noted the strong
943 resemblance with abelisaurid teeth. Hendrickx *et al.* (2015a) finally considered NHMUK
944 R4190 as almost certainly representing the shed tooth crown of an abelisaurid.**Description.**
945 NHMUK R4190 is an almost complete lateral shed tooth crown missing the basalmost crown,
946 especially in its distal part where a piece of the basalmost portion of the distal surface was lost
947 (Fig. 15). Due to that, the cervical line as well as the distalmost denticles of the mesial and
948 distal carinae are not preserved. Despite being relatively complete, the crown is poorly

preserved as the enamel layer exhibits a punctuate appearance where spots of the enamel surface are worn out. The external surface of most of the mesial and distal denticles are also broken off, especially mesially at the crown apex. The specimen represents a typical ziphodont crown with denticulated mesial and distal carinae extending basally up to or very close to the root. Both mesial and distal carinae are straight or very weakly bowed and centrally placed on the mesial and distal profiles of the crown, respectively (Fig. 15.3-15.4). The crown, therefore, has a subsymmetrical appearance in basal view where the two carinae are aligned on a plane passing through the center of the crown and where the labial and lingual surfaces have the same convexity, with the apex mesially displaced and positioned at the level two-fifths of the crown (Fig. 15.5). The crown is medium in size (CH of 2.5 cm), moderately compressed (CBR of 0.48), and poorly elongated (CHR of 1.6). The mid-crown is only slightly more compressed than the crown base (MCR of 0.46). In lateral view, the mesial profile is symmetrically convex whereas the distal profile is straight so that the crown apex lies at the same level as the basalmost portion of the distal carina.

Denticles are present all along the carina length and appear to have crossed the apex. Based on the preserved denticles, the basalmost mesial denticles and apicalmost distal ones are smaller than those at mid-crown. We counted 8.5 and 10 mesial and distal de/5 millimeters at mid-crown, respectively, 13.75 at the base of the mesial carina and 11.87 in the apical portion of the distal carina. The mesial denticles are subquadrangular, project perpendicular from the mesial profile of the crown, and their external margin is either asymmetrically convex or apically hooked (Fig. 15.7). Conversely, the distal denticles are horizontally elongated, project diagonally from the distal profile, and the external surface is asymmetrically convex (Fig. 15.8). Well-developed interdenticular sulci curving basally are visible between distal denticles on the labial side of the crown (Fig. 15.1). Short sulci are also present between the best preserved mesial denticles. No marginal or transverse undulations

appear to be present on the crown, which is too badly preserved to rule out their presence. The specimen neither exhibits flutes or elongated grooves or ridges labial/lingual depressions. The best-preserved part of the crown surface clearly shows an irregular texture of the enamel (Fig. 15.9).

Identification. NHMUK R4190 exhibits all dental features present in abelisaurid lateral crowns: the crown is relatively large (CH~2.5 cm), moderately compressed (CBR~0.5), poorly elongated (CHR<2), and subsymmetrical is basal and mesial/distal views, with symmetrically convex labial and lingual profiles; the denticulated mesial and distal carinae extend to the root (or very close to it) and are centrally positioned on the mesial/distal surface; the mesial denticles are apically hooked or asymmetrically convex; the distal denticles project apically from the distal profile and show well-developed interdenticular sulci; and the enamel surface texture is irregular (Hendrickx *et al.*, 2020a). Only abelisaurid lateral teeth display such a combination of dental features, and the specimen is confidently referred to this clade based on its external morphology, the results of the cladistic and machine learning analyses, and the stratigraphic and geographic context given the abundance of abelisaurid material in Maastrichtian deposits of India (Wilson *et al.*, 2003; Novas *et al.*, 2004, 2010; Khosla and Lucas, 2023). Based on the results of the phylogenetic relationships on ceratosaurs obtained by Hendrickx *et al.* (2024), we additionally tentatively assign this specimen to Majungasaurinae, as all abelisaurids from the latest Cretaceous of India are classified to this clade by these authors.

DISCUSSION

Paleogeographic implications

The presence of isolated abelisaurid teeth in Upper Cretaceous deposits of Patagonia, northern Argentina, and India is not surprising, since abelisaurid theropods are among the typical apex terrestrial predators in all Late Cretaceous ecosystems of Argentina (Calvo *et al.*, 2004; Novas

et al., 2013; Ezcurra and Novas, 2016; Cerroni *et al.*, 2020; Agnolín *et al.*, 2022) and India (Wilson *et al.*, 2003; Novas *et al.*, 2004, 2010). Likewise, an isolated tooth identified as belonging to an abelisaurid was already reported from the Kimmeridgian–Tithonian Tacuarembó Formation of Uruguay by Soto *et al.* (2023) and the identification of a second abelisaurid tooth (Fig. 10) from these deposits provides further support for the presence of this clade in South America during the Late Jurassic. Conversely, the referral of isolated theropod teeth from the Middle Jurassic of Madagascar (Fig. 9) to Abelisauridae is particularly interesting and provides crucial information on the paleogeographic distribution and evolutionary history of this important theropod clade. Although the dental material from the Middle Jurassic of Madagascar was already regarded as likely representing abelisaurid teeth by Maganuco *et al.* (2005) and Soto *et al.* (2023), our study is the first to confirm this referral with computational techniques, corroborating the presence of Abelisauridae in Gondwana before the Late Jurassic.

Pol and Rauhut (2012) were the first to argue the presence of this clade in the Middle Jurassic based on a particularly complete skeleton from the Cañadón Asfalto Formation of Cerro Cóndor, Chubut Province, Patagonia. By giving the genus name *Eoabelisaurus*, they showed that this medium-sized (6-6.5 m; Pol and Rauhut, 2012) theropod was clearly an abelisaurid, making it the earliest member of this clade and pushing back its origins to the Middle Jurassic while abelisaurid theropods were thought to be restricted to the Cretaceous (Carrano and Sampson, 2008; Novas *et al.*, 2013). Remains from the Jurassic referred to abelisaurid theropods are meager and their referral to this clade is either tentative (Rauhut, 2011; Rauhut and Pol, 2021) or debated (e.g., Novas *et al.*, 2013; Tortosa *et al.*, 2014; Gerke and Wings, 2016; Hendrickx *et al.*, 2020a; Soto *et al.*, 2023). To this day, Jurassic remains attributed to Abelisauridae includes *Eoabelisaurus* from the Cañadón Asfalto Formation (now dated to the Toarcian, Early Jurassic; Cúneo *et al.*, 2013; Rauhut and Pol, 2019; Fantasia *et*

al., 2021) of Patagonia (Pol and Rauhut, 2012), two isolated teeth from the Kimmeridgian-Tithonian of Portugal (Hendrickx and Mateus, 2014), one single isolated tooth from the Late Jurassic of Uruguay (Soto *et al.*, 2023), one isolated tibia from the Kimmeridgian-Tithonian Tendaguru beds of Tanzania (Rauhut, 2011), an anterior cervical vertebra and a set of fragmented cranial and postcranial remains from the Oxfordian–Kimmeridgian Cañadón Calcáreo Formation of Chubut, Patagonia (Rauhut and Pol, 2021), and an isolated tooth from the Late Jurassic or the Early Cretaceous of the Araripe basin, Brazil (Ribeiro *et al.*, 2025). The postcranial material from the Late Jurassic of Tanzania and Patagonia were, however, tentatively referred to Abelisauridae (Rauhut, 2011; Rauhut and Pol, 2021), and many authors cast doubt on the abelisaurid affinity of the two isolated teeth from the Late Jurassic Portugal, which may instead belong to early branching tetanurans such as allosauroids (Gerke and Wings, 2016; Malafaia *et al.*, 2017; Hendrickx *et al.*, 2020b; Soto *et al.*, 2023; C.H. pers. obs.). The abelisaurid affinity of *Eoabelisaurus*, which is by far the most complete of the putative abelisaurid material from the Jurassic, was also challenged by various authors whose results of the cladistic analyses performed on independent datamatrices classify it as an early branching neoceratosaur (Aranciaga Rolando *et al.*, 2021; Hendrickx *et al.*, 2024), a non-abelisaurid abelisauroid (Tortosa *et al.*, 2014; Rauhut and Pol, 2021), or a ceratosaurid (Delcourt, 2018), restricting all taxa recovered among Abelisauridae to the Cretaceous. This study is, therefore, one of the few to confidently refer theropod material from the Jurassic to Abelisauridae using cladistic techniques.

Our referral of the dental material from Madagascar (Fig. 9) to a Jurassic abelisaurid could be challenged in two ways: i) the dental material from Madagascar is not from an abelisaurid but from a ziphodont theropod with a similar dental morphology; or ii) it is from an abelisaurid that lived in the Cretaceous. Although distantly related theropods can superficially exhibit similar dental morphologies (e.g., Hendrickx *et al.*, 2019), we reject the

first hypothesis on the ground that no theropod clades other than Abelisauridae have teeth that have a combination of the numerous dental features present in the mesialmost, transitional, and lateral dental morphotypes from Madagascar. Based on an extensive survey of the dentition of ziphodont theropods by four of us (C.H., M.S., J.G.M., S.M.), none other than abelisaurids bear teeth with both mesial and distal denticulated carinae extending to the root, a straight to convex distal profile of the crown, and an irregular enamel surface texture; mesialmost teeth with a weak constriction between crown and root, a parlinon-shaped cross-section outline, and a CBR close to 0.7; transitional teeth with a parlinon cross-section having lingual concavities adjacent to the carinae; and lateral teeth with centrally positioned mesial and distal carinae, hooked distal and sometime mesial denticles, and well-developed interdenticular sulci. If the presence of Middle Jurassic non-abelisaurid theropods that convergently acquired abelisaurid dental morphology cannot be rejected, we disregard this hypothesis based on our current knowledge on theropod dental anatomy. The second hypothesis, which would appear to be more conceivable based on the presence of the abelisaurid *Majungasaurus* in the Mahajanga basin, whose dental morphology is surprisingly similar to that of the dental morphotypes here described, is also confidently rejected. Maganuco *et al.* (2005) indeed wrote that "despite the lacking of more specific stratigraphic data, the general features of such well exposed, subhorizontal continental deposits, locally containing heteropies with transgressive marine sediments, as evidenced by petrographic features and faunal assemblages, allow us to state that the material pertains without doubt to a single Subunit referable to the Isalo IIIb" (Maganuco *et al.*, 2005, p. 166), a unit formerly known as the "Faciès mixte - dinosauriens" of Besairie and Collignon (1972) and currently referred to as the Sakaraha Formation, well-dated to the Bathonian (Geiger *et al.*, 2004; Maganuco *et al.*, 2005, 2007; Bindellini and Dal Sasso, 2021; Flynn *et al.*, 2022). The abelisaurid affinity of the teeth from the Middle Jurassic of Madagascar consequently

provides strong support for the presence and radiation of this clade in Gondwana as early as the Middle Jurassic, as claimed by Pol and Rauhut's (2012).

Implications on the earliest discovery of non-avian theropod and abelisaurid remains in the world

Using both cladistic and machine learning techniques, this study is the first to reveal that NHMUK R4190 (Fig. 15) from the Lameta Formation of Takli, India, and representing, to our knowledge, the first published record of a non-avian theropod in Asia (Hendrickx *et al.*, 2015a), can confidently be referred to an abelisaurid theropod. This is the second record of abelisaurid dental material representing the earliest record of non-avian theropod body fossils in the scientific literature on a continent. In 1896, French palaeontologist Charles Depéret (1896a, 1896b) reported two theropod teeth, an ungual phalanx, and a caudal vertebra from the Maastrichtian Maevarano Formation of northwestern Madagascar (Fig. 16.1-16.3). Krause *et al.* (2007) provided details on the history of the discovery of these remains that were collected by Mr. Landillon during an expedition led by French military physician Dr. Félix Salètes in the area of the village Maevarana, on the northeastern bank of the Betsibokar River in 1895. If the provenance of the dinosaur postcranial material is unknown, Depéret (1896a) stated that the two theropod teeth came from Locality 2, which lies just north of the Amboanemba Escarpment (Krause *et al.*, 2007: figs. 2, 5). The brief report of the existence of dinosaur remains in Madagascar by Depéret (1896b) from the 24th of February 1896 represents the first published record of non-avian theropod skeletal remains in Africa (Hendrickx *et al.*, 2015a). Depéret (1896a) provided a description and several illustrations of the dinosaurian material in an article from the 16th of March 1896 in which he referred the theropod remains to the new *Megalosaurus* species *M. crenatissimus*. The two teeth, which are now deposited at the Faculté des Sciences de Lyon under specimen number FSL

92.306a,b (Fig. 16.2-16.3), were referred to *Majungasaurus crenatissimus* by Krause *et al.* (2007) and Smith (2007). The latter explored the taxonomic affinity of the dental material using discriminant analysis and confidently referred the most complete crown (FSL 92.306a) to this abelisaurid species, noting that it was similar to the distal dentary teeth of *Majungasaurus* (2007). Based on Smith's (2007) expertise on *Majungasaurus* dental anatomy, combined with the paleogeographic and stratigraphic context of the material, we fully agree that the two shed teeth reported by Depéret (1896a, 1896b) almost certainly belong to *Majungasaurus*, making them (along with the two vertebrae and the pedal ungual phalanx) the earliest non-avian theropod remains from Africa to be published in the literature.

Interestingly, the discovery and earliest reports on isolated theropod teeth are intrinsically linked to the first discoveries of theropod remains in the world and the emergence of theropod palaeontology in the 18th and 19th century. In Europe, 125 years before the description of *Megalosaurus* by Buckland (1824), Welsh naturalist Edward Lhuyd (1699) identified in his *Lithophylacii Britannici Ichnographica* specimen 1328 from Stonesfield as the tooth of a fish; however, plate 16 illustrating the specimen suggests that this crown likely belonged to *Megalosaurus*, making it the second published record of a non-avian dinosaur only 22 years after Robert Plot's (1677) description of the distal portion of a *Megalosaurus* femur famously labelled "Scrotum Humanum" by Richard Brookes (1763). In North America, a set of isolated theropod teeth recovered from Upper Cretaceous deposits at the confluence of the Missouri and Judith rivers of Montana were used by Joseph Leidy (1856) to erect the new species *Troodon formosus* and *Deinodon horridus* and represent the first body fossils of a non-avian theropod described in the scientific literature outside Europe (Hendrickx *et al.*, 2015a; Hendrickx and Carrano, 2016). In South America, the description of the first Argentine dinosaur to be named, *Loncosaurus argentinus* (initially named *Megalosaurus argentinus*; Huene, 1929), by palaeontologist Florentino Ameghino (1899) based on a

theropod tooth and a femur later referred to an ornithopod (Coria and Salgado, 1996) from the Cenomanian Mata Amarilla Formation of Par-Aik, Río Sehuen, Santa Cruz Province of Argentina (Fig. 16.4-16.5), only predates by six years the earliest published record of non-avian theropod body fossils in South America by Lydekker (1893) (Hendrickx *et al.*, 2015b; Hendrickx and Carrano, 2016). This tooth crown was illustrated as complete by Ameghino (1900, 1906) but Huene (1929), who provided a detailed description of the tooth, noted that it had been reconstructed, preventing referral to a specific theropod clade. The probable abelisaurid tooth MACN 18.172 reported by del Corro (1966) may, therefore, represent the earliest published record of abelisaurid material in Argentina, 19 years before the erection of the clade Abelisauridae by José Bonaparte and Fernando Novas in 1985 (Bonaparte and Novas, 1985). It also likely represents the second published record of abelisaurid dental material from the New World after Price's (1960) report of two isolated theropod teeth, one of which confidently referred to an abelisaurid (Ribeiro *et al.*, 2024a), from the Amazon forest of Brazil. In Europe, if the earliest non-avian theropod remains published in the literature all belong to megalosauroids (Delair and Sarjeant, 2002; Buffetaut, 2010; Spalding and Sarjeant, 2012; Hendrickx *et al.*, 2015a), the first published record of abelisaurid material occurred as early as the late 19th century (Buffetaut, 2025b). According to Buffetaut (2025b), the right femur from the Maastricht beds of the Maastricht area, southern Netherlands, and referred to *Megalosaurus bredai* by Harry Govier Seeley in 1883 (Seeley, 1883) belongs to an abelisaurid, making it the first published record of a definite abelisaurid in Europe and the latest known occurrence of this clade on this continent (Buffetaut, 2025b). Buffetaut (2025b) further argued that the isolated theropod teeth from the Campanian Gosau Formation of Muthmannsdorf, Lower Austria, described by Seeley (1881) as *Megalosaurus pannoniensis* (Fig. 16.6-16.7) may represent the earliest published record of abelisaurid remains from Europe, noting that even though these teeth were referred to non-abelisaurid theropods by

various authors (Ősi *et al.*, 2010; Malafaia *et al.*, 2025), an abelisaurid affinity cannot be excluded. We, however, concur with Ősi *et al.* (2010) and Malafaia *et al.* (2025) that the tooth illustrated by Ősi *et al.* (2010: fig. 6C) likely belongs to an early branching tetanuran based on the well-visible braided surface texture of the enamel, a dental feature absent in abelisaurid teeth (Hendrickx *et al.*, 2020a).

Dental evolution in Abelisauridae

The particularly incomplete, if not fully unpreserved, dentition of many abelisauroids (e.g., *Eoabelisaurus*, *Vespersaurus*, *Dahalokely*, *Ilokelesia*, *Carnotaurus*, *Koleken*) combined with the highly debated classification of ceratosaurs (e.g., the placement of elaphrosaurines within noasaurids or at the base of the ceratosaur clade) currently prevents a more confident understanding of dental evolution in Abelisauridae. Even though abelisaurid teeth exhibit many diagnostic features such as a mesial carina extending to the root (char. 89:1-2), a straight or slightly convex distal profile of the crown (char. 79:1-2), hooked distal denticles (char. 99:2), well-developed interdenticular sulci between distal denticles (char. 116:2), an irregular enamel surface texture (char. 128:0), and mesial teeth with a salinon cross-section outline at the base crown (char. 51:2), it is the combination of these dental features that allows the identification of isolated abelisaurid teeth. Indeed, lateral teeth with a mesial carina reaching the cervix is seen in all ceratosaurs, a straight or slightly convex distal margin is present in the lateral teeth of ceratosaurids and *Noasaurus*, some of the lateral teeth of *Masiakasaurus* bear hooked distal denticles, *Ceratosaurus* lateral teeth have well-developed interdenticular sulci, the enamel surface texture is irregular in *Saltriovenator* and *Noasaurus*, and a salinon cross-section outline at the base crown also characterizes the mesialmost teeth of *Masiakasaurus* (Hendrickx *et al.*, 2019). Results of the dental evolution analysis indeed shows that none of these crown-based characters evolved in abelisaurids. Instead, it is the

proportion of different parts of the dentition that appeared to have changed during the radiation of Abelisauridae, the latter being diagnosed by having mesialmost dentary teeth significantly smaller than mid- and distal dentary teeth (char. 30:2) and the tallest crowns in the middle portion of the maxilla (char. 42:1) (Fig. 5). An increase in the number of dentary teeth to more than 15 (char. 28:2) and the development of interdenticular sulci between distal denticles in mesial teeth (char. 69:2) also evolved in Abelisauridae when Elaphrosaurinae forms an early radiation of ceratosaurs (Fig. 5.1). It must be noted that our analysis is significantly biased, as it is limited to Cretaceous abelisaurids. The dentition of the only putative abelisaurid from the Jurassic, *Eoabelisaurus*, is extremely fragmentary and restricted to a single unerupted tooth from a small portion of the maxilla (Pol and Rauhut, 2012). Photos shared by colleagues show that this average maxillary tooth (3-3.5 cm) features a mesial denticulated carina extending to or near the root, a weakly concave distal profile, and comparatively small mesial and distal denticles (~10 de/5 mm). This extremely limited dental information is insufficient to draw any conclusion on dental changes in the early evolution of Abelisauridae, assuming *Eoabelisaurus* is indeed an abelisaurid. The abelisaurid teeth from Madagascar nonetheless offer an opportunity to better understand dental evolution in this clade during the Middle Jurassic. The external morphology of the mesial, transitional, and lateral teeth from Madagascar clearly indicates that the acquisition of typical abelisaurid crown-based traits occured early in the evolutionary history of Abelisauridae, the mesialmost teeth having already the two concave surfaces adjacent to the carinae lingually, a constriction between crown and root, convex mesial and distal profiles with denticulated carinae extending over the whole crown height, and a salinon-cross section outline with a strongly convex labial surface and a biconcave lingual one (Fig. 9.1-9.8). Lateral teeth are also identical to those of Cretaceous abelisaurids in having a straight to slightly convex distal profile, centrally positioned mesial and distal carinae on the crown extending to the root, hooked distal

denticles, and long interdenticular sulci curving basally (Fig. 9.16-9.22). The only plesiomorphic dental features we could observe in the putative abelisaurid lateral teeth from the Middle Jurassic of Madagascar (Supplementary data Appendix 1: Fig. A1) and the Late Jurassic of Uruguay (Fig. 10) is the presence of a mesial denticulated carina that does not extend to the root, a trait also seen in the ceratosaurids *Genyodectes* and possibly *Ceratosaurus* (C.H. pers. obs.). With a crown height not exceeding 2.5 cm, the abelisaurid dental material from Madagascar additionally aligns with the apparent reduction in body size that abelisaurids seem to have undergone from the Early Jurassic, with the medium-bodied (5.82 m in body length) *Eoabelisaurus* with maxillary teeth of ~3.5 cm, to the Early Cretaceous with the small-bodied (1.42 m in body length; Pereyra *et al.*, 2025) *Spectrovenator ragei* (Zaher *et al.*, 2020) from the Barremian-Aptian of Brazil (1.4 cm for mx6; n.b., this taxon might, however, represent a juvenile individual; see below) and the medium-bodied (3.56 m) *Genusaurus sisteroni* (Accarie *et al.*, 1995; Buffetaut *et al.*, 1995; Buffetaut, 2025a) from the Albian of France (Grillo and Delcourt, 2017; Pereyra *et al.*, 2025). However, more data is needed to confirm such a trend.

Our understanding of dental evolution in Early Cretaceous forms is essentially based on the dentition of *Spectrovenator ragei* (Zaher *et al.*, 2020), which is extremely similar to that of Late Cretaceous abelisaurids. Our dental analysis indeed reveals that its dentition only differs from that of more derived abelisaurids in the absence of apically inclined distal denticles in lateral teeth (Fig. 5.1-5.2). Based on the plesiomorphic morphology of the temporal region, the reduced dorsoventral depth of the dentary, and the absence of a kinetic intramandibular joint, *Spectrovenator* was described by Zaher *et al.* (2020) as retaining a more generalized feeding strategy comparable to that of other theropods and differing from the specialized feeding strategy of Late Cretaceous abelisaurids (Therrien *et al.*, 2005; Canale *et al.*, 2009). The dental morphology of *Spectrovenator*, however, does not support this

hypothesis and instead concurs with the results of Pereyra *et al.*'s (2025) recent study on maxilla morphology in ceratosaurs, which finds that the hunter specialization already appeared in Early Cretaceous abelisaurids. We additionally note that the particularly small body size of *Spectrovenator* may result from the immaturity of this abelisaurid, whose feeding strategy may have differed from adult individuals. We, indeed, observe that the mesial denticles from the lateral dentition of *Spectrovenator* are significantly smaller than the distal ones (DSDI>1.2), a dental feature observed in juvenile abelisaurids (Fanti and Therrien, 2007). The distal denticles from the maxillary teeth are also relatively large in proportion to crown height (DCR of 2.46-2.71); however, this dental feature is also observed in *Kryptops* from the Early Cretaceous of northern Africa (C.H. pers. obs.), suggesting that a decrease in denticle size compared to crown height (DCR<2) may have occurred in Late Cretaceous abelisaurids.

Even though the dentition of Late Cretaceous abelisaurids is relatively well-known, their debated relationships complicate our understanding of dental evolution in later branching Abelisauridae. Mapping dental apomorphies on two hypotheses of abelisaurid relationships (i.e., Hendrickx and Cau's topologies; Fig. 5.1, 5.3) shows that abelisaurids more derived than *Rugops* developed mesialmost and mid-maxillary teeth of similar size. Similarly, dental evolution in members of the clade Brachyrostra + Majungasaurinae, as recovered in Hendrickx's topology (Fig. 5.1), is marked by an increase in crown height (crowns between 3 and 6 cm; char. 41:2), a trend probably linked to the body size increase observed in some Late Cretaceous abelisaurids. Dental evolution within Brachyrostra and Abelisaurinae involves minor changes, primarily concerning denticle shape and the development of interdenticular sulci. Brachyrostra is indeed diagnosed by having subquadrangular mesial denticles in lateral teeth (char. 102:1) when it includes *Skorpiovenator*, *Abelisaurus* and *Aucasaurus* (Hendrickx's topology) and subrectangular distal denticles in lateral teeth (char. 103:1) when

it includes *Arcovenator*, *Skorpiovenator*, *Llukalkan*, and *Aucasaurus* (Pol's topology). Likewise, Abelisaurinae is diagnosed by poorly developed interdenticular sulci between distal denticles of the lateral crowns (char. 116:1) when *Abelisaurus* is closely related to *Majungasaurus* and *Indosuchus* (Pol's topology; Fig. 5.2), and biconvex mesial denticles in lateral crowns (char. 105:1) when *Abelisaurus* forms a clade with *Aucasaurus* (Cau's topology; Fig. 5.3). Functionally speaking, Sampson and Witmer (2007) argued that the dentition of *Majungasaurus* and other closely related abelisaurids with short-crowned lateral teeth and robust premaxillary teeth (e.g., *Indosuchus*, *Rugops*, *Kryptops*, *Aucasaurus*, Kem Kem abelisaurid taxon), combined with other suite of non-dental features such as a broad and abbreviated skull, particularly high bite forces, as well as expanded occiput and neck musculature, were adaptation towards a bite-and-hold feeding behavior. According to Sampson and Witmer (2007), such a mode of predation entailed relatively few long penetrating bites followed by powerful neck retraction to produce massive wounds in a struggling large-bodied prey.

All Late Cretaceous abelisaurids did not have the same dental morphology as *Majungasaurus* and other closely related taxa from the Southern Hemisphere. Our study shows that *Chenanisaurus* from the Maastrichtian of Northern Africa (Longrich *et al.*, 2017) and *Arcovenator* from the Campanian of Southern Europe (Tortosa *et al.*, 2014) have the largest number of dental apomorphies among Abelisauridae, suggesting a particularly derived dental morphology. We, however, note that the high number of apomorphic dental features in *Chenanisaurus* most likely results from its rather early branching placement among Abelisauridae (Longrich *et al.*, 2017), a position that should be seen as tentative owing to the incompleteness of this taxon (i.e., *Chenanisaurus* only preserves an anterior portion of the dentary and three isolated teeth). We will, therefore, focus solely on the distinctive dentition of *Arcovenator* previously noted by Hendrickx *et al.* (2020a), as the various phylogenetic

positions of *Arcovenator* among abelisaurids do not have any influence on the number (6) and type of dental autapomorphies diagnosing this abelisaurid (Fig. 5). In all three topologies, the lateral dentition of *Arcovenator* is indeed diagnosed by a strongly concave distal margin of the crowns (char. 79:0), a strongly labially deflected distal carina (char. 94:1) extending far below the cervical line (char. 92:1), a denticle crown ratio lower than 1 (i.e., the distal denticles are particularly small compared to the crown; char. 97:1), lower number of denticles apically than at the mid-crown (char. 111:1), and distal denticles larger than mesial ones (DSDI>1.2; char. 112:2). Lateral crowns with such a combination of dental features are peculiar among abelisaurids and reminiscent to those of piatnitzkysaurids (Hendrickx *et al.*, 2019), possibly reflecting similar feeding strategies among members of the latter clade and *Arcovenator*. We, indeed, reject the hypothesis that the isolated teeth assigned to *Arcovenator* belong to a non-abelisaurid theropod for the following reasons: i) one of the teeth was recovered in a single sedimentary layer within a limited area with the rest of the holotypic material of *Arcovenator* (Tortosa *et al.*, 2014); ii) unlike the Apulian archipelago of eastern Europe where medium-bodied early branching tetanurans were also present during the Late Cretaceous, abelisaurids are the unique large-bodied theropods with tall (>3 cm) ziphodont crowns that inhabited the Ibero-Armorican domain of southern Europe during the latest part of the Cretaceous (e.g., Le Loeuff and Buffetaut, 1991; Ősi *et al.*, 2010; Csiki-Sava *et al.*, 2015; Isasmendi *et al.*, 2022, 2024; Malafaia *et al.*, 2025). Although the discovery of additional cranial and postcranial material in *Arcovenator* is needed to support such a hypothesis, its dental morphology suggests that the feeding ecology of this taxon and other closely related Iberian abelisaurids with similar dental morphologies (Torices *et al.*, 2015; Pérez-García *et al.*, 2016; Isasmendi *et al.*, 2024; Malafaia *et al.*, 2025) differed from other Late Cretaceous abelisaurids from the Southern Hemisphere.

The combined results of the WMPD, morphospace, and phylogenetically informed regression analyses provide an idea of the evolutionary patterns in ceratosaur dental morphology. WMPD values reveal higher morphological disparity during the Early Cretaceous for both mesial and lateral teeth, followed by a notable decline in the Late Cretaceous (Fig. 6). This temporal shift suggests an initial phase of morphological niche or ecological differentiation in ceratosaurs, likely linked to an adaptive radiation, followed by increasingly conservative morphology, potentially associated with particular ecological specialization. Morphospace occupation patterns reinforce this interpretation. Early Cretaceous ceratosaur taxa exhibit a more restricted distribution within the morphospace, while Late Cretaceous forms occupy a broader range of morphological variation, particularly in the lateral dentition (Fig. 7.2). Notably, certain clades such as Noasauridae and non-brachyrostran abelisaurids maintain distinct positions within morphospace, whereas brachyrostrans and majungasaurines display partial overlap, with *Chenanisaurus* and *Arcovenator* deviating notably from the occupation of Gondwanan abelisaurids (Fig. 7.2), evidence of taxa-specific morphological specialization in northern Africa and Europe. Finally, pGLS analyses demonstrate no significant correlation between body size and PCo1 of dental variation for either mesial or lateral dentition, indicating that morphological disparity in abelisaurid teeth was not driven by body size (Fig. 8). Together, these results suggest that ecological and functional factors—rather than allometry—played a primary role in shaping dental morphology in this clade.

CONCLUSIONS

The identification of a set of abelisaurid shed tooth crowns from various Jurassic and Cretaceous localities of Gondwana using advanced phylogenetic and machine learning techniques reveal several important points that can be summarized as follows: i) abelisaurids were present in what is now Madagascar during the Middle Jurassic, providing strong support

for the radiation of this clade as early as the Early Jurassic; ii) teeth of Middle Jurassic abelisaurids are particularly similar to those of Cretaceous forms, suggesting that abelisaurid crown-based traits were acquired early in the evolution of Abelisauridae; iii) dental evolution in Early Cretaceous abelisaurids is characterized by a decrease in size of the mesialmost dentary dentition, a displacement of the tallest crowns towards the middle part of the maxilla, and a possible increase in the number of dentary teeth; iv) in Late Cretaceous abelisaurids, dental evolution is characterized by the development of mesialmost and mid-maxillary teeth of similar size, a possible increase in crown height to more than 3 cm, and, in more derived abelisaurid subclades, subtle dental changes mainly related to denticle shape; v) the strongly apomorphic lateral dentition of *Arcovenator* suggests that the dietary ecology of this taxon and other closely related species from the latest part of Cretaceous in southern Europe departed from the specialized feeding strategies of Gondwanan abelisaurids; vi) two isolated abelisaurid teeth identified in this study, NHMUK R4190 mentioned by Hislop (1861) and MACN 18.172 reported by del Corro (1966), represents, to our knowledge, the earliest historical record of a non-avian theropod in Asia and the first published record of an abelisaurid from Argentina, respectively.

This study is the first to use cladistic methods conducted on datasets separated into tooth row partitions using two fully constrained topological trees representing alternative hypotheses of theropod relationships to classify shed dinosaur teeth, further helping to identify isolated theropod teeth from the mesial and lateral dentition with better confidence. Likewise, our new morphometric-driven machine-learning pipeline presented here streamlines the identification of isolated dinosaur teeth, offering a demonstrably cleaner and more transparent workflow than earlier rule-based or ad-hoc approaches. By systematically testing four algorithms across graded reference sets, we show that model architecture is almost immaterial; once biases introduced by uneven taxon sampling and body size effects are

minimized, all classifiers converge on the same answers with comparable accuracy. Crucially, the protocol's emphasis on balanced, size-controlled training data and explicit probability outputs mitigates the "hidden" omissions and subjective weighting that affected previous methods, allowing palaeontologists to quantify both confidence and error rates. In short, these techniques provide a reproducible, bias-aware framework in which the reliability of clade assignments remains modest but now with a firm basis and clear path drawn; thereby raising the bar for future studies that rely on isolated dental material.

This study is additionally the first to apply WMPD, morphospace, and phylogenetically informed regression analyses to theropod teeth. Our results show that ceratosaur dental disparity was greater during the Early Cretaceous than in the Late Cretaceous. This shift suggests an initial phase of ecological diversification followed by increasing conservative morphology. Morphospace analyses also highlight the distinct positioning of certain groups such as Noasauridae and non-brachyrostran Abelisauridae, as well as taxa such as *Chenanisaurus* and *Arcovenator*, underscoring the presence of taxon-specific morphological trends in abelisaurids from the Northern Hemisphere that may reflect particular adaptations. Finally, pGLS analyses reveal no significant correlation between body size and dental morphology, indicating that variation in ceratosaur teeth was largely decoupled from allometric scaling and more likely shaped by functional and ecological pressures more complex.

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FIGURES

Figure captions

Figure 1. Geographic and stratigraphic distribution of the isolated abelisaurid teeth from the Jurassic of Gondwana. **1,** Paleogeographic map of what is now South America, Africa and India during the Middle Jurassic (170 Mya; map from Ronald Blakey; modified). **2,** Geological map of a portion of the Mahajanga Basin of north-western Madagascar (from Bindellini and Dal Sasso, 2021); used with permission; modified). The material from the Sakaraha Formation (in light blue with dark blue dots) comes from several sites marked by the red asterisks. **3,** Paleogeographic map of what is now South America and Africa during the Late Jurassic (150 Mya; map from Ronald Blakey; modified). **4,** Geological map of Uruguay (from Soto *et al.*, 2020b); modified). The material from the Tacuarembó Formation (in blue) is marked by a red asterisk.

Figure 2. Geographic and stratigraphic distribution of the isolated abelisaurid teeth from the Cretaceous of Gondwana. **1,** Paleogeographic map of what is now South America, Africa and India during the Late Cretaceous (70 Mya; map from Ronald Blakey; modified). **2,** Geological map of the main Deccan Volcanic Province from Western India (from Prasad and Parmar, 2022; modified). The material from the Lameta Formation (in dark red) is marked by the black arrow and a red asterisk. **3,** Geological map of the Somuncurá-Cañadón Asfalto Basin, central Chubut Province, Patagonia (from Umazano *et al.*, 2017; modified). The material from the Bayo Overo Member (with black stripes) of the Cerro Barcino Formation probably comes

from the top right of the geological map. **4,** Geological map of the El Brete site, southern Salta Province, Northern Argentina (from Hendrickx *et al.*, 2024; modified). The material from the Lecho Formation (in dark blue) is marked by a yellow asterisk.

Figure 3. Results of the cladistic analyses performed on a revised version of Hendrickx *et al.*'s (2024) data matrix focused on the non-avian theropod dentition (148 dental characters scored in 127 saurischians) using a constrained tree and the dental material under study as floating OTUs. All specimens/morphotypes were recovered among ceratosaurs so that the figure is focused on this clade. Results of the cladistic analysis showing the whole theropod trees are available in the supplementary information. **1-2,** Strict consensus trees of **1,** eight; and **2,** 24 most parsimonious trees resulting from a cladistic analysis performed on the data matrix of 32 mesial crown-based characters using the first **1,** and **2,** second tree topology and all floating taxa. **3-4,** Strict consensus trees of **3,** 1712 and **4,** 371 most parsimonious trees resulting from a cladistic analysis performed on the data matrix of 56 lateral crown-based characters using **3,** the second tree topology and all floating taxa; and **4,** the first tree topology after the exclusion of PVL 3672 and MACN 18.172. Mada I, II, III, IV, V are the dental morphotypes I, II, III, IV, and V from the Middle Jurassic of Madagascar and Salta I, II, III are the dental morphotypes I, II, and III from the Upper Cretacerous of the Salta Province, Argentina. Black silhouettes by Scott Hartman (*Ceratosaurus* and *Majungasaurus*; CC BY-NC-SA 3.0), Tasman Dixon (*Masiakasaurus* and *Spectrovenator*; CC0 1.0 and CC BY 4.0, respectively), Jagged Fang Designs (*Ekrixinatosaurus*; CC0 1.0), and *Limusaurus* (from Wang *et al.*, 2017, modified).

Figure 4. Results of the machine learning analysis. The first thirteen graphs present the results for the teeth we aimed to classify into specific clades, using various datasets: the

complete dataset (light blue), the complete dataset restricted to large theropods (salmon), the personal dataset (green), and the personal dataset restricted to large theropods (dark blue). The second-to-last graph (bottom center) compares different algorithms across these datasets, showing the macro-accuracy for the best-performing model, such as Random Forests. Note that macro-accuracy remains relatively stable across algorithms. The last graph (bottom right) illustrates the percentage of correct identifications as Abelisauridae, summarizing the top predictions from each algorithm when all teeth sampled are grouped together. Theropod silhouettes by Scott Hartman (CC BY-NC 3.0 and CC BY-NC-SA 3.0).

Figure 5. Dental evolution in Ceratosauria. Dentition-based synapomorphies mapped on three topological trees representing alternative phylogenetic hypotheses of ceratosaur relationships following the topology obtained by **1,** Hendrickx *et al.* (2024); **2,** Pol *et al.* (2024); and **3,** Cau and Paterna (2025). Black circles indicate non-homoplasious changes (synapomorphies or autapomorphies; here restricted to the clade Ceratosauria) whereas white circles show homoplasies. Ceratosaur silhouettes by Julio Francisco Garza Lorenzo (*Dilophosaurus*; CC BY 3.0), Ville-Veikko Sinkkonen (*Limusaurus*; CC BY-NC-SA 3.0), de Souza *et al.* (2021; *Berthasaura*; modified), Tasman Dixon (*Spectrovenator*; CC0 1.0), and Scott Hartman (all others; CC BY-NC-SA 3.0).

Figure 6. Morphological disparity within Abelisauroidea across the Early–Late Cretaceous intervals, including WMPD values. **1,** WMPD based on the mesial dentition matrix; and **2,** WMPD based on the lateral dentition matrix. Skull silhouette of *Majungasaurus* from Sampson and Witmer (2007; modified).

Figure 7. Morphological disparity of Ceratosauria. **1,** Morphospace distribution based on the first two PCO axes, and PCO1 vs. PCO3 based on the mesial dentition matrix; and **2,** Morphospace distribution based on the first two PCO axes, and PCO1 vs. PCO3 based on the lateral dentition matrix. Filled convex hulls in 1 and 2 represent the two selected time bins: Early Cretaceous (light blue) and Late Cretaceous (light green). Convex hulls delimited by plain and dashed lines in 2 represent early branching abelisaurids (dashed lines) and the two abelisaurid subclades Abelisaurinae from South America (light green) and Majungasaurinae from India, Africa, and Europe (dark green).

Figure 8. Phylomorphospace in Ceratosauria illustrating the relationship between the logarithm of body length and PCo1, based on the reduced consensus tree from Hendrickx *et al.* (2024) with a time-calibrated topology. **1,** Phylomorphospace plotting based on the mesial dentition matrix; and **2,** phylomorphospace plotting based on the lateral dentition matrix.

Figure 9. Isolated abelisaurid teeth from the Bathonian (Middle Jurassic) Sakaraha Formation of the Mahajanga Basin, Madagascar. **1-8,** Mesialmost shed tooth crown (MSNM V5778; Morphotype I) in **1,** labial; **2,** lingual; **3,** distal; and **4,** mesial views; with close-up on **5,** distal; and **6,** mesial denticles at mid-crown in lateral view, and **7-8,** cross-sectional outlines at **4,** the crown-base; and **8,** mid-crown. **9-15,** Lateral shed tooth crown of an adult individual (MSNM V5779; Morphotype III) in **9,** labial; **10,** lingual; **11,** distal; and **12,** mesial views; with close-up on **13,** distal; and **14,** mesial denticles at mid-crown in lateral view; and **15,** cross-sectional outline at the crown-base. **16-22,** Lateral shed tooth crown of a possible juvenile individual (MSNM V5799; Morphotype IV) in **15,** labial; **17,** lingual; **18,** distal; and **19,** mesial views; with close-up on **20,** the distal; and **21,** mesial denticles at mid-crown in lateral view; and **22,** cross-sectional outline at the crown-base. Abbreviations: **cos,** concave surface; **dca,** distal

carina; **hod,** hooked denticle; **las,** labial surface; **lis,** lingual surface; **ids,** interdenticular sulcus; **mca,** mesial carina; **tun,** transverse undulation. Scale bars equal 1 cm (1-4, 9-12), 5 mm (16-19), and 1 mm (5-6, 13-14, 20-21).

Figure 10. Possible isolated abelisaurid tooth (cf. Abelisauridae; MGT-1161) from the Kimmeridgian? (Upper Jurassic) Tacuarembó Formation of Tacuarembó city, Uruguay. **1-8,** Lateral shed tooth crown in **1,** labial; **2,** lingual; **3,** mesial; **4,** distal, **5,** basal; and **6,** apical views; with close-up on **7,** distal denticles; and **8,** enamel surface texture in lateral views. Abbreviations: **dca,** distal carina; **ens,** enamel surface texture, **hod,** hooked denticle; **ids,** interdenticular sulcus; **mca,** mesial carina; **tun,** transverse undulation. Scale bars equal 1 cm (1-6), 5 mm (8), and 1 mm (7).

Figure 11. Probable isolated abelisaurid tooth (cf. Abelisauridae; MACN 18.172; "*Megalosaurus inexpectatus*" of del Corro 1966) from the Cenomanian (Upper Cretaceous) Cerro Barcino Formation of Cerro Barcino, Chubut Province, Patagonia, Argentina. **1-9,** Lateral shed tooth crown in **1,** lingual; **2,** labial; **3,** distal; **4,** mesial, **5,** basal; and **6,** apical views; with close-up on **7,** the distocentral; and **8,** mesio-apical denticles; and **9,** the enamel surface texture in lateral views. Abbreviations: **dca,** distal carina; **mca,** mesial carina. Scale bars equal 1 cm (1-6) and 2 mm (7-9).

Figure 12. Isolated abelisaurid teeth from the Campanian–Maastrichtian (Upper Cretaceous) Los Blanquitos Formation of La Candelaria, Salta Province, northern Argentina. **1-6,** Lateral shed tooth crown (PVL 4173; Morphotype III) in **1,** labial; **2,** lingual; **3,** distal; **4,** mesial; **5,** apical; and **6,** basal views. **7-10,** Lateral? shed tooth crown (PVL 4174; Morphotype III?) in **7,** labial; **8,** lingual; and **9,** basal views; with close-up on **10,** the mesial denticles at mid-crown

2125 in lateral view. **11-16,** Transitional shed tooth crown (PVL 4175; Morphotype II) in **11,** labial;
2126 **12,** lingual; **15,** apical; and **16,** basal views; with close-up on **13,** the distal; and **14,** mesial
2127 denticles at mid-crown in lateral view. Abbreviations: **dca,** distal carina; **hod,** hooked
2128 denticle; **ids,** interdenticular sulcus; **mca,** mesial carina. Scale bars equal 1 cm (1-6, 7-10, 11-
2129 12, 15-16) and 1 mm (9, 13-14).
2130
2131 **Figure 13.** Isolated abelisaurid teeth from the Maastrichtian (Upper Cretaceous) Lecho
2132 Formation of El Brete, Salta Province, northern Argentina. **1-7,** Lateral shed tooth crown
2133 (PVL 4062-1; Morphotype III) in **1,** lingual; **2,** labial; **3,** mesial; **4,** distal; **5,** basal; and **6,**
2134 apical views; with close up on **7,** distal denticles in lateral view. **8-14,** Lateral shed tooth
2135 crown (PVL 4062-2; Morphotype III) in **8,** lingual; **10,** labial; **11,** mesial; **12,** distal; **13,** basal;
2136 and **14,** apical views; with close-up on **9,** the enamel surface texture and distocentral denticles
2137 at mid-crown in lateral view. **15-17,** Transitional tooth (PVL 4062-4; Morphotype II) in **15,**
2138 labial; **16,** distal; and **17,** apical views. **18-25,** Mesialmost shed tooth crown (PVL 4062-5;
2139 Morphotype I) in **18,** labial; **19,** lingual; **20,** mesial; **21,** mesial, **24,** basal; and **25,** apical
2140 views; with close-up on **22,** distocentral; and **23,** mesiocentral denticles in lateral view.
2141 Abbreviations: **dca,** distal carina; **ids,** interdenticular sulcus; **mca,** mesial carina; **mun,**
2142 marginal undulation; **tun,** transverse undulation. Scale bars equal 1 cm (1-6, 8, 10-21, 24-25)
2143 and 1 mm (7, 9, 22-23).
2144
2145 **Figure 14.** Isolated abelisaurid tooth (PVL 3672) from the Maastrichtian (Upper Cretaceous)
2146 Yacoraite Formation of La Candelaria, Salta Province, Northern Argentina. **1-9,** lateral shed
2147 tooth crown in **1,** labial; **2,** lingual; **3,** mesial; **4,** distal, **5,** basal; and **6,** apical views; with
2148 close-up on **7,** the mesioapical and, **8,** distocentral denticles; and **9,** the enamel surface texture

in lateral views. Abbreviations: **hod,** hooked denticle; **mca,** mesial carina. Scale bars equal 1 cm (1-6) and 1 mm (7-9).

Figure 15. Isolated abelisaurid and possible majungasaurine tooth (NHMUK R4190; '*Massospondylus rawesi*' of Lydekker, 1890) from the Maastrichtian (Upper Cretaceous) Lameta Formation of Takli, Nagpur area, Maharashtra State, India. **1-9,** Lateral shed tooth crown in **1,** labial; **2,** lingual; **3,** mesial; **4,** distal, **5,** basal; and **6,** apical views; with close-up on **7,** mesial, and **8,** distal denticles at mid-crown; and **9,** enamel surface texture in lateral views. Abbreviation: **mca,** mesial carina. Scale bars equal 1 cm (1-6) and 1 mm (7-9).

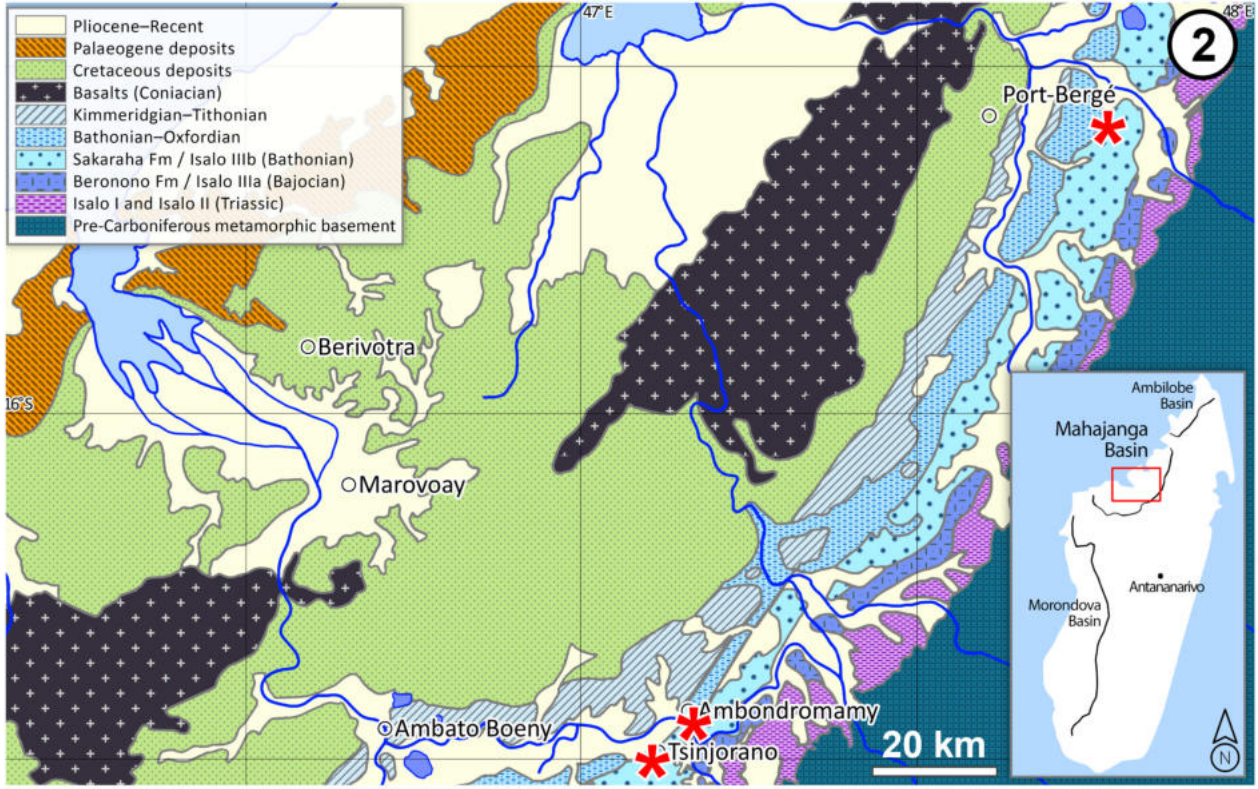
Figure 16. Isolated theropod teeth from early discoveries in Africa, South America, and Europe. **1-4,** Two *Majungasaurus* shed tooth crowns referred to *Megalosaurus crenatissimus* by Depéret (1896a) and representing the earliest body fossils of a non-avian theropod published in the literature from Africa; **1-2,** are illustrations by Depéret (1896a, plate 6, figs. 4-5) showing the teeth in lateral (4, 5) and basal (4a, 5a) views; and **3-4,** are photos of the original teeth (FSL 92.306) by Krause *et al.* (2007: fig. 4A; modified) in lateral view (scale bar equals 1 cm). **5-6,** Isolated theropod tooth in lateral view from the Cenomanian Mata Amarilla Formation of Par-Aik, Santa Cruz Province, Argentina, referred to *Loncosaurus argentinus* by Ameghino (1899) and representing the first theropod dental material to be described in the literature in South America; **5,** are from Ameghino (1900, p. 160) and Ameghino (1906: fig. 8); and **6,** are from Huene (1929, plate 41). **7-8,** Isolated theropod tooth from the Campanian Gosau Beds of Muthmannsdorf, Austria, referred by Seeley (1881) as *Megalosaurus pannoniensis* and thought by Buffetaut (2025b) to possibly represent the first abelisaurid remains from Europe; **7,** illustration by Seeley (1881) showing the tooth in lateral

and mesial views; and **8,** photo of the original tooth by Ősi *et al.* (2010: fig. 2A) in lateral view (scale bar equals 5 mm).

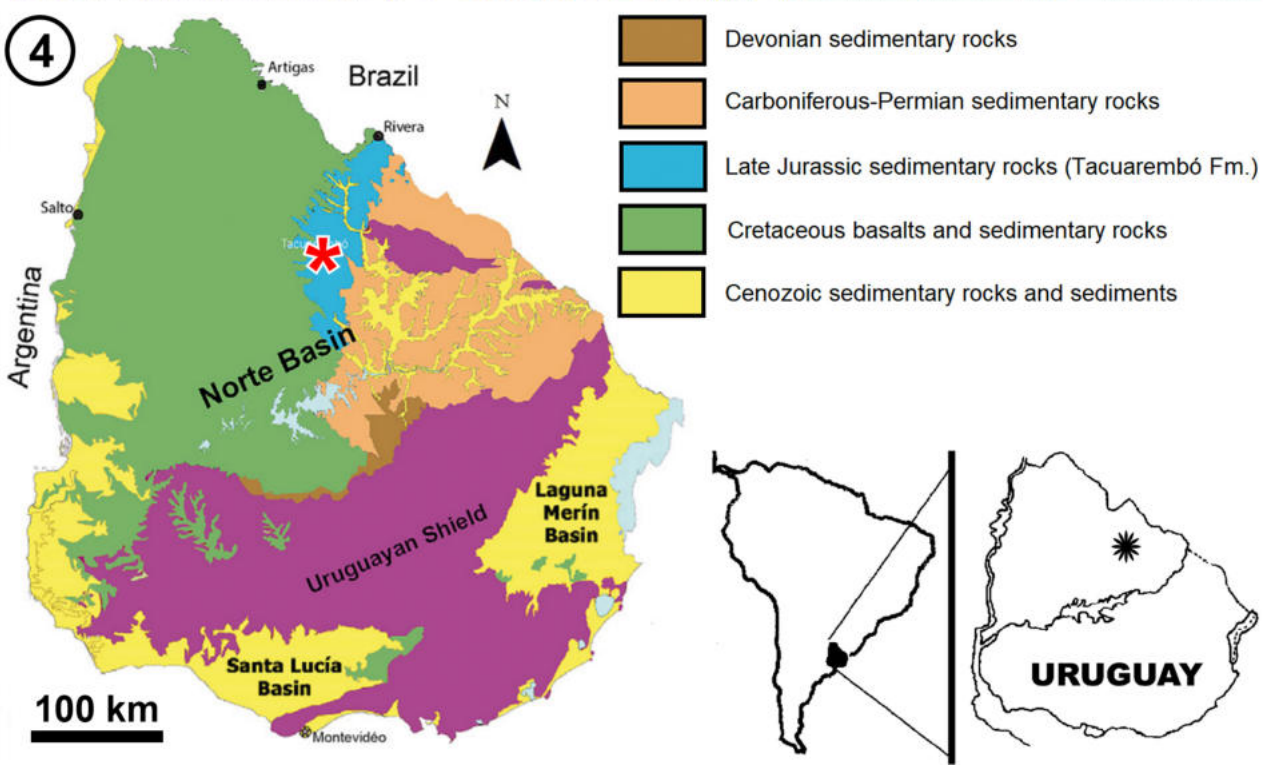
APPENDIX. SUPPLEMENTARY INFORMATION

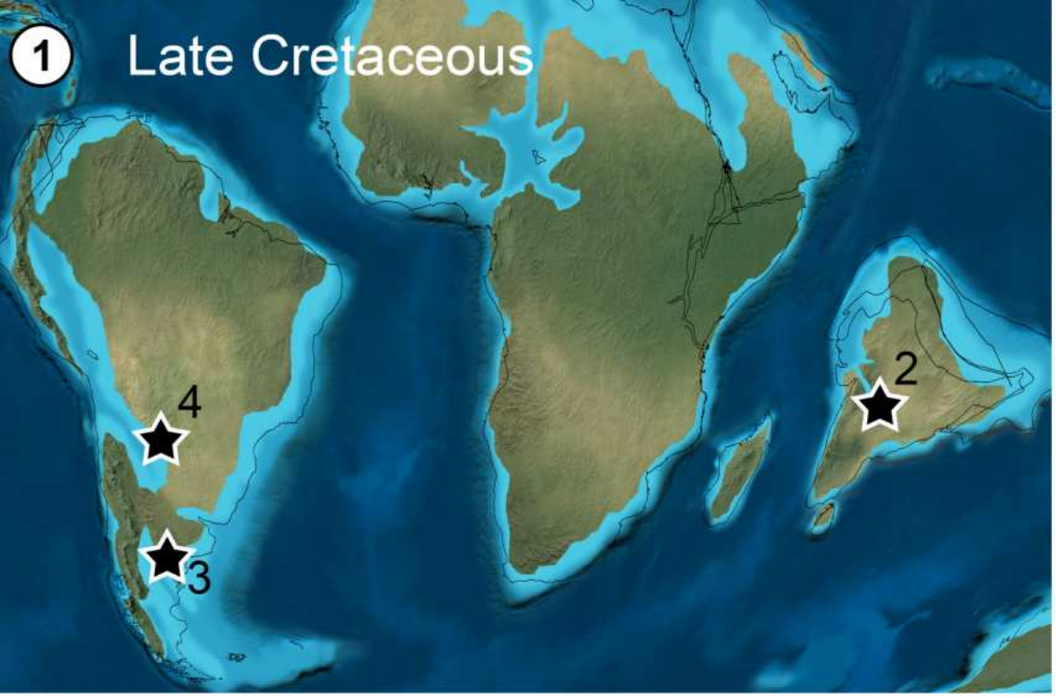
Supplementary information related to this article includes Appendix 1 with an illustration of the second and fifth dental morphotypes from Middle Jurassic of Madagascar, the files used in the phylogenetic and machine learning analyses, and the results of these analyses.

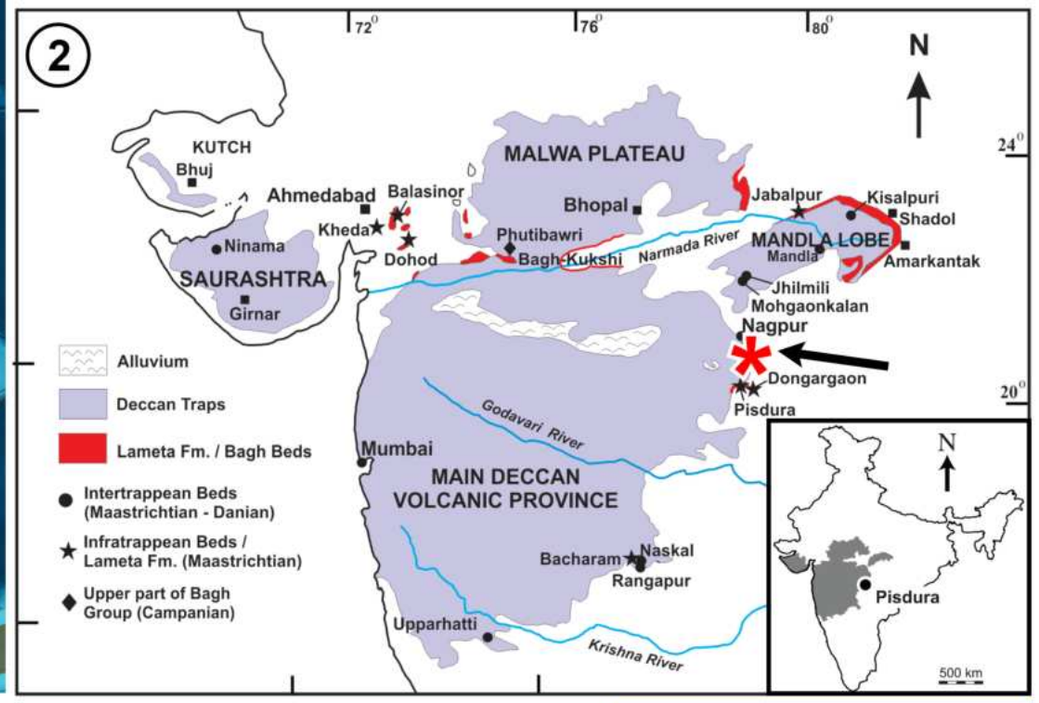

1
Middle Jurassic

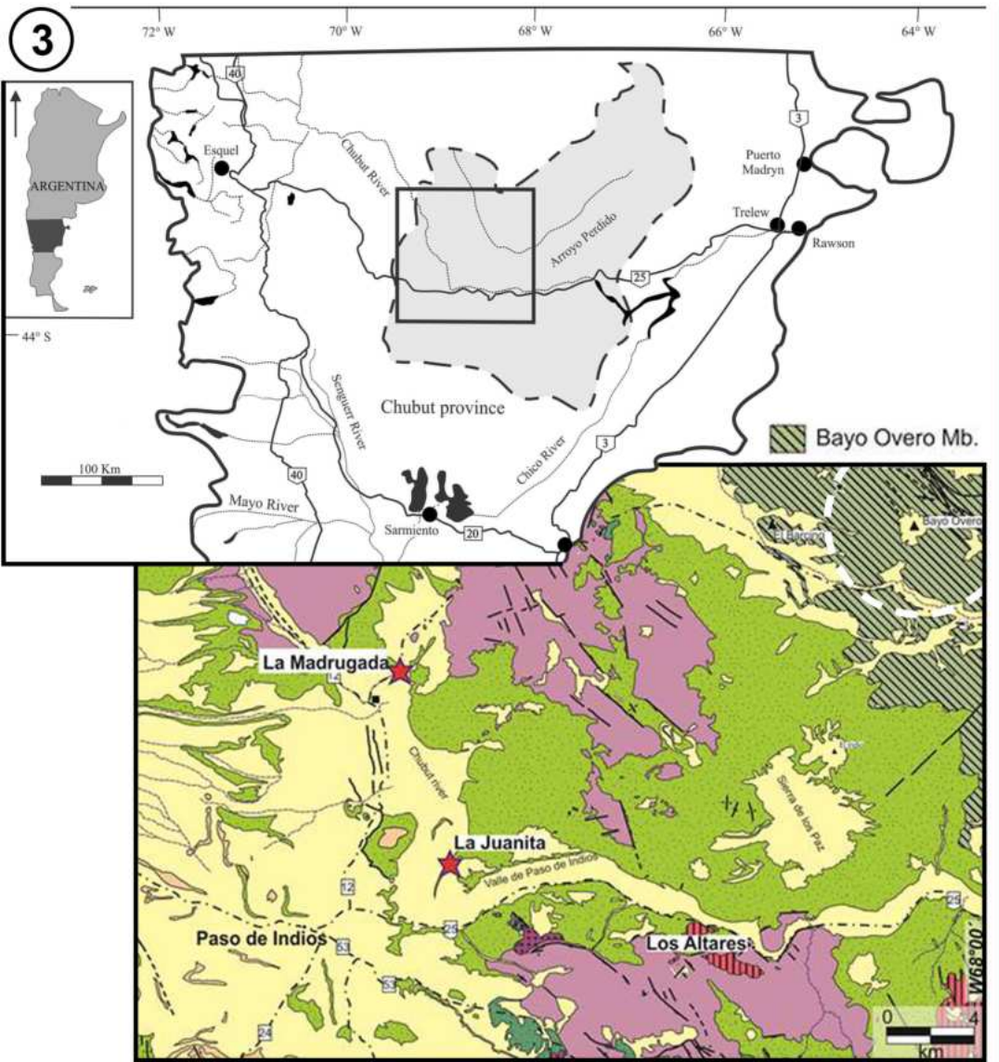

2
Pliocene–Recent
Palaeogene deposits
Cretaceous deposits
Basalts (Coniacian)
Kimmeridgian–Tithonian
Bathonian–Oxfordian
Sakaraha Fm / Isalo IIIb (Bathonian)
Beronono Fm / Isalo IIIa (Bajocian)
Isalo I and Isalo II (Triassic)
Pre-Carboniferous metamorphic basement
47°E
48°E
16°S
Port-Bergé
Berivotra
Marovoay
Ambato Boeny
Ambondromamy
Tsinjorano
20 km
Ambilobe Basin
Mahajanga Basin
Antananarivo
Morondova Basin
N

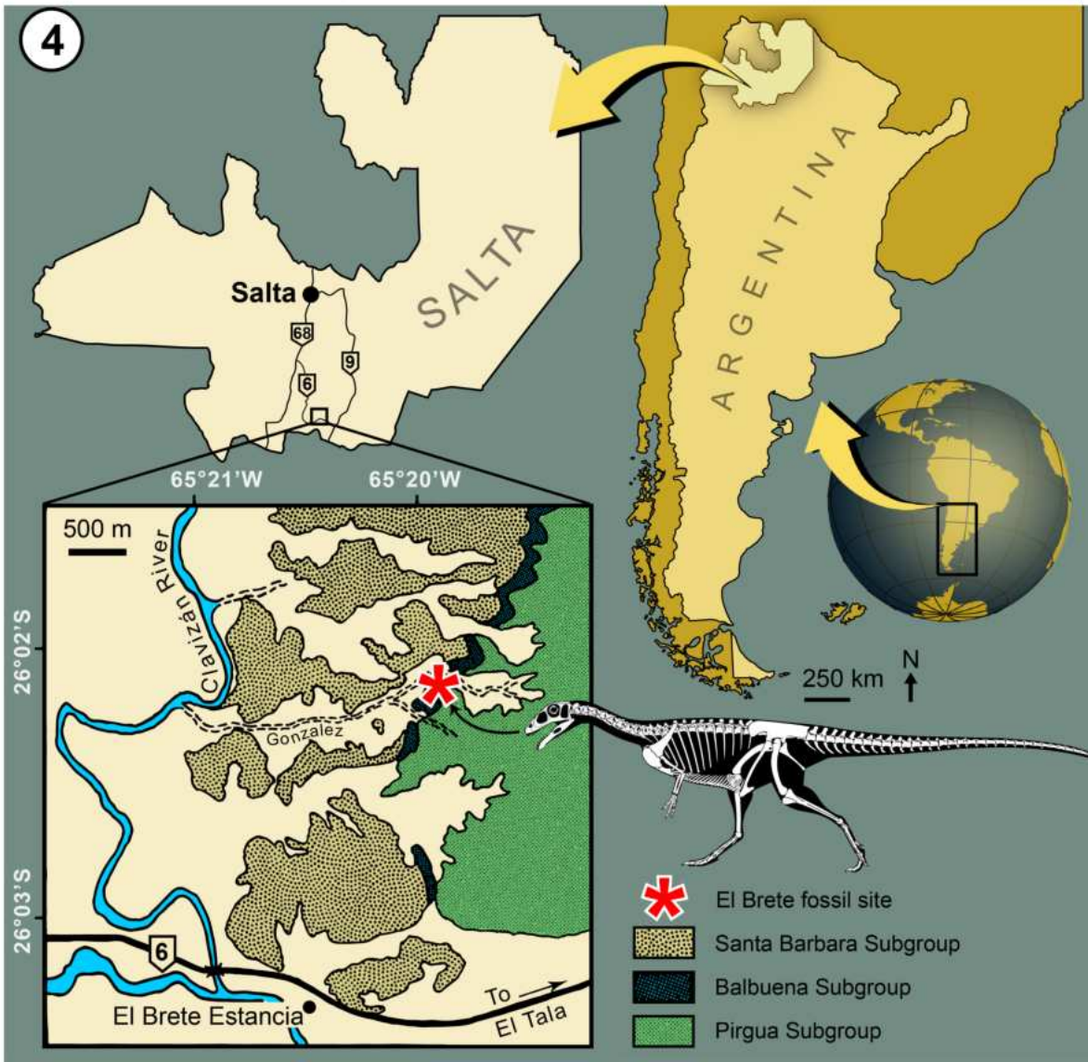

3
Late Jurassic


4
Artigas
Brazil
N
Rivera
Salto
Argentina
Norte Basin
Uruguayan Shield
Laguna Merín Basin
Santa Lucía Basin
100 km
Montevidéo
Devonian sedimentary rocks
Carboniferous-Permian sedimentary rocks
Late Jurassic sedimentary rocks (Tacuarembó Fm.)
Cretaceous basalts and sedimentary rocks
Cenozoic sedimentary rocks and sediments
URUGUAY


1
Late Cretaceous
2
3
4


2
72°
76°
80°
24°
20°
N
KUTCH
Bhuj
Ahmedabad
Balasinor
Kheda
Dohod
Ninama
SAURASHTRA
Girnar
MALWA PLATEAU
Bhopal
Jabalpur
Kisalpuri
Shadol
Phutibawri
Bagh-Kukshi
Narmada River
MANDLA LOBE
Mandla
Amarkantak
Jhilmili
Mohgaonkalan
Nagpur
Dongargaon
Pisdura
Godavari River
Mumbai
MAIN DECCAN
VOLCANIC PROVINCE
Bacharam
Naskal
Rangapur
Upparhatti
Krishna River
Alluvium
Deccan Traps
Lameta Fm. / Bagh Beds
Intertrappean Beds
(Maastrichtian - Danian)
Infratrappean Beds /
Lameta Fm. (Maastrichtian)
Upper part of Bagh
Group (Campanian)
N
Pisdura
500 km


3
72° W
70° W
68° W
66° W
64° W
ARGENTINA
44° S
Esquel
Chubut River
Arroyo Perdido
Puerto
Madryn
Trelew
Rawson
Chubut province
Bayo Overo Mb.
Senguerr River
Chico River
Mayo River
Sarmiento
100 Km
La Madrugada
La Juanita
Paso de Indios
Los Altares
Bayo Overo
Sierra de los Paz
0
4
km


4
Salta
SALTA
ARGENTINA
65°21'W
65°20'W
500 m
26°02'S
26°03'S
Clavijan River
Gonzalez
6
El Brete Estancia
To
El Tala
250 km
N
El Brete fossil site
Santa Barbara Subgroup
Balbuena Subgroup
Pirgua Subgroup

1

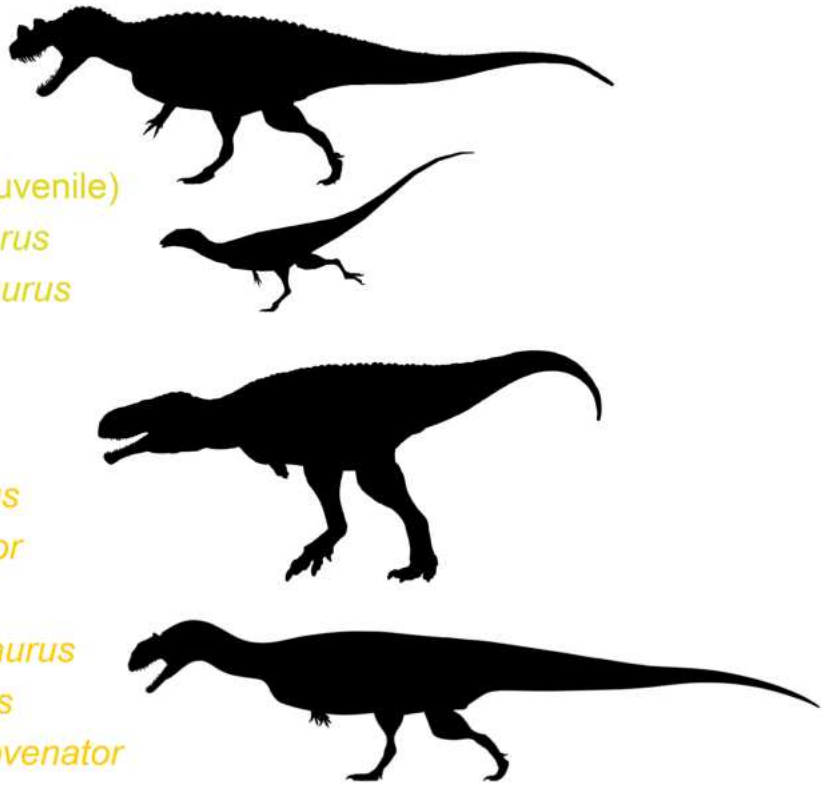
- *Limusaurus* (juvenile)
- *Genyodectes*
- *Ceratosaurus*
- *Vespersaurus*
- *Masiakasaurus*
- *Spectrovenator*
- Salta II
- Salta I
- Mada I
- *Chenanisaurus*
- Mada II
- *Majungasaurus*
- *Indosuchus*
- *Skorpiovenator*
- *Abelisaurus*

Abelisauridae

2

- *Genyodectes*
- *Ceratosaurus*
- *Limusaurus* (juvenile)
- *Vespersaurus*
- *Masiakasaurus*
- Salta II
- Salta I
- Mada I
- *Chenanisaurus*
- *Spectrovenator*
- Mada II
- *Majungasaurus*
- *Indosuchus*
- *Skorpiovenator*
- *Abelisaurus*

Abeli-sauridae



3

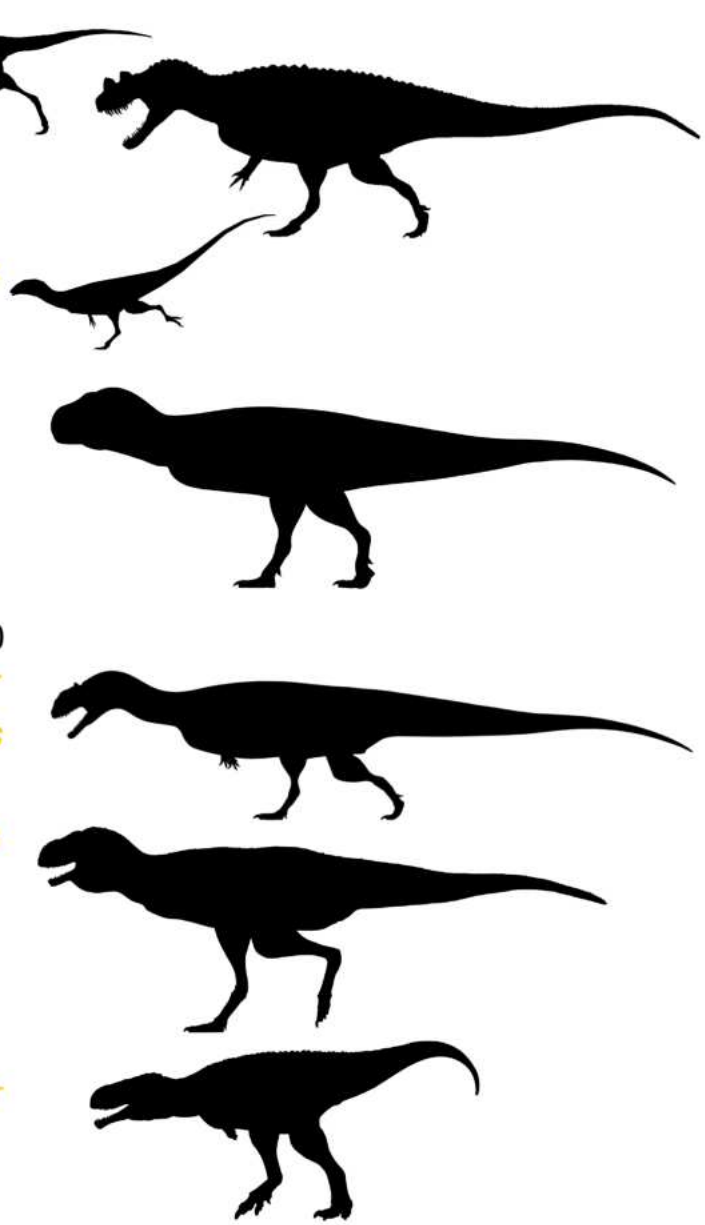
- *Berberosaurus*
- *Genyodectes*
- *Ceratosaurus*
- PVL 3672
- Salta III
- Mada V
- Mada IV
- Mada III
- MGT 1161
- MACN 18.172
- NHMUK R4190
- *Skorpiovenator*
- *Majungasaurus*
- *Indosuchus*
- *Chenanisaurus*
- *Arcovenator*
- *Aucasaurus*
- *Abelisaurus*
- *Rugops*
- *Llukalkan*
- *Kryptops*
- *Spectrovenator*
- *Masiakasaurus*
- *Noasaurus*
- *Limusaurus* (juvenile)

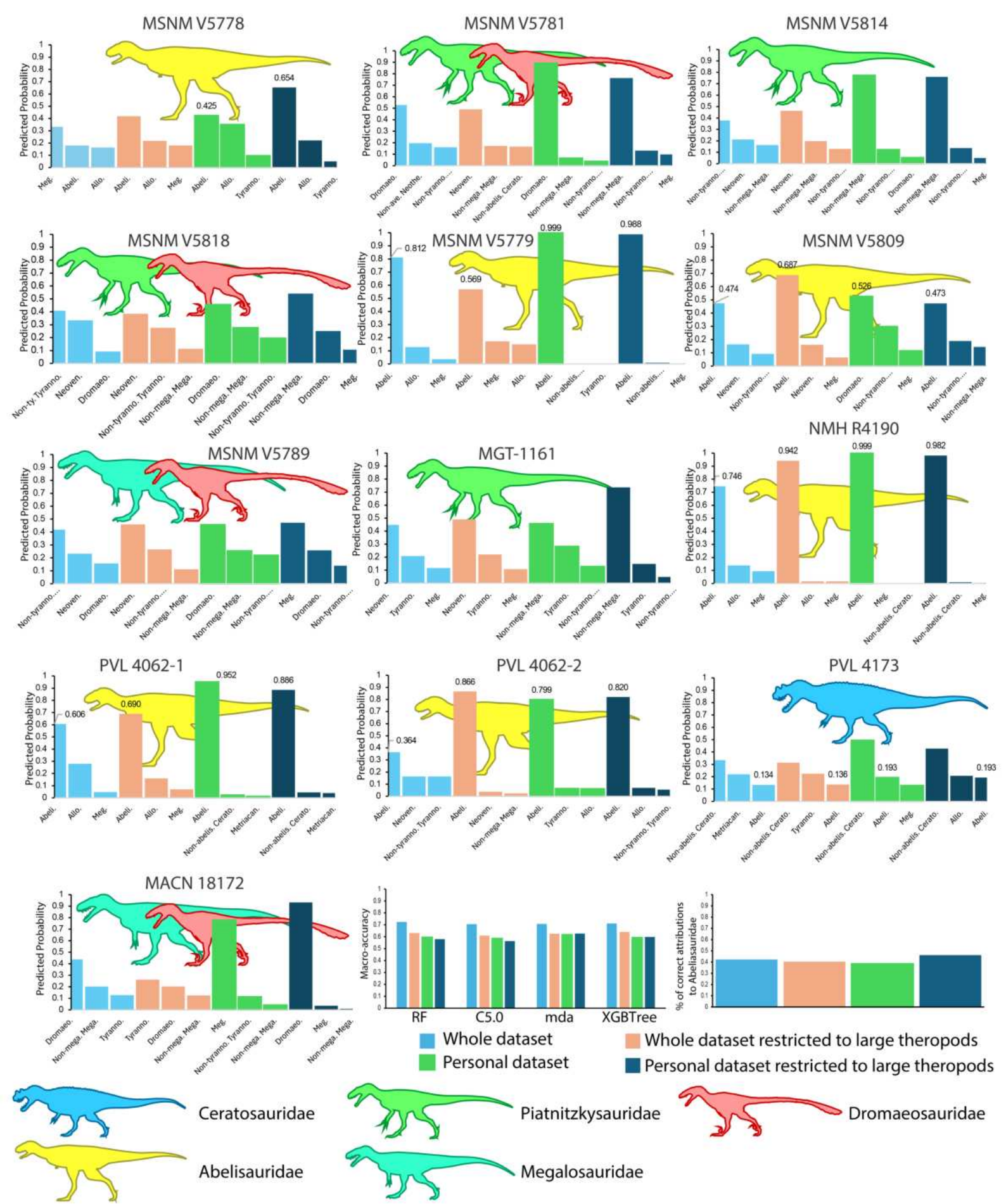
Abeli-sauroidea

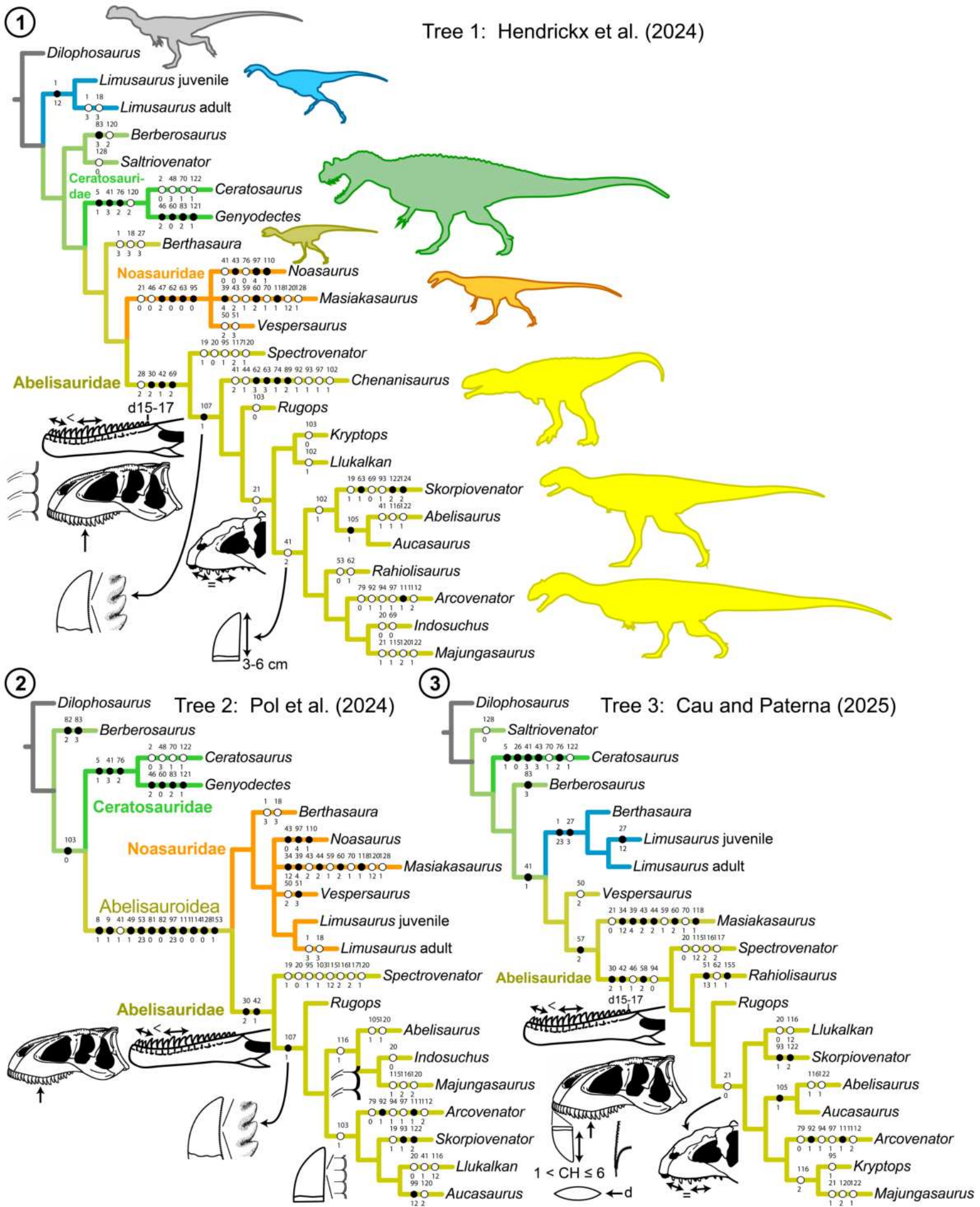
4

- *Limusaurus* (juvenile)
- *Genyodectes*
- *Ceratosaurus*
- *Berberosaurus*
- *Masiakasaurus*
- *Noasaurus*
- Salta III
- Mada V
- Mada IV
- Mada III
- MGT 1161
- NHMUK R4190
- *Skorpiovenator*
- *Majungasaurus*
- *Indosuchus*
- *Chenanisaurus*
- *Arcovenator*
- *Aucasaurus*
- *Abelisaurus*
- *Rugops*
- *Spectrovenator*
- *Llukalkan*
- *Kryptops*

Abelisauridae




MSNM V5778
MSNM V5781
MSNM V5814
MSNM V5818
MSNM V5779
MSNM V5809
MSNM V5789
MGT-1161
NMH R4190
PVL 4062-1
PVL 4062-2
PVL 4173
MACN 18172
Predicted Probability
Macro-accuracy
% of correct attributions to Abeliasauridae
RF
C5.0
mda
XGBTree
Whole dataset
Personal dataset
Whole dataset restricted to large theropods
Personal dataset restricted to large theropods
Ceratosauridae
Abelisauridae
Piatnitzkysauridae
Megalosauridae
Dromaeosauridae


1
Tree 1: Hendrickx et al. (2024)
Dilophosaurus
Limusaurus juvenile
Limusaurus adult
Berberosaurus
Saltriovenator
Ceratosauri-
dae
Ceratosaurus
Genyodectes
Berthasaura
Noasauridae
Noasaurus
Masiakasaurus
Vespersaurus
Abelisauridae
Spectrovenator
Chenanisaurus
Rugops
Kryptops
Llukalkan
Skorpiovenator
Abelisaurus
Aucasaurus
Rahiolisaurus
Arcovenator
Indosuchus
Majungasaurus
d15-17
3-6 cm
2
Tree 2: Pol et al. (2024)
Dilophosaurus
Berberosaurus
Ceratosaurus
Genyodectes
Ceratosauridae
Berthasaura
Noasauridae
Noasaurus
Masiakasaurus
Vespersaurus
Abelisauroidea
Limusaurus juvenile
Limusaurus adult
Spectrovenator
Abelisauridae
Rugops
Abelisaurus
Indosuchus
Majungasaurus
Arcovenator
Skorpiovenator
Llukalkan
Aucasaurus
3
Tree 3: Cau and Paterna (2025)
Dilophosaurus
Saltriovenator
Ceratosaurus
Berberosaurus
Berthasaura
Limusaurus juvenile
Limusaurus adult
Vespersaurus
Masiakasaurus
Spectrovenator
Abelisauridae
Rahiolisaurus
d15-17
Rugops
Llukalkan
Skorpiovenator
Abelisaurus
Aucasaurus
Arcovenator
Kryptops
Majungasaurus
1 < CH ≤ 6
d

① Mesial

Disparity (WMPD)

0.55

0.50

0.45

0.40

0.35

② Lateral

Disparity (WMPD)

0.6

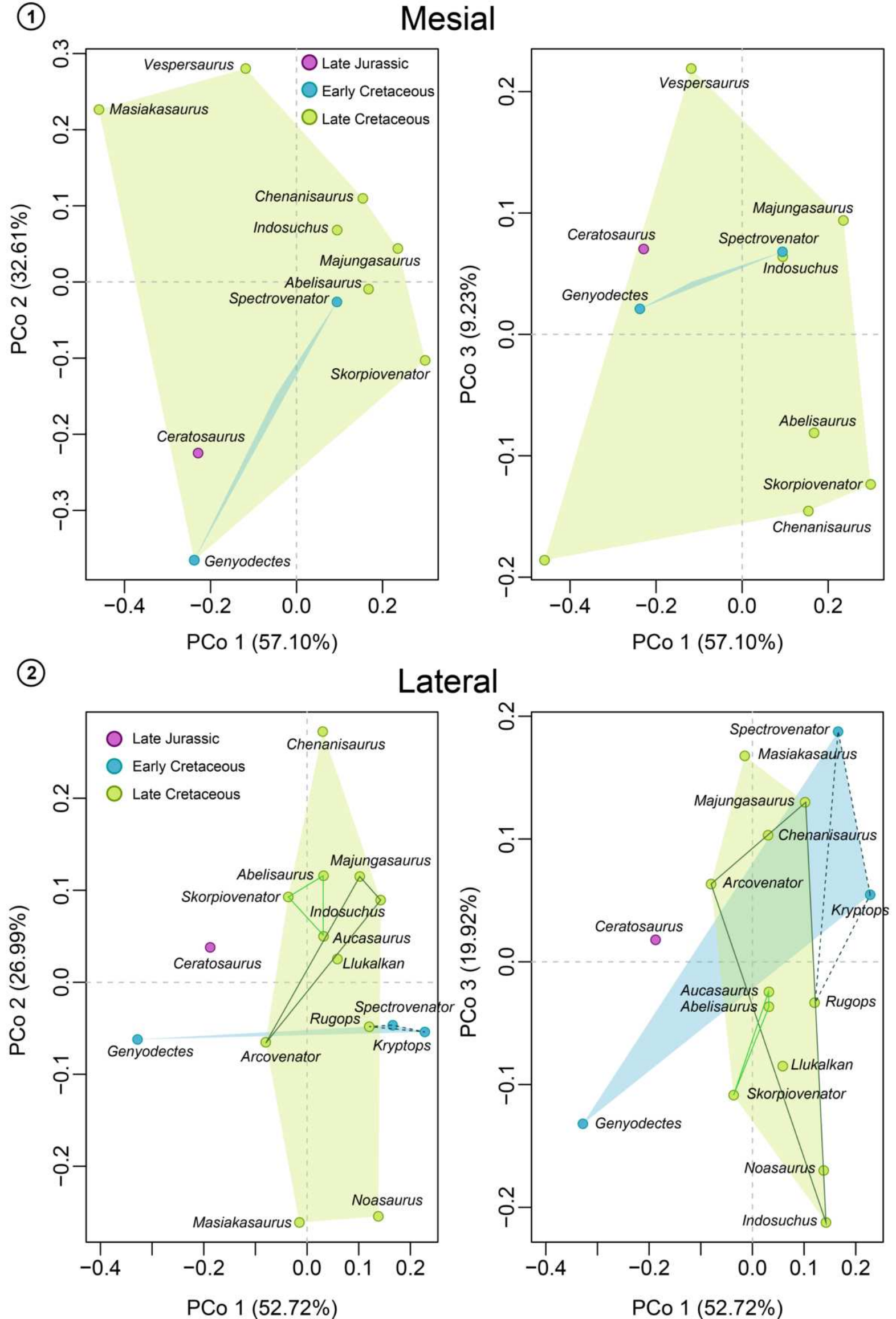
0.5

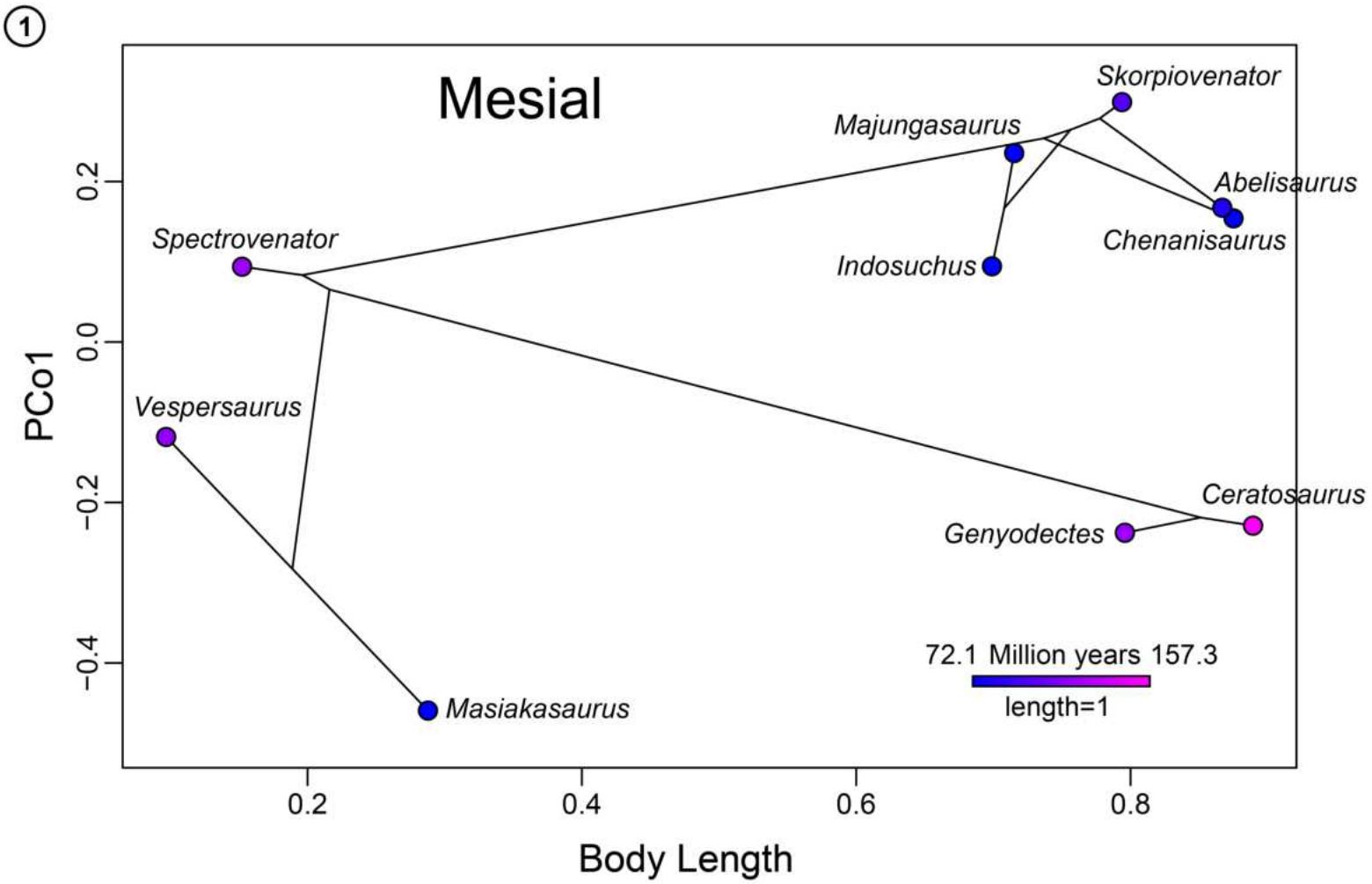
0.4

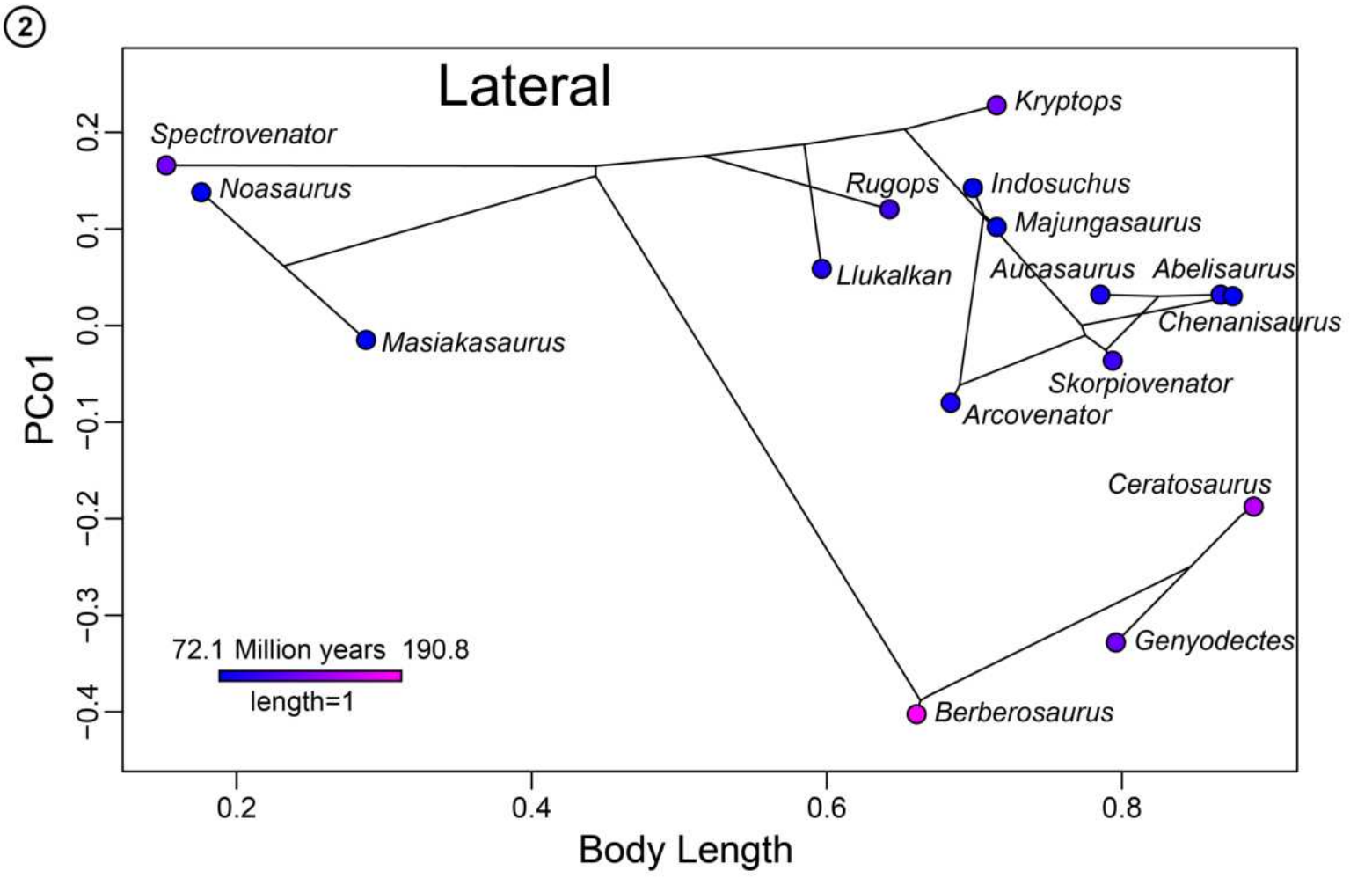
0.3

Ber	Val	Ha	Bar	Apt	Alb	Cen	Tur	Co	Sa	Cam	Maa
Lower						Upper					
Cretaceous											

145 140 130 120 110 100 90 80 70 66


1
Mesial
Late Jurassic
Early Cretaceous
Late Cretaceous
Vespersaurus
Masiakasaurus
Chenanisaurus
Indosuchus
Majungasaurus
Abelisaurus
Spectrovenator
Skorpiovenator
Ceratosaurus
Genyodectes
PCo 2 (32.61%)
PCo 1 (57.10%)
PCo 3 (9.23%)
PCo 1 (57.10%)
2
Lateral
Late Jurassic
Early Cretaceous
Late Cretaceous
Chenanisaurus
Majungasaurus
Abelisaurus
Skorpiovenator
Indosuchus
Aucasaurus
Llukalkan
Ceratosaurus
Spectrovenator
Rugops
Kryptops
Genyodectes
Arcovenator
Noasaurus
Masiakasaurus
PCo 2 (26.99%)
PCo 1 (52.72%)
PCo 3 (19.92%)
PCo 1 (52.72%)


1
Mesial
Skorpiovenator
Majungasaurus
Abelisaurus
Chenanisaurus
Spectrovenator
Indosuchus
Vespersaurus
Ceratosaurus
Genyodectes
Masiakasaurus
72.1 Million years 157.3
length=1
PCo1
0.2
0.0
−0.2
−0.4
0.2
0.4
0.6
0.8
Body Length


2
Lateral
Kryptops
Spectrovenator
Noasaurus
Rugops
Indosuchus
Majungasaurus
Llukalkan
Aucasaurus
Abelisaurus
Chenanisaurus
Masiakasaurus
Skorpiovenator
Arcovenator
Ceratosaurus
Genyodectes
72.1 Million years 190.8
length=1
Berberosaurus
PCo1
0.2
0.1
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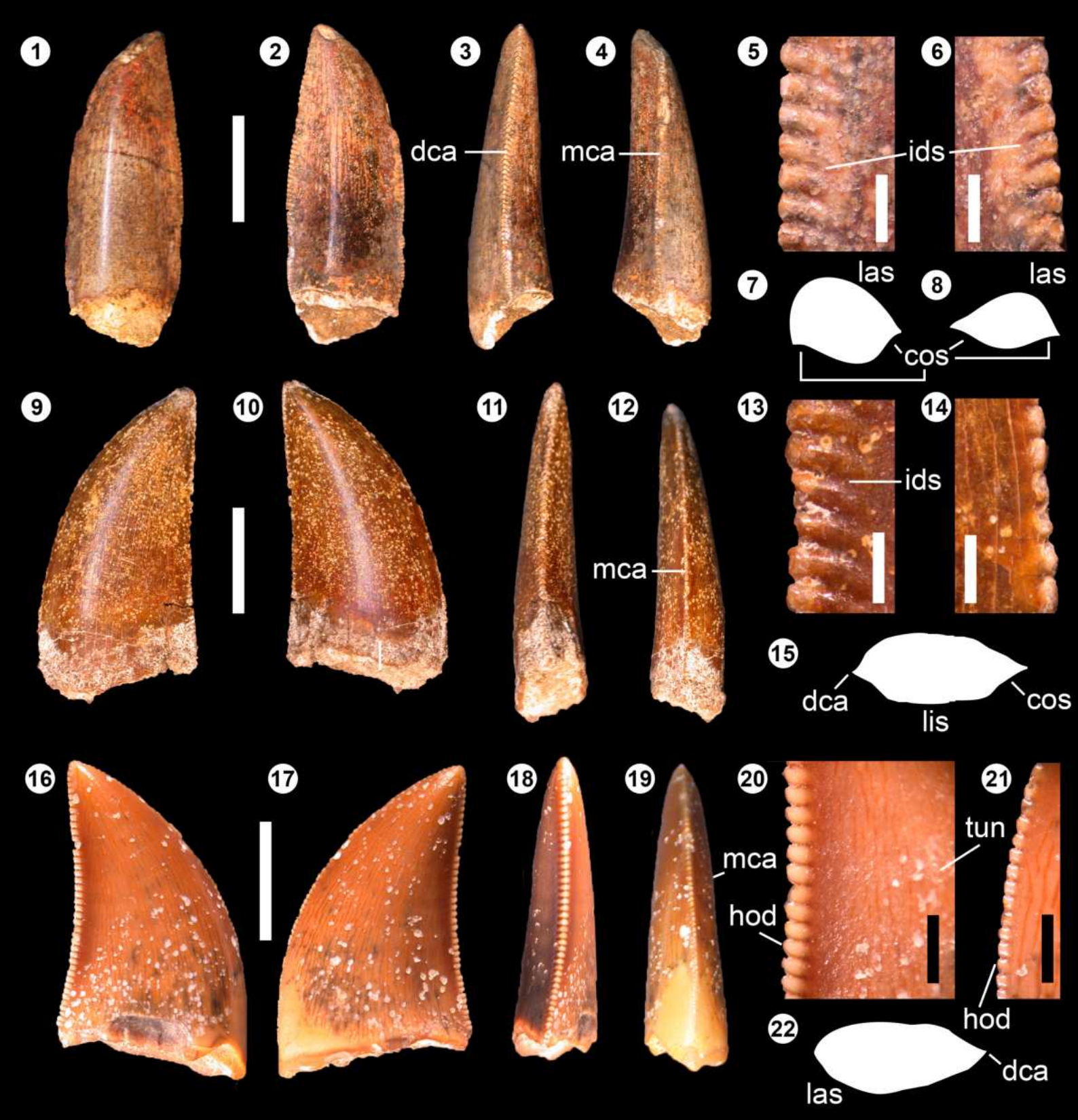
−0.1
−0.2
−0.3
−0.4
0.2
0.4
0.6
0.8
Body Length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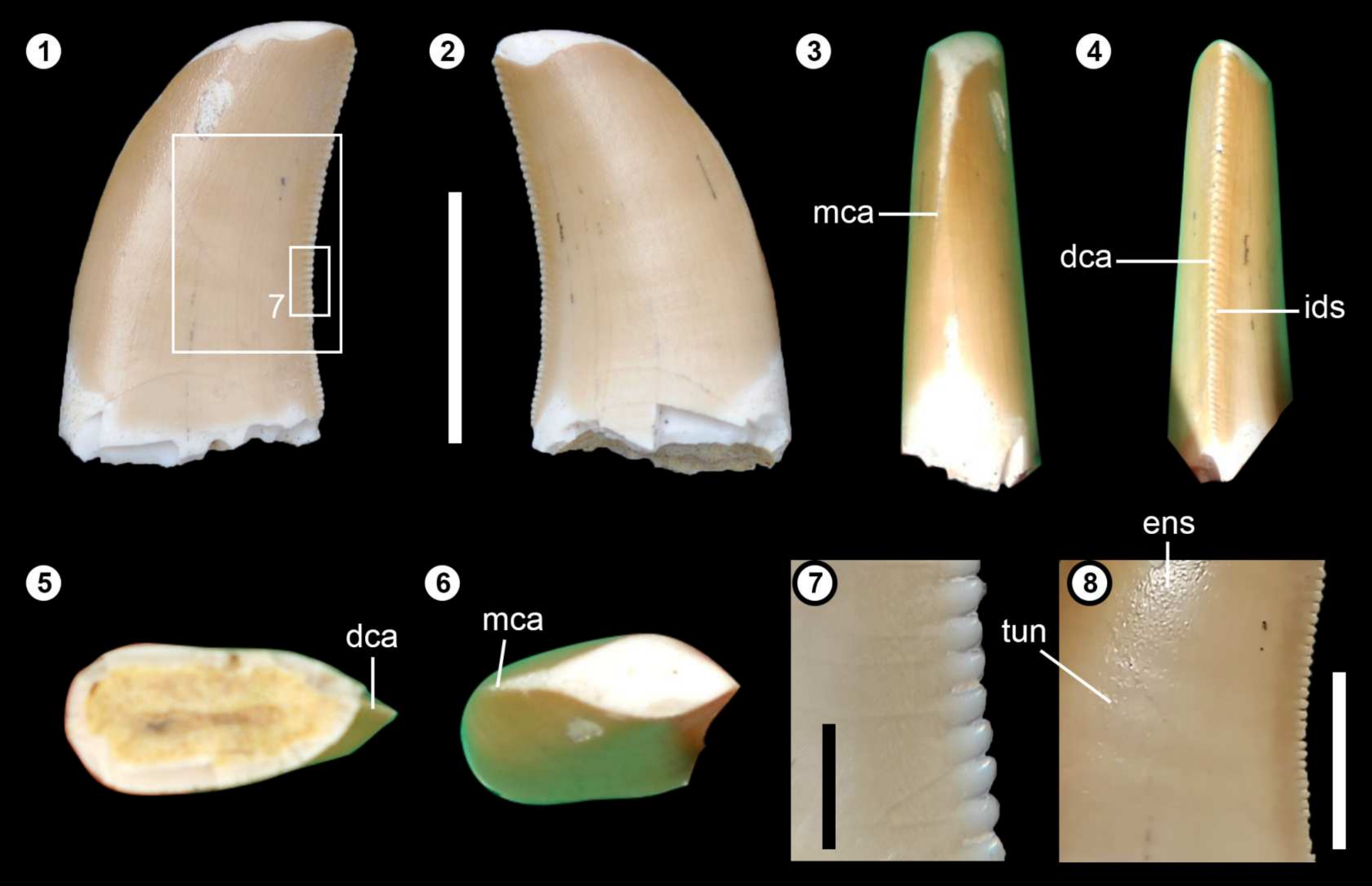
dca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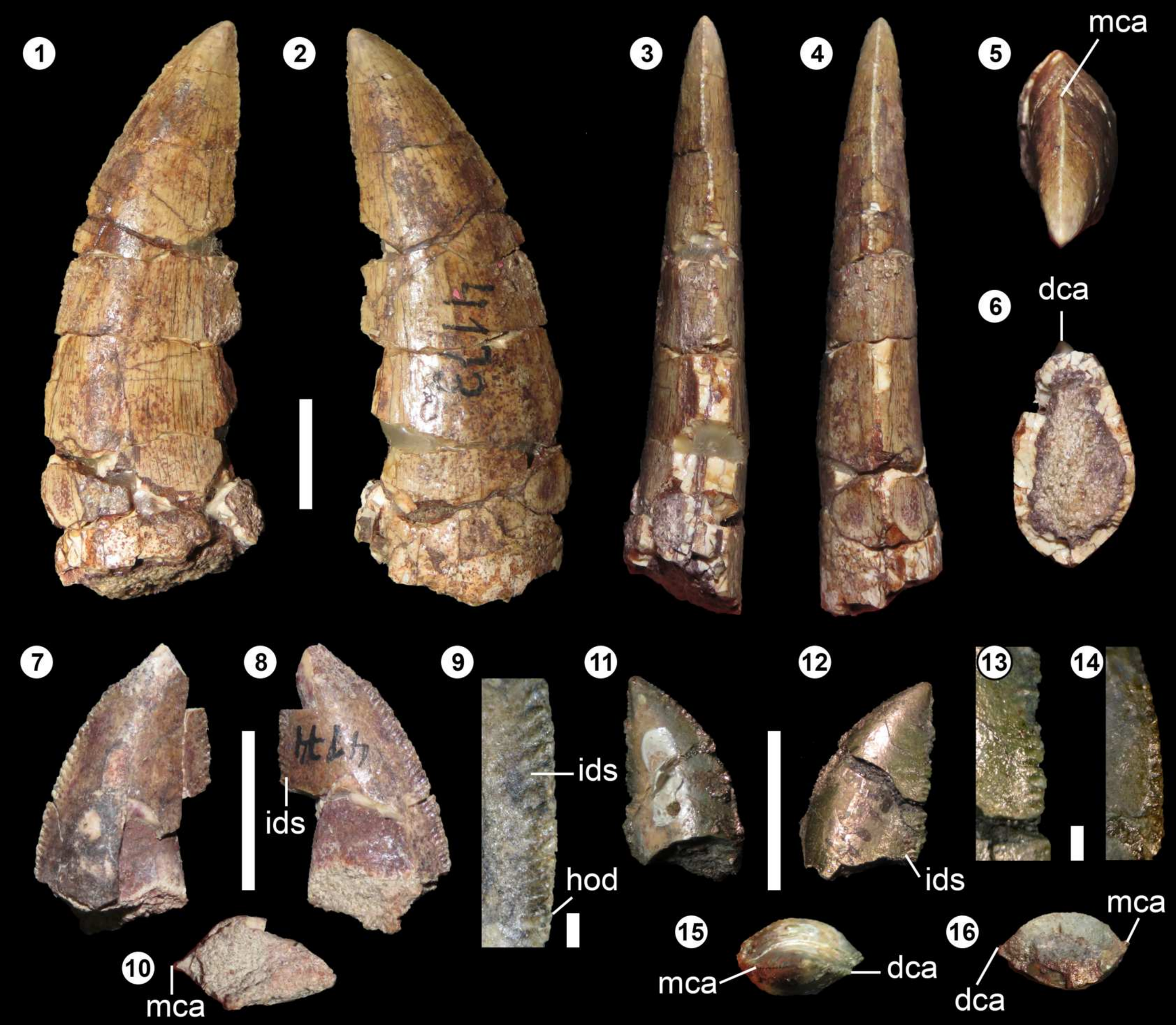
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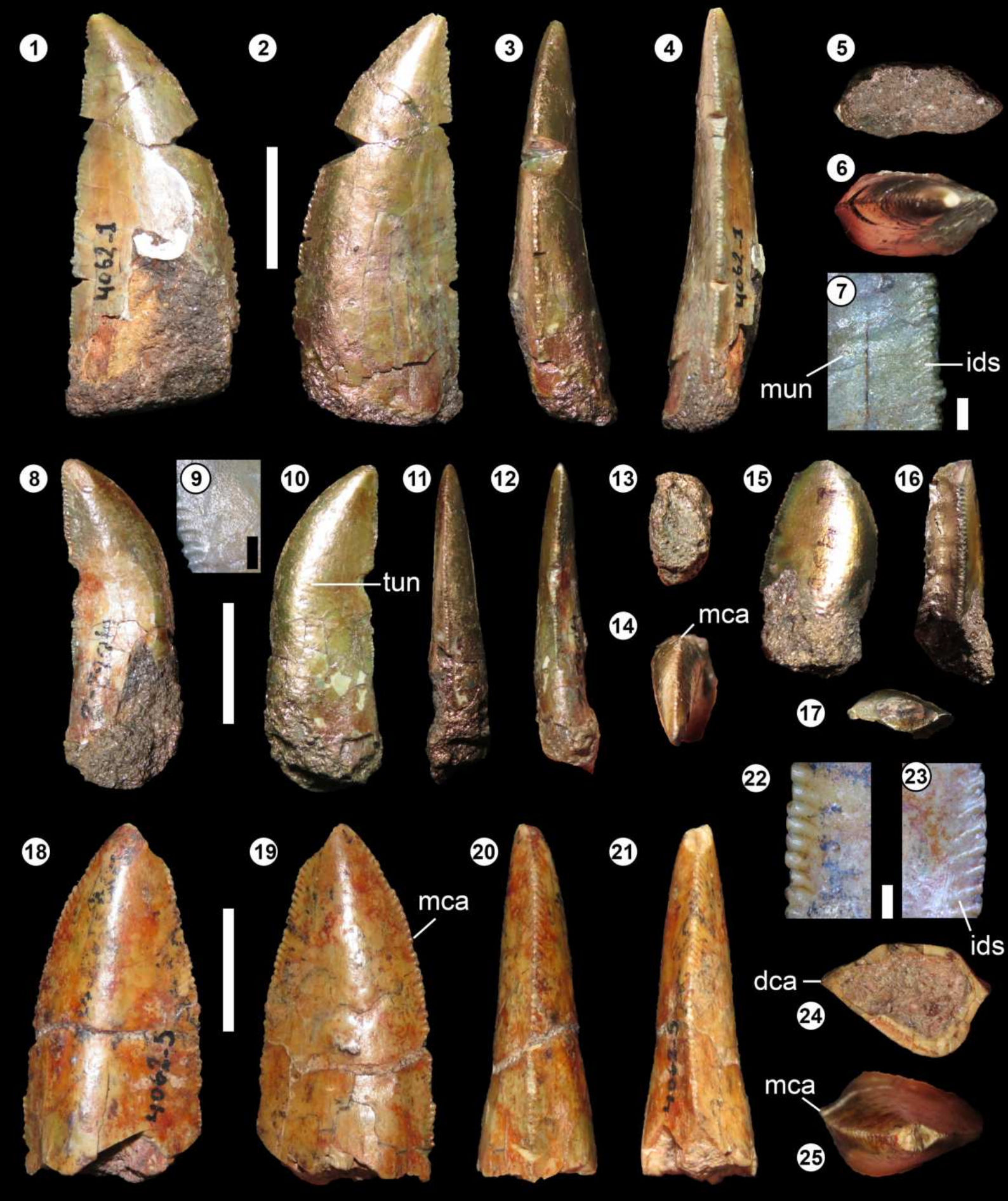
dca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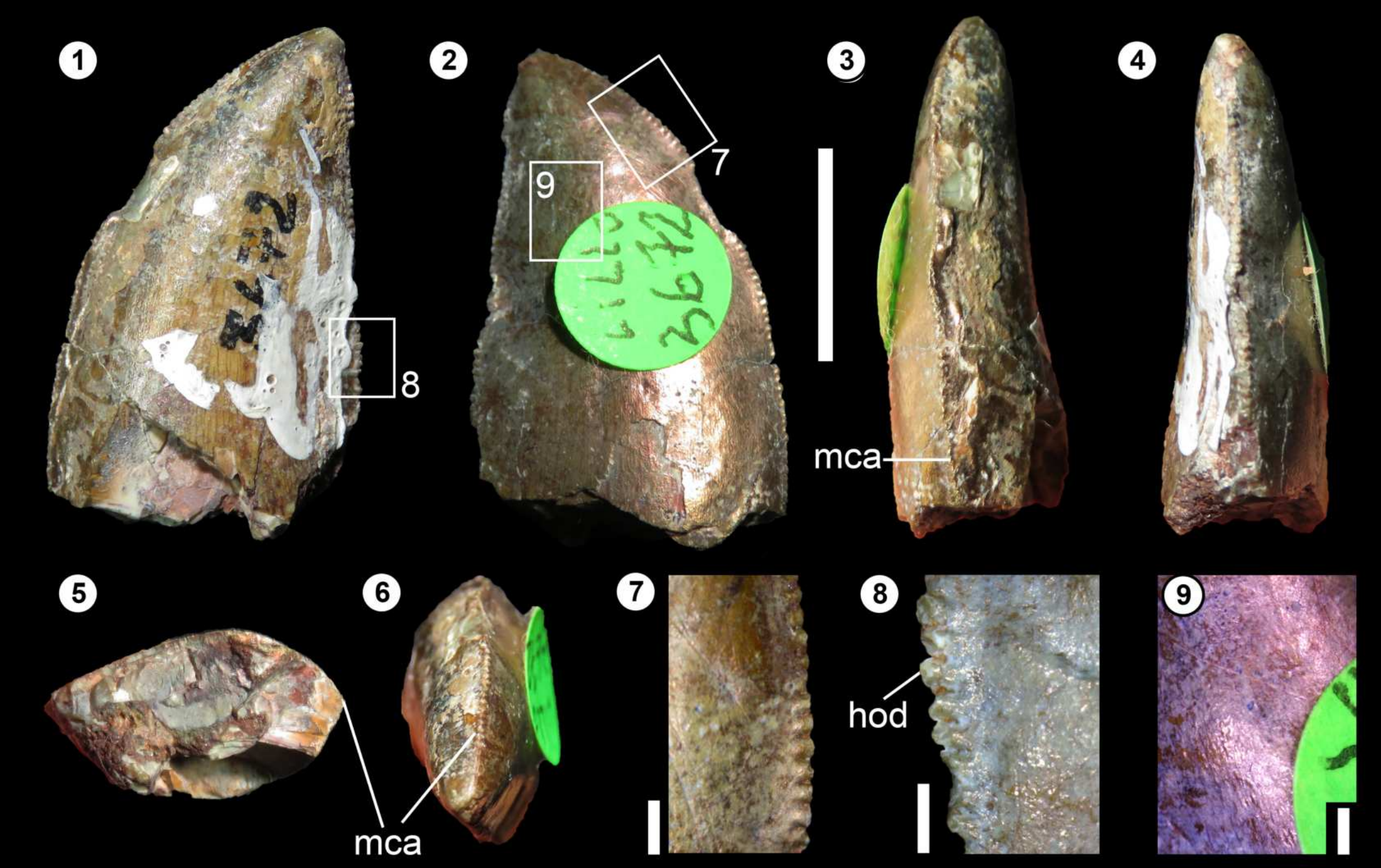
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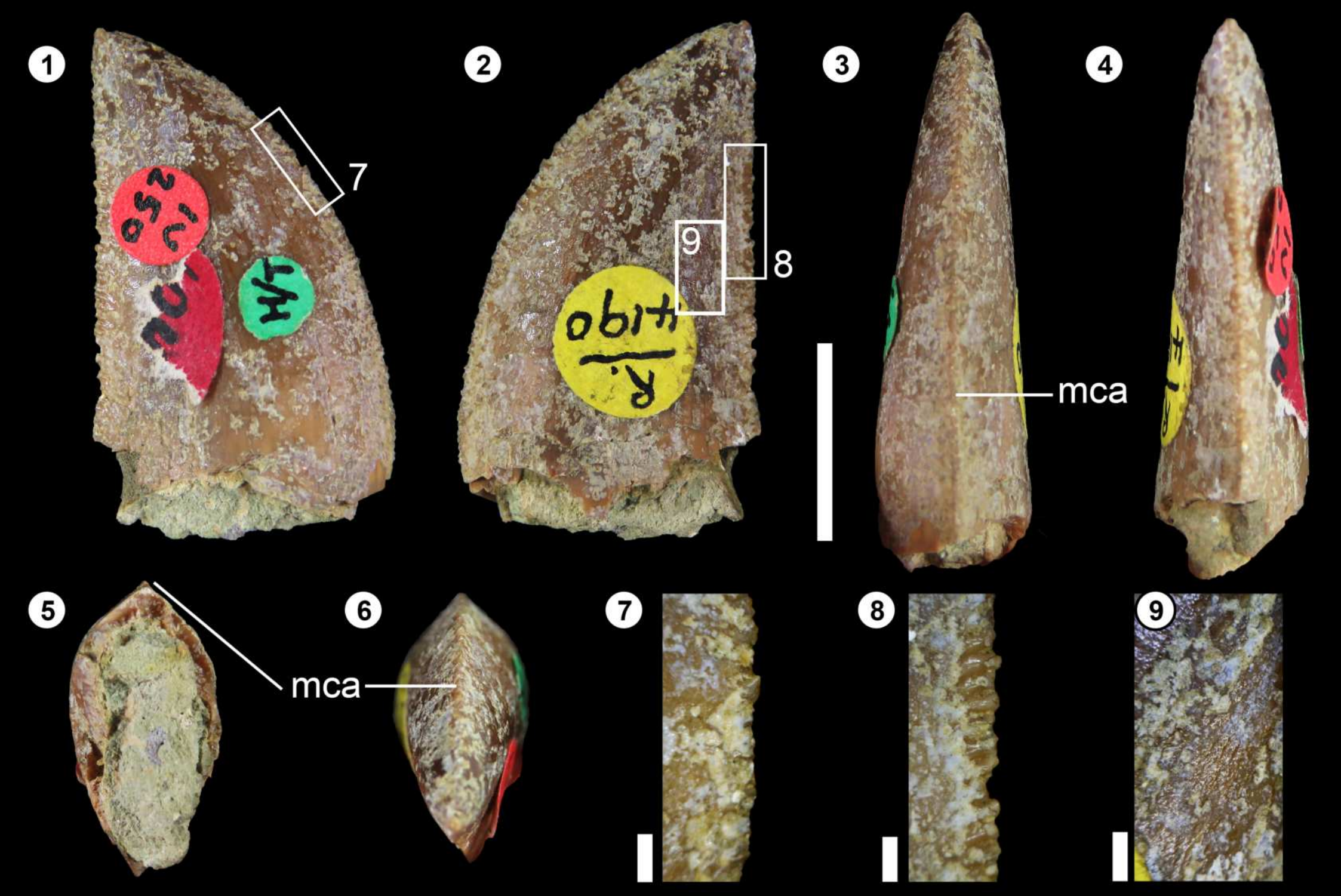
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mca
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mca
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8
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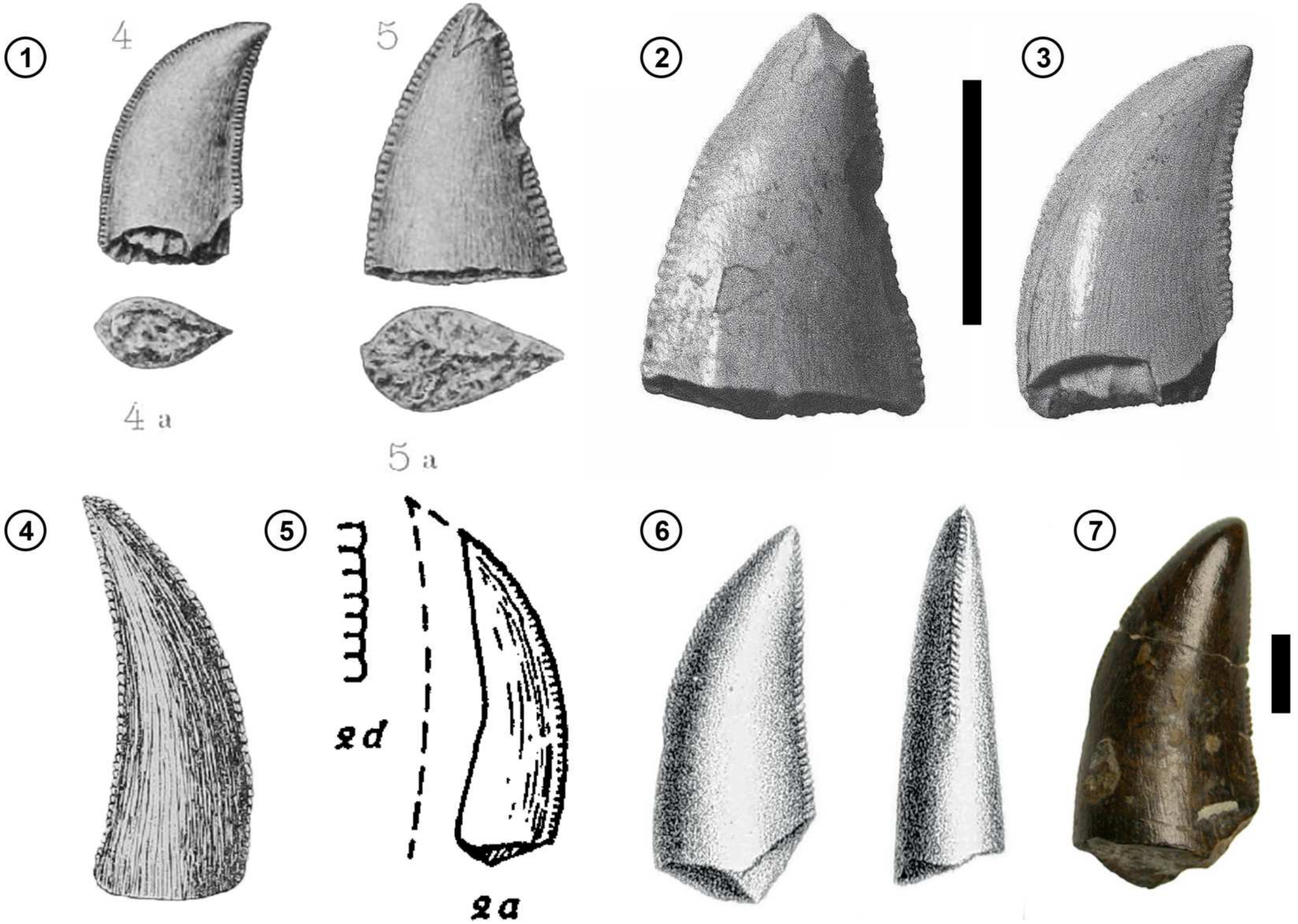
1
4
4 a
5
5 a
2
3
4
5
2 d
2 a
6
7

TABLE 1. Measurements of the abelisaurid dental material from the Mesozoic of Gondwana.

Specimen	Position	CBL	CBW	CH	AL	CBR	CHR	MCL	MCW	MCR
MSNM V5778	M I	10.5	7.4	25.2	26.7	0.7	2.4	10.5	5.4	0.51
MSNM V5781	L IV	6.6	3.6	9.1	10.3	0.55	1.38	5.6	2.6	0.46
MSNM V5799	L IV	8.0	3.4	11.8	?	0.43	1.48	?	?	?
MSNM V5814	L V	8.9	4.9	16.1	18.2	0.55	1.81	7.4	4.0	0.54
MSNM V5818	L V	8.4	4.3	14.6	17.3	0.51	1.74	7.1	3.0	0.42
MSNM V5779	L III	14.1	6.4	24.4	30.3	0.45	1.73	11.7	4.9	0.42
MSNM V5809	T II	9.2	5.2	17.3	21.2	0.57	1.88	7.6	3.8	0.5
MSNM V5789	L IV	8.6	4.4	17.1	18.4	0.51	1.99	7.1	3.3	0.46
MGT-1161	L IV	10.19	5.01	16.71	19.88	0.49	1.64	8.87	4.3	0.48
FC-DPV 3531	L	14.63	7.24	?	?	0.49	?	13.35	5.14	0.39
NHMUK R4190	L	15.36	7.35	24.67	27.45	0.48	1.61	13	6.01	0.46
PVL 3672	L III	14.86	7.75	>21.18	>24.63	0.52	?	?	?	?
PVL 4062-1	L III	13.41	6.36	30.71	29.02	0.47	2.29	12.23	5.62	0.46
PVL 4062-2	L III	8.45	4.3	18.06	16.94	0.51	2.14	8.28	3.45	0.42
PVL 4062-4	T II	8.38	4.58	>10.11	>10.97	0.55	?	?	?	?
PVL 4062-5	M I	14.31	9.28	>25.84	29.03	0.65	?	12.29	6.18	0.5
PVL 4173	L III	~18.87	10.37	~45.84	46.17	~0.55	~2.43	16.46	7.63	0.46
PVL 4174	L III	?	?	?	>16.69	?	?	?	?	?
PVL 4175	T II	7.83	~4.86	>11.47	>12.48	~0.63	?	?	?	?
MACN 18.172	L III	12.13	5.68	27.04	28.88	0.47	2.23	8.79	3.95	0.45

Specimen	Position	MDE	MA	MC	MB	DA	DC	DB	DSDI	DCR
MSNM V5778	M I	0	17	13	?	17	13	12	1	1.53
MSNM V5781	L IV	0	>28	25	?	22	20	?	1.25	2.75
MSNM V5799	L IV	0	?	25	?	?	18	?	1.389	2.35
MSNM V5814	L V	~3	26	23	23	20	18	17	1.278	1.73
MSNM V5818	L V	2.4	?	22	?	?	17	?	1.294	2.01
MSNM V5779	L III	0	12	10	?	11	10	10	1	2.05
MSNM V5809	T II	0	16	13	12	14	13	13	1	2.22
MSNM V5789	L IV	0	25	22	>22	15	14	?	1.571	2.09
MGT-1161	L IV	>0	?	?	20-25	15	15	20	?	1.99
FC-DPV 3531	L	?	?	14.5	21	?	15	17.5	0.967	?
NHMUK R4190	L	0	?	8.5	13.75	11.9	10	?	0.85	2.03
PVL 3672	L III	0?	13.33	11.66	13	11.3	11.7	?	1	?
PVL 4062-1	L III	0	11.25	10	?	11.3	11	15	0.909	1.48
PVL 4062-2	L III	0	11.66	12.5	15	14	13.3	20	0.938	2.08
PVL 4062-4	T II	0	?	15	18.33	?	14.2	17.5	1.059	?
PVL 4062-5	M I	?	?	8	10	?	8.5	?	0.941	?
PVL 4173	L III	?	15	11.25	?	12.5	11.7	?	0.965	~0.93
PVL 4174	L III	?	?	9	10.5	?	8.75	?	1.029	?
PVL 4175	T II	?	17.5	12.5	?	15	12.5	?	1	?
MACN 18.172	L III	0	?	?	?	?	?	?	?	?

TABLE 2. Corrected or revised phylogenetic definitions given by Hendrickx et al. (2024) for Berthasauridae, Elaphrosaurinae, and Noasaurinae.

Taxon	First definitional author	First phylogenetic definition	Definition type	New definition	Definitional author
Berthasauridae (Hendrickx et al., 2024)		The most inclusive clade containing *Berthasaura leopoldinae* but not *Noasaurus leali*, *Elaphrosaurus bambergi* or *Ceratosaurus sastrei*	Stem-based	The most inclusive clade containing *Berthasaura leopoldinae* but not *Noasaurus leali*, *Elaphrosaurus bambergi*, *Abelisaurus comahuensis*, or *Ceratosaurus nasicornis*	Modified from Hendrickx et al. (2024)
Elaphrosaurinae (Rauhut & Carrano, 2016)	Rauhut and Carrano 2016	All noasaurids that are more closely related to *Elaphrosaurus* than to *Noasaurus*, *Abelisaurus*, *Ceratosaurus*, or *Allosaurus*	Stem-based	The most inclusive clade containing *Elaphrosaurus bambergi* but not *Noasaurus leali*, *Abelisaurus comahuensis*, or *Ceratosaurus nasicornis*	Modified from Hendrickx et al. (2024)
Noasaurinae (Bonaparte & Powell, 1980)	Rauhut and Carrano 2016	All noasaurids that are more closely related to *Noasaurus* than to *Elaphrosaurus*, *Abelisaurus*, *Ceratosaurus*, or *Allosaurus*	Stem-based	The most inclusive clade containing *Noasaurus leali* but not *Elaphrosaurus bambergi*, *Abelisaurus comahuensis*, or *Ceratosaurus nasicornis*	Modified from Hendrickx et al. (2024)