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A Unified Framework for Predatory Dinosaur Macroevolution

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ABSTRACT - Known since the 19th Century, the compsognathids are among the smallest predatory dinosaurs, and include the first feathered non-avian species found. Traditionally, compsognathids have been considered small and unspecialized coelurosaurs, closer to birds than large-bodied forms like allosauroids and megalosaurids. Yet, all known compsognathids are based on skeletally-immature specimens, and this challenges the accuracy of their traditional phyletic placement. Despite the role of heterochrony in dinosaur evolution is widely recognized, the impact of ontogenetic-biased miscodings in shaping theropod phylogenetics is mostly underestimated. Herein, I show that the standard framework of theropod macroevolution is biased by a series of coding artifacts which violate semaphoront equality prescribed by phylogenetic systematics. I introduce "Ontogenetic State Partitioning" (OSP), a novel coding protocol which integrates ontogenetic and morphological variation under a total evidence approach, and apply it to a densely sampled data set focusing on Mesozoic theropods. The phylogenetic analysis dismissed "Compsognathidae" from being a natural group: its members are identified as juvenile morphs nested among several non-maniraptoriform tetanuran lineages. Conservatism in the immature body plan and greater disparity among large-sized adults differentiate the predatory communities dominated by non-coelurosaurian species (e.g., the so called "triumvirates") from the maniraptoriform-tyrannosaurid faunas (herein named "tyrannies"). This clade-specific differentiation among the communities is confirmed by an analysis of the predatory guild structures including all growth stages: triumvirates and tyrannies result as particular cases along a continuum of communities regulated mainly by alternative contributions of the small- and medium-sized classes. The oldest tyrannies (early Late Cretaceous in age) cluster among non-tyranny communities, supporting the hypothesis that tyrannosaurid-dominated faunas acquired their peculiar structure only after the extinction of the non-coelurosaurian components. The macroevolutionary trajectory that led the maniraptoriforms to realize the avian-like biology may have precluded them from occupying hypercarnivorous large-bodied niches: this bauplan constraint would have favored the tyrannosauroids in opportunistically assuming the apex predatory roles in Late Cretaceous Asiamerica but not elsewhere. The large-scale structure of the Cenozoic radiation of birds is coherent with the framework introduced herein.

Goliath looked at David with disgust. He saw that David was only a handsome, healthy boy (1 Samuel 17:42).

In consideration therefore of the enormous magnitude which this saurian attains, I have ventured, in concurrence with my friend and fellow-labourer, the Rev. W. Conybeare, to assign to it the name of Megalosaurus (William Buckland, February 20th, 1824).

The very remarkable reptile, Compsognathus longipes*, has many affinities with the Megalosauridae, Scelidosauridae, and Iguanodontidae, but it presents, at the same time, so many differences from all these, and so much of its structure is left unrevealed by the solitary specimen which exists, that perhaps the most convenient course which can be adopted, at present, is to make it the representative of a group equivalent to them* (Thomas Huxley, 1870).

INTRODUCTION

The theropod dinosaurs include the largest terrestrial predators of the Phanerozoic. The giant size (up to a dozen meters in length and body mass estimated up to ten tons), combined with their obligate bipedal body plan, radically distinguishes the iconic theropods of the second half of the Mesozoic from any modern analogous (Paul, 1988). Gigantism has been shown to be a recurrent phenomenon in theropod evolution since the beginning of the Jurassic (Bakker et al., 1992; Brusatte et al., 2010; Benson et al., 2014; Dal Sasso et al., 2018), with at least four distinct lineages approaching multiple times the biophysical upper limit for a terrestrial bipedal vertebrate (Alexander, 1985; Coria & Salgado, 1995; Erickson et al., 2004; Therrien & Henderson, 2007; Campione et al., 2014). Less spectacular than the iconic giant species, the small-sized theropods played a fundamental role for the modern vertebrate diversity being the ancestral condition from which emerged the avian bauplan (Cau, 2018). A miniaturization trend along the theropod lineage drove the acquisition of a peculiar biology among the avian precursors and their closest relatives, promoting, among others, paedomorphosis in skull anatomy and allometric

changes in limb proportions (Dececchi et al., 2011, 2013; Bhullar et al., 2012; Benson et al., 2014; Brusatte et al., 2014; Lee et al., 2014; Qin et al., 2021). This scenario requires that the ancestral body size among most non-avian theropods was distinctly larger than among the closest bird relatives (i.e., the maniraptorans), and implies that a small body (less than 10 kg in mass) represents a key innovation restricted to the taxa morphologically closest to *Archaeopteryx* (e.g., the anchiornithids; Godefroit et al., 2013). Another theropod, found in the same years and from similar units of the "Urvogel" *Archaeopteryx*, challenges the notion that a miniaturized body plan is restricted to the maniraptoran relatives of birds. For over a century, *Compsognathus longipes* Wagner, 1859, from the Upper Jurassic of Germany, was universally considered "the smallest dinosaur" (Ostrom, 1978). The peculiar morphology of this fossil was first noted by Huxley (1870) who interpreted it a key element in linking birds and dinosaurs. Huxley (1870) considered *Compsognathus* a relative but not a true member of Dinosauria and included both in a larger group he named Ornithoscelida. Under Huxley's (1870) taxonomy, *Compsognathus* differed from dinosaurs in the much smaller body size and in some axial and appendicular proportions. The distinction between *Compsognathus* and dinosaurs was not followed by other authors, who considered it as a member of the small-sized gracile-limbed predatory group, later named Coelurosauria (Huene, 1914). A second specimen of *Compsognathus*, found a century later from penecontemporary levels in France, is 50% larger than the German specimen but appears very similar in overall morphology (Ostrom, 1978; Peyer, 2006). Ostrom (1978) suggested an immature status for the *Compsognathus* holotype and questioned the validity of a "coelurosaurian group" including all gracile-limbed small-sized theropods. Yet, the referral of *Compsognathus* to Coelurosauria persisted after the application of the phylogenetic systematics (Hennig, 1966) to dinosaur taxonomy, and has never been questioned by the numerous analyses focusing on theropod relationships (e.g., Gauthier, 1986; Holtz et al., 2004; Hwang et al., 2004; Choiniere et al., 2013; Brusatte et al., 2014; Dal Sasso & Maganuco, 2011). During the last three decades, newly discovered theropods have dethroned *Compsognathus* from the iconic status of the "smallest dinosaur" (Xu et al., 2000). Furthermore, other taxa have been included in the compsognathid lineage or have been suggested to be members of the same coelurosaurian grade: *Sinosauropteryx* (Chen et al., 1998; Chen & Currie, 2001); *Scipionyx* (see Dal Sasso & Maganuco, 2011); *Huaxiagnathus* (Hwang et al., 2004); *Mirischia* (Naish et al., 2004); *Juravenator* (Göhlich & Chiappe, 2006); *Sinocalliopteryx* (Ji et al., 2007; Xing et al., 2012); and *Xunmenglong* (Xing et al., 2019). A specimen referred to *Sinosauropteryx* by Currie & Chen (2001), NGMC 2124, differs in several features from the former and represents a distinct taxon (Longrich, 2002). A few, very fragmentary, small-bodied theropods from the Lower Cretaceous of UK have been referred to Compsognathidae (e.g., *Aristosuchus*; see Naish, 2002). Yet, aside overall similarity with compsognathids (Naish, 2002), no unambiguous synapomorphies of that group can be identified in the British material: it is provisionally excluded from the analysis, pending a redescription. Another purported compsognathid from China, *Beipiaognathus* (Hu et al., 2016), is based on a heavily restored skeleton, several elements of which have been erroneously repositioned (e.g., the pectoral girdle is attached ventral to the iliac blades; pers. obs. on high resolution photographs provided by X. Wang). Since it lacks compsognathid-like features and shows derived maniraptoran apomorphies in the appendicular skeleton (pers. obs.), it is excluded from the discussion.

All the valid compsognathid taxa share with the eponymous genus a small body size (in all cases, less than 2.5 meters in length, often less than 1.5 meters), and a proportionally large skull which bears enlarged orbits, is devoid of specializations and lacks cranial ornamentations. Despite the generalized body plan, compsognathids show a few peculiarities including a characteristic shape of the tooth crowns (Peyer, 2006), slender ("hair-like") cervical ribs, fan-shaped dorsal neural spines, moderately short forelimbs, and relatively elongate proportions of the hindlimbs (Hwang et al., 2004; Dal Sasso & Maganuco, 2011). Yet, they show a significant intra-clade diversity in several elements of the skeleton, including the snout and cheek bones, the vertebrae, and in the forelimb proportions (pers. obs.). Although some compsognathids share a peculiar stout morphology of the hand (Chen & Currie, 2001; Gishlick & Gauthier, 2007), others show a more gracile condition (e.g., Hwang et al., 2004; Dal Sasso & Maganuco, 2011). Exceptional preservation in most of the known compsognathids, which suggests a taphonomic filter in their known distribution, has provided direct evidence of both scales and filamentous integument (e.g., Currie & Chen, 2001; Ji et al., 2007; Foth et al., 2020; Bell & Hendrickx, 2021), internal organs (see Naish et al., 2004; Dal Sasso & Maganuco, 2011) and gut contents (e.g., Ostrom, 1978; Currie & Chen, 2001; Ji et al., 2007; Dal Sasso & Maganuco, 2011) directly supporting a carnivorous diet including lepidosaurs (Ostrom, 1978; Dal Sasso & Maganuco, 2011), fish (Dal Sasso & Maganuco, 2011), mammals (Currie & Chen, 2001) and other small-bodied dinosaurs (Xing et al., 2012).

The discovery of *Sciurumimus* from the Upper Jurassic of Germany (Rauhut et al., 2012) has introduced a novel phyletic scenario for at least some compsognathid-like forms. Rauhut et al. (2012) interpreted *Sciurumimus*, and possibly also *Juravenator*, as immature members of the non-coelurosaurian group Megalosauroidea. Subsequent phylogenetic analyses have not supported a megalosauroid status for *Sciurumimus* or *Juravenator* (e.g., Godefroit et al., 2014; Cau, 2018), recovering them among the earliest diverging coelurosaurs. Foth et al. (2020) discussed the possibility that *Juravenator* was not a coelurosaurian. In a discussion on the affinities of *Scipionyx*, Cau (2021) extended the hypothesis of Rauhut et al. (2012) arguing that Compsognathidae is a polyphyletic group which clusters together immature individuals from distinct tetanuran lineages. Assuming such hypothesis, Cau (2021) showed that when the compsognathid taxa are replaced by coding strings describing their autapomorphies alone, the phylogenetic analysis clustered them among distinct non-coelurosaurian lineages. Yet, that analysis assumed the non-monophyly of Compsognathidae as working hypothesis, but did not properly test it. Such task is the main aim of this contribution.

The ontogenetic issue in theropod phylogenetics

The "compsognathid problem" briefly discussed by Cau (2021) represents a palaeontological case of the more general biological issue of integrating the ontogenetic information in the phylogenetic reconstruction. Under the phylogenetic systematics paradigm (Hennig, 1966), none of the developmental stages (the semaphoronts) holds a priviliged status as source of evolutionary information. Although the mature/adult morphs are often assumed as the main source of phylogenetic data, the evolutionary novelties can occur at every moment of phenotype development and could eventually be expressed and result adaptive at one single stage (Hennig, 1966; Alberch et al., 1979): the whole ontogenetic sequence is thus the proper operational taxonomic unit of the phylogenetic investigation. Some elements of the phenotype are fixed at one moment and persist along the whole life (e.g., the obliteration of sutures), others are remodelled and transformed along the entire ontogeny (e.g., the shape of the skull roof bones; e.g., Carr, 2020; Voris et al., 2021): since the sequence of modifications could be taxon-specific, each stage represents a source of phylogenetically-significant information and should not be excluded from the analysis.

The biological issue of including all developmental stages in the phylogenetic analysis is particularly challenging in palaeontology, for two reasons: the first is the intrinsic incompleteness of the fossil record; the second is that in the majority of taxa, the developmental series (the proper taxonomic unit) cannot be directly observed in any body fossil specimen because the latter documents only one moment of the biological life (i.e., peri-mortem), and thus it expresses just the semaphoront of that single (and contingent) point of the ontogeny. In radical contrast from living organisms whose ontogeny can be directly observed (and constitutes evidence), in fossils like those of the vertebrates, the ontogenetic sequence is always a hypothesis linking two or more specimens which have previously been assumed to belong to the same species (e.g., Erickson & Currie, 2006; Griffin, 2018; Carr, 2020). The definition of the ontogenetic series of a dinosaur is thus intimately linked to the prior delimitation of the inclusiveness (morphologic, geographic and stratigraphic) of its species.

Since the advent of the phylogenetic systematics, various methods have been developed to integrate the morphological characters across the ontogenetic series. These methods span from data partitioning to a posteriori reconciliation of trees obtained from separate subsets of stage-specific characters (see review in Sharma et al., 2017). In theropod phylogenetics, the most-frequently followed approaches have been to focus uniquely to mature stages or, when taxa based solely on immature stages were included in the taxon sample, to follow coding protocols aiming to "mitigate" the impact of the immature morphs in the phylogenetic reconstruction (Fig. 1a; e.g., Dal Sasso & Maganuco, 2011; Choiniere et al., 2013). This "contingent coding" strategy assumes that some features are "ontogenetically variable", i.e., that the state of the character is contingent to the ontogenetic stage of the coded specimen(s) (Choiniere et al., 2013): accordingly, coding such characters for taxonomic units based uniquely on immature specimens is believed to be

misleading, because it cannot be excluded that the states expressed by the immature semaphoronts differ from those expressed by the mature semaphoronts of the same taxon. The implicit assumption of the "contingent coding" is thus the epistemological subordination of the immature morphologies relative to the mature morphologies: yet, this violates the equivalence of all semaphoronts which is explicitly defined by the Phylogenetic Systematics (Hennig, 1966). The underestimation of the immature semaphoronts in theropod phylogenetics is even more concerning in light of the rich literature demonstrating the importance of the heterochronic processes in dinosaur evolution and in bird origins (e.g., Farke et al., 2013; Foth et al., 2016; Wang et al., 2017). The prevalent focus on the adult morphology in theropod phylogenetics might be justified by the rarity and fragmentary nature of the immature specimens (Hone & Rauhut, 2009), which are believed to not provide sufficient phylogenetic information compared to the more abundant and better preserved mature specimens. Nevertheless, there is no reason to assume that some preservational or ecological processes selectively removed the immature individuals of large-bodied taxa from the fossil record yet at the same time they allowed the preservation of the comparably-sized adult individuals of small-bodied taxa. Whatever the biological or taphonomic reasons penalizing the preservation of immature specimens of large theropods, why the tiny compsognathid-grade taxa of the same size class (sensu Holtz, 2021) are instead usually found in exquisite conditions (e.g., Chen & Currie, 2001; Dal Sasso & Maganuco, 2011; Rauhut et al., 2012)? One solution of this paradox could be to reconsider the "compsognathids" themselves as the missing juveniles of the large theropods (Cau, 2021).

As stated above, there is not justification for assuming that some growth stages (e.g., the adult morphs) are phylogenetically more significant than others, thus any a priori exclusion of semaphoronts or any coding protocol aiming to "mitigate" the presumed homoplastic effect of a growth stage introduces coding artifacts and removes information. In principle, a phylogenetic analysis should instead be assembled under a "total evidence perspective", i.e., using as much as data as possible from various ontogenetic stages to construct a single and comprehensive code string for each taxon (Fig. 1b; Hennig, 1966; Sharma et al., 2017). Any departure from the total evidence approach inevitably leads to topological artifacts due to the unequal contributions of the ontogenetic stages. Furthermore, and regardless the coding strategy followed, the behavior of a taxonomic unit based on a growth stage different from those defined as target of the character statements (e.g., *Aorun*, Choiniere et al., 2013; *Scipionyx*, Dal Sasso & Maganuco, 2011; both based on juvenile specimens and coded in data matrices targeting adult morphs) does not necessarily reflect the behavior of other semaphoronts of the same taxon. As shown by cases of more semaphoronts of the same species included in a phylogenetic analysis, the reconstructed placement of an immature semaphoront in the adult-targeting sample is variable and likely taxon-specific. In some cases, the conspecific semaphoronts cluster together relative to the other included taxa (suggesting a weak homoplastic effect by the ontogeny, e.g., *Limusaurus*, Wang et al., 2016), in other cases, one semaphoront is reconstructed
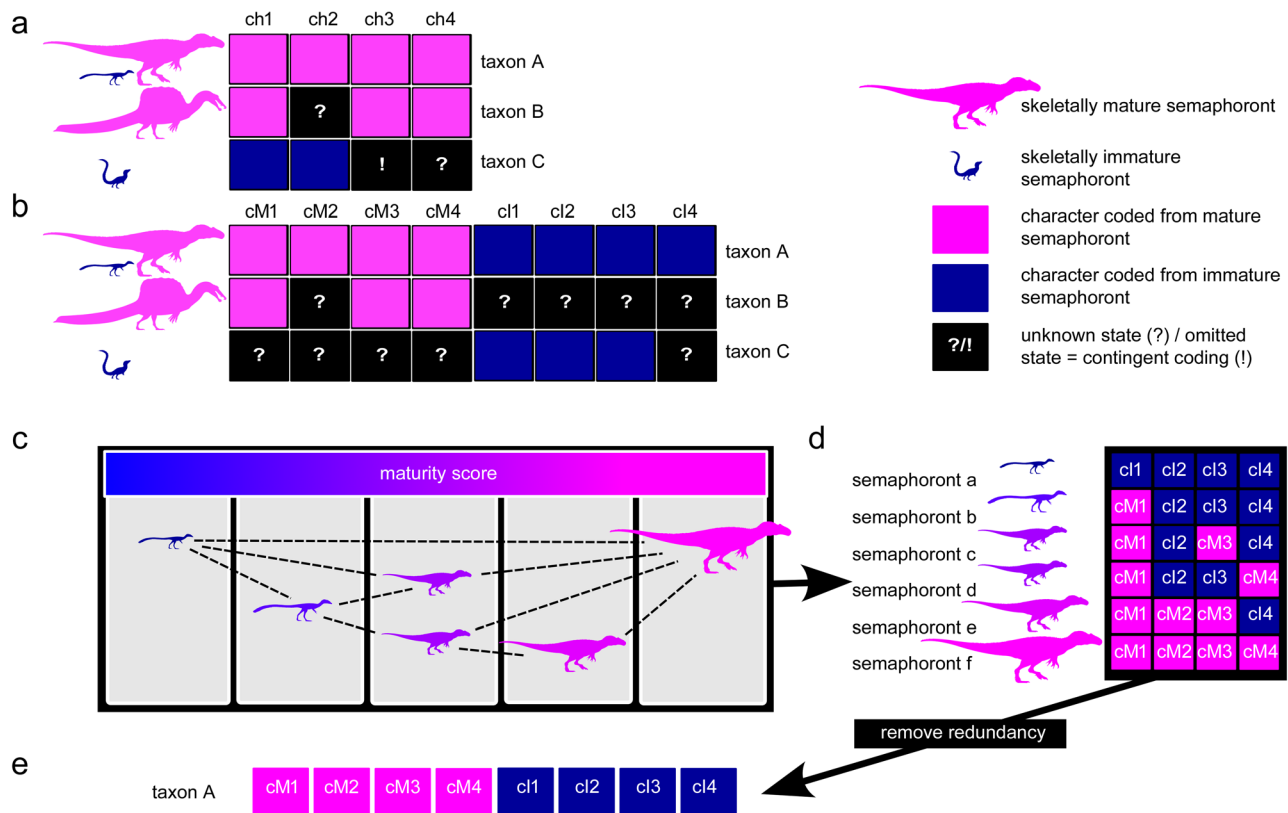
Fig. 1 - Rationale for the new coding protocol. a-b) Comparison between the traditional coding protocol (a) (used for topology shown in Fig. 3) and the OSP protocol (b) (used for topology shown in Fig. 4). In the example, the data set includes three taxa coded for four morphological features. Semaphoronts known for each taxon indicated by the silhouettes (i.e., two semaphoronts for taxon "A", only one for both taxa "B" and "C"). Note that, in protocol (a): one semaphoront of taxon "A" (the immature) is arbitrarily ignored; character "3" is not coded in taxon "C" (simulating contingent coding, sensu Choiniere et al., 2013); and characters "1" and "2" combine both mature and immature conditions in the same apomorphy-state distribution. All these coding artifacts are avoided following the protocol shown in (b). c-e) Biological basis for coding protocol shown in (b). The ontogenetic structure of taxon "A" (see Griffin, 2018) is shown in (c) and is described by the series of ontogenetic coding strings of its semaphoronts (d): the proper OTU is derived from the whole set of strings after pruning of redundant codes and describes the complete state distribution of both immature and mature features (e). Silhouettes from PhyloPic.org (details in Acknowledgements).

in a node more inclusive than that containing the other semaphoront (a paradoxical "double placement" for the same taxon which implies a significant homoplastic effect by the ontogeny; e.g, *Tarbosaurus*, Tsuihiji et al., 2012). In the absence of mature conspecifics to bracket the inclusiveness of taxa coded uniquely from immature semaphoronts (e.g., Dal Sasso & Maganuco, 2011, or Choiniere et al., 2013), the accuracy of their phyletic placement is thus undeterminable.

These cases show that any "contingent coding" strategy so far suggested is not a valid solution for the integration of ontogeny and phylogeny, from both theoretical and practical points of view.

Implicit semaphoront coding bias

A second type of coding artifact stems from the inclusion in the phylogenetic analysis of several taxa coded uniquely from immature semaphoronts, which are clustered together by the analysis due to the similarity of their immature morphologies. The hypothesis discussed here is that the phylogenetic analyses including the compsognathids so far published have been further biased by an implicit form of coding strategy named "semaphoront coding" (Sharma et al., 2017). The adjective "implicit" refers to the non-intentional nature of such coding artifact, which distinguishes the cases here discussed from the "explicit" use of semaphoront coding as a phylogenetic protocol (see Sharma et al., 2017, for a discussion of why the semaphoront coding itself is antithetic to the proper concepts of phylogenetic systematics). The implicit semaphoront coding (ISC) is the inclusion of two or more taxonomic units based on specimens which represent growth stages distinct from the stage(s) meant (even just implicitly) to be the actual target of the analysis. Like its "explicit" version (Sharma et al., 2017), the ISC is predicted to produce spurious nodes clustering together terminal units coded from comparable growth stages regardless of their actual phylogenetic relateness. The impact of the ISC is expected to be the more significant the greater the morphological disparity between the semaphoronts of the same taxon (i.e., in peramorphic and/or giant-sized taxa). Given the considerable —and in many cases, unexpected— ontogenetic disparity documented in Theropoda (e.g., *Limusaurus*, Wang et al., 2016; *Tyrannosaurus*, Carr, 2020), in absence of mature semaphoronts it is not possible to predict the amount of morphological difference between the latter and the available immature stages.

In this paper: 1) I test the hypothesis that Compsognathidae is not monophyletic, i.e., it is an artifact due to implicit semaphoront coding; 2) I introduce a total evidence coding protocol which is not biased by the coding artifacts discussed above and use it to reconstruct the affinities of the "compsognathids" and all other Mesozoic theropods; 3) I discuss the macroevolutionary implications of this new phylogeny at the level of the predatory dinosaur communities.

MATERIAL AND METHODS

Semaphoront coding test

In order to test the hypothesis that Compsognathidae is a phylogenetic artifact due to ISC, I built an explicitly semaphoront-coded data set, and showed that such data set supports spurious clades diagnosed by skeletally-immature morphotypes, one of which is equivalent to Compsognathidae. The character statements were based on Cau (2018) with the inclusion of 163 new morphological characters (total number of characters = 1944). The taxon sample includes 543 Operational Taxonomic Units (OTUs), each one based on, alternatively, immature or mature semaphoronts of a densely sampled set of Mesozoic pan-avians and two archosauromorph outgroups, all coded with no ontogenetic-contingent restrictions (sensu Choiniere et al., 2013). Accordingly, a subset of the sample includes immature and mature morphs of the same taxon, here treated as separated terminal units (as dictated by the explicit semaphoront coding protocol; Sharma et al., 2017): the two alternative ontogenetic categories of the OTUs are indicated by the prefix "mature_" or "immature_" included in each OTU name. The phylogenetic analysis was performed in TNT (Goloboff et al., 2008) and followed the tree search strategy of Cau (2018: 100 "New Technology" search runs followed by exploration of the sampled tree island using "Traditional Search" runs, with "maxtree" set at 10000 trees). The most inclusive subtree topology reconstructed from the shortest trees found was used as framework for ancestral state reconstruction at nodes using Reconstruct Ancestral State in Phylogenies (RASP; Yan et al., 2011). To infer the probability that semaphoront coding leads to reconstruct immature morphotypes as spurious adult conditions at some nodes, each terminal taxon was coded for a binary character statement describing the ontogenetic stage of the material used to code the OTU (i.e., "immature" vs "mature"). The Bayesian inference analysis in RASP used default settings for the Bayesian Binary Markov (BBM) Chain Monte Carlo analysis (Yan et al., 2011). The hypothesis tested is that the inferred topology is biased by ISC, resulting in a non-omogeneous distribution of the immature OTUs in the topology (i.e., the difference between the distribution of the ontogeny states coded for the OTUs and that of the ontogeny states inferred at nodes by the RASP analysis is statistically significant).

Ontogenetic State Partitioning

I introduce "Ontogenetic State Partitioning" (OSP), a coding protocol for phylogenetic analysis which integrates the developmental diversity and is not affected by semaphoront inequality bias. The rationale for this novel coding protocol stems directly from Hennig's (1966) seminal work on Phylogenetic Systematics, which defines semaphoronts' equality and their hierarchical subordination relative to the Operational Taxonomic Unit (OTU) (see Sharma et al., 2017). The proper OTU is thus the set of all state strings describing the semaphoronts' morphologies. Following Griffin et al. (2021), I focus on the developmental stage of the individual morphological features and not on the ontogenetic category of the whole individual: accordingly, the terms "mature" and "immature" refer to mature/immature skeletal features and not to "holistic" developmental stages. Griffin (2018) showed that regardless the number of semaphoronts in a well-sampled theropod population, each semaphoront could be described by a unique combination of immature and mature states. Each immature or mature condition itself is a potential phylogenetically significant character statement, the latter describing the variation between plesiomorphic and apomorphic states. Redundancy in the ontogenetic stages of the individual features among sections of the semaphoront strings does not impact the state combination in the complete OTU obtained merging all semaphoronts: this implies that we can ignore the actual number of semaphoronts or their peculiar combination of ontogenetic states and directly describe the OTU using a string which maps the apomorphy-state distribution in the complete set of both immature and mature character statements (Fig. 1c-e).

Protocol for assembling the OSP data set from an available data matrix

STEP 1 - Character statement list is obtained duplicating the original character list of N characters (in this case, that used in the semaphoront coding test, which describes 1944 binary character statements), producing two ontogenetically-segregated versions of the same series of morphological features. The two subsets of series act as data partitions focusing on, alternatively, the mature and immature stages of each feature: in this case, the first N character statements describe the apomorphy-state distribution of the mature morphological conditions, the remaining N character statements describe the apomorphy-state distribution of the immature morphological conditions of the same features (i.e., character "x" [with $x < N+1$] describes the alternative states of the mature condition of a particular feature, character "x+N" describes the alternative states of the immature condition of the same feature). Note that the order of the characters in each partition must remain the same as the original data set to facilitate the translation of entire strings to the corresponding OSP partition.

STEP 2A - The codings of the OTUs that in the original data set were based on immature semaphoronts are directly translated to the second half of the OSP matrix (i.e., their character codes are changed from the original position "x" to the new position "x+N"). [Note that a new OTU based uniquely on a single developmental stage can be directly created adding a string of N "?", alternatively, at the beginning of the original string (if the semaphoront is immature), or at the end of the original string (if the semaphoront is mature). In cases when the author defines some character as non-ontogenetically variable and fixes all its scores to just one of the two corresponding

character statements describing the state variation, the corresponding column in the other ontogenetic partition is coded as "?". Also, note that a column so coded has no impact on the phylogenetic analysis, and is included uniquely to keep consistency among the positions of all characters in both partitions].

STEP 2B - If two OTUs in the original matrix are interpreted as alternative mature/immature semaphoronts of the same taxon, they are merged into a single OTU in the OSP matrix, each occupying the relative ontogenetic partition.

STEP 3 - If a specimen of a taxon is interpreted as a semaphoront expressing a combination of immature and mature features, each feature of the specimen is coded in the relative ontogenetic partition of the OSP matrix (see Griffin, 2018).

Some taxonomic units included in the OSP analysis, and originally considered as distinct taxa, have been merged together on the hypothesis that they represent distinct semaphoronts of the same taxon. The rationale for their synonymy is based on a combination of palaeobiogeographic, stratigraphic and morphologic criteria.

The genus *Corythoraptor* (Lü et al., 2017) is considered a junior synonym of *Banji* (Xu & Han, 2010). The type specimen of *Banji* is an immature oviraptorid skull from the Nanxiong Formation of China. *Corythoraptor* is based on an adult oviraptorid from the same unit of *Banji*: the two share a peculiar set of features (subnarial process of premaxilla extended posterodorsally to overlap the lacrimal bar, unforked subnarial ramus of premaxilla, apex of nasal crest at level of lacrimal bar, posterodorsal margin of nasal crest with an abrupt elevation relative to the skull roof, pneumatic pockets on the nasal crest), and differ uniquely in features which are ontogeny-related in dinosaurs (relative size and development of the nasal crest, proportions of the skull fenestrae; see Griffin et al., 2021). The shallow and elongate proportions of the external naris in the *Banji long* holotype are also reported in *Corythoraptor* (Lü et al., 2017) but questioned by Funston (2024): yet, that feature is widespread among immature coelurosaurs (e.g., Hwang et al., 2004; Ji et al., 2007; Porfiri et al., 2014) and does not necessarily represent a diagnostic character differentiating the two taxa. Pending additional information on the ontogeny of the cranial crest in oviraptorids (Funston, 2024), the differences between *Banji* and *Corythoraptor* do not invalidate the hypothesis that the two morphotypes are semaphoronts of the same ontogenetic trajectory. The two taxa are provisionally coded in the same OTU (i.e., "*Corythoraptor*" OTU was used for coding the mature features of the *Banji* OTU, the original "*Banji*" OTU was used for coding the immature features).

The genus *Dubreuillosaurus* (Allain, 2002, 2005) is considered a junior synonym of *Poekilopleuron* (see Allain & Chure, 2002). The type material of *Dubreuillosaurus* is based on a juvenile specimen from the same unit and locality of the *Poekilopleuron* material. Immature features of the *Dubreuillosaurus* holotype include the lack of fusion among the elements of the braincase and in all vertebrae. The two taxa differ uniquely in the shape and inclination of the ribs, accessory spur and zygapophyses in

the middle caudal vertebrae (Allain, 2005): yet, the same diversity in the mentioned elements is observed among *Allosaurus* caudal series (Gilmore, 1920; Madsen, 1976) and thus could be interpreted as merely a combination of positional and individual variation. The two taxa are here considered synonyms and coded in the same OTU (i.e., the original "*Poekilopleuron*" OTU was used for coding the mature features, the codes of "*Duibreuillosaurus*" OTU were used for the immature features).

The genus *Epidexipteryx* (Zhang et al., 2008) is considered a junior synonym of *Epidendrosaurus* (Zhang et al., 2002). All specimens of both taxa were collected from the Daohugou Beds (Zhang et al., 2008) and differ each-other uniquely in ontogeny-related features. The two specimens of *Epidendrosaurus* are very-immature individuals showing an elongate tail lacking any co-ossification of the distal centra (Czerkas & Yuan, 2002). The only known specimen of *Epidexipteryx* is a much larger and more mature individual showing a proportionally shorter tail and incipient co-ossification of the distalmost ten caudal centra. Contra Zhang et al. (2008), the actual length of the presacral series is unknown in the specimens of *Epidendrosaurus* (Czerkas & Yuan, 2002; Zhang et al., 2002), and cannot be compared to *Epidexipteryx*. Furthermore, the difference in the number of preserved tail vertebrae in the two taxa is less dramatic than claimed by Zhang et al. (2008), i.e., at least 22 caudal vertebrae are reported in *Epidendrosaurus* vs at least 16 caudal vertebrae in *Epidexipteryx* (Czerkas & Yuan, 2002; Zhang et al., 2008); yet, in the *Epidexipteryx* holotype, the distal part of the tail is not oriented with the long axis of the body, and a gap in the sequence separates the co-ossified distal centra from the rest of the tail (see figs 1 and 2 in Zhang et al., 2008): these features suggest that an unknown number of tail vertebrae is missing. Despite the claimed differences in the caudal series, the morphology of the first six tail vertebrae is very similar in the two taxa (Czerkas & Yuan, 2002; Zhang et al., 2008). Taking into account the possible missing elements between the middle and distal vertebrae in *Epidexipteryx*, tail diversity in the two taxa recalls the variation seen in the ontogenetic series of other maniraptorans (O'Connor & Sullivan, 2014). Since *Epidexipteryx* was differentiated from *Epidendrosaurus* on the basis of features in the tail (Zhang et al., 2008), their taxonomic distinction is not strongly supported. All specimens are provisionally coded in the same OTU (i.e., the original "*Epidendrosaurus*" OTU was used for coding the immature features, the codes of "*Epidexipteryx*" OTU were used for the mature features).

The genus *Jixiangosaurus* (Pu et al., 2013) is considered a junior synonym of *Beipiaosaurus* (Xu et al., 1999). Both taxa were collected from the Yixian Formation (Pu et al., 2013), and differ mainly in size and body proportions. In particular, the type material of *Jiaxiangosaurus* is juvenile and more gracile than the specimens of *Beipiaosaurus*. Several features stated to differentiate the two taxa are ontogeny-controlled (see Kundrát et al., 2008) or size-related (e.g., in *Jixiangosaurus*, the skull is longer than the femur, the tooth crowns are less robust, the manual unguals are slender, the preacetabular process is shallower and not flared, the iliac peduncles are subequal in size, the ischial foot is less prominent, and the femur lacks a ridge on the anterior surface). Other features are problematic (e.g.,

Jixiangosaurus is stated to have a "short lateral articular surface" on manual phalanx I-1) or not significantly different (e.g., shape and position of the manual flexor tubercles is comparable to *Beipiaosaurus*; see Liao et al., 2021). The holotype of *Jianchangosaurus* is provisionally coded in the *Beipiaosaurus* OTU (i.e., used to code the immature features).

Following OSP protocol, I assembled a new character-taxon matrix describing the distribution of 3888 character statements in a set of 502 OTUs. The phylogenetic analysis followed the tree search strategy used for the semaphoront coding test (see above).

Theropod guild analysis

I compared the structure of predatory theropod communities using a data set modified from Holtz (2021) and updated with the inclusion of the Chorrillo Formation dinosaur fauna (Maastrichtian of Argentina; Novas et al., 2019). A few taxa listed in Holtz (2021, e.g., *Dakotaraptor*, *Latenivenatrix* and the Bissekty Formation carcharodontosaurid) were removed from the sample or referred to sympatric taxa (see Cau & Madzia, 2018; Sues et al., 2022). In particular, the holotype of the dromaeosaurid *Dakotaraptor* is problematic and is provisionally excluded from the analysis. The specimen was collected from a multitaxon bonebed (DePalma et al., 2015) and has been shown to include non-dinosaurian material (Arbour et al., 2016). The quarry map of the type locality shows a substantial disarticulation of the material (DePalma et al., 2015, appendix 3), compatible with the multitaxon association. The dinosaurian elements of the *Dakotaraptor* holotype hypodigm are problematic when compared to other dromaeosaurids. None of the caudal vertebrae is complete and some show pathologic features (DePalma et al., 2015). The best preserved vertebra (DePalma et al., fig. 5) is dromaeosaur-like in the elongation of the prezygapophyses, yet they differ from those of dromaeosaurids in having much deeper and more posteriorly extended bases, recalling ornithomimids (e.g., Longrich, 2008). Most forelimb elements lack the majority of the articular ends (e.g, DePalma et al., 2015, figs 2 and 3) which are the most phylogenetically-informative parts of the theropod long bones. The presence of feather papillae in *Dakotaraptor* ulna does not necessarily support a paravian status since it is also known in caenagnathids (e.g., *Apatoraptor*; Funston & Currie, 2016). The hindlimb elements are proportionally more gracile and elongate than comparably-sized dromaeosaurids (DePalma et al., 2015) and recall those of more cursorial theropods (e.g., caenagnathids; Lamanna et al., 2014; Currie et al., 2016). The tibia of *Dakotaraptor* lacks unambiguous dromaeosaurid apomorphies, yet it shows a hooked fibular crest as in some caenagnathids (e.g., Currie et al., 2016). Based on the published photographs (DePalma et al., 2015, fig. 12), the large falciform ungual referred to the second toe lacks the asymmetric placement of the collateral grooves (contra DePalma et al., 2015) diagnostic of dromaeosaurids. The flattened pedal ungual 3 with reduced flexor tuber is unusual for a dromaeosaurid and more closely recalls the ornithomimosaurs (e.g., Longrich, 2008). Since the type material of *Dakotaraptor* is currently housed in a private collection (DePalma et al., 2015), it is unclear if it is available for further examination.

Pending new published evidence, and given analogous cases of theropod species from multitaxon assemblages which resulted chimaerae once restudied (e.g., Słowiak et al., 2024), currently the hypothesis that the hypodigm of *Dakotaraptor* is not a single theropod taxon cannot be dismissed.

Size classes and categories follow Holtz (2021). For brevity, "small", "middle" and "large" classes refer to, respectively, classes 1 to 2; classes 3 to 5, and classes 6 to 7. The term "tyranny" used here (and inspired by the analogous "triumvirate" sensu Sereno & Brusatte, 2008) equates to "tyrant-dominated fauna" of Holtz (2021).

I introduce an additional metric for community comparison, named "Relative Size Class" (RSC) which describes the relative contribution of each size class to the whole predatory community when all ontogenetic stages of the community species are taken into account. The metric stems from the assumption that at any given time of community history, and excluding selective migration patterns restricted to some growth stages, any population of the community should occupy all size classes spanning from hatchling to their adult stage (Fig. 2). Reproductive constraints related to oviparity predict that all theropods, regardless of adult body size, hatched at size class 1 (e.g., Funston et al., 2021), thus the number of size classes occupied by a given taxon is the numeral of the adult size class coded. For example, *Tyrannosaurus rex* is reported to occupy size class 7 of the Upper Hell Creek Formation community (Holtz, 2021): thus, the *T. rex* population must occupy all size classes from 1 to 7 in that community. The RSC of a size class is the ratio between the number of species which occupy that size class (regardless to as immature or mature stages) and the total number of size classes occupied by the whole community. I calculated the RSC of all seven size classes for all communities sampled and performed a Principal Component Analysis (PCA) of the community-RSC matrix. To reject the hypothesis that the RSC may be biased by sampling artifacts, I compared the distribution of the RSC values of the theropod communities with those calculated from a sample of 500 randomly-generated
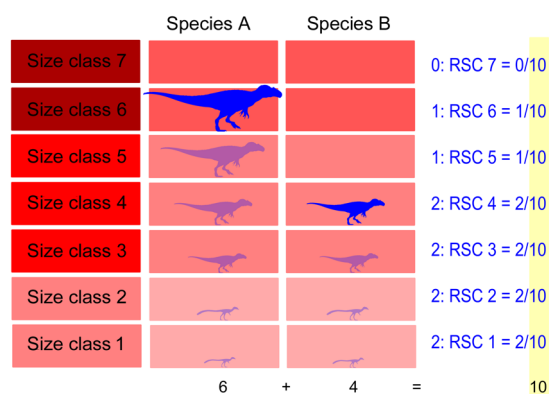

Fig. 2 - Example of calculation of the Relative Size Class values for a predatory theropod community. In the example, the community is formed by two species, one of maximum size class 6 and one of maximum size class 4. Silhouettes from PhyloPic.org (details in Acknowledgements).

communities having a diversity similar to those sampled by Holtz (2021; maximum number of species per size class set as = 10). For each size class, I compared the RSC ranges between tyrannies and non-tyrannies. For each community, I calculated the ratio between the number of coelurosaurian species (according to the topology resulted in the OSP coded analysis) and the total number of predatory theropod species ("Coelurosaurian Ratio"). All analyses were performed in PAST vers. 4 (Hammer et al., 2001).

Institutional abbreviations

MCF-PVPH, Museo Municipal "Carmen Funes", Paleontología de Vertebrados Plaza Huincul, Provincia de Neuquén, Argentina; NGMC, Geological Museum of China, Beijing, China; OPH, Ophis Museo Paleontologico e Centro Erpetologico, Teramo, Italy.

RESULTS

Semaphoront coding test

The reduced strict consensus of the shortest trees reconstructed by the phylogenetic analysis of the data set explicitly assembled using semaphoront coding is well-resolved. The topology mostly agrees with results of previous iterations of this data set (e.g., Cau, 2018) and —in the overlapping clades— with the large-scale phylogenetic analyses of Theropoda published recently (e.g., Choniere et al., 2013; Brusatte et al., 2014) (Fig. 3a, see also the figure in the Supplementary Online Material 1 - SOM 1). The distribution in the topology of the OTUs based on the immature semaphoronts is not homogeneous. Some couples of OTUs, originally coded from both immature and mature semaphoronts of the same taxon, have been reconstructed in direct sister taxon relationships, supporting their original ontogenetic unity, whereas the two members of other conspecific couples have not been reconstructed as closely related. In particular, the correctly-identified semaphoront couples are distributed in two distinct regions of the topology: among non-tetanuran taxa (e.g., *Lesothosaurus*, *Ceratosaurus*) or among paravian coelurosaurs (e.g., *Almas*, *Archaeopteryx*, *Meleagris*, *Sapeornis*). On the contrary, the majority of the OTUs based on immature semaphoronts and nested among non-paravian tetanurans was clustered with other OTUs based on immature semaphoronts. Such "nursery nodes" excluding mature semaphoronts are concentrated among the earliest diverging branches of Coelurosauria (Fig. 3b). Accordingly, the ontogenetic stage reconstructed at nodes using RASP shows part of the nodes among non-paravian Tetanurae which are diagnosed uniquely by the immature morphology of the included OTUs (posterior probability > 0.95; Fig. 3b). The distribution of the ontogeny states reconstructed at nodes is significantly different from that expected from a homogeneous distribution of the OTUs not biased by their ontogenetic stage. The difference between the ontogeny-code median and the ontogeny-state inferred at node median is statistically significant (Kruskal-Wallis test for equal medians; H [χ^2]: 552.6; Hc [tie corrected]: 620.9; $p < 0.0001$). Thus, the null hypothesis of non-influence of the ISC on topology is rejected: the test confirms that the relative distribution of the OTUs coded from immature semaphoronts is biased by their ontogenetic stage, and that both topology and diagnosis at nodes were artifacted by semaphoront coding.

Phylogenetic analysis

A detailed description of the result of the phylogenetic analysis based on the OSP data set is beyond the aims of this contribution. Here, I briefly mention the most significant elements of the topology reconstructed, and discuss in detail the affinities of the compsognathid-like OTUs. The analysis found 10000 shortest trees of 16578 steps each (Consistency Index excluding uninformative characters = 0.1671; Retention Index = 0.5904). The reduced consensus tree after the pruning of the less stable "wildcard" OTUs is well-resolved and supports the monophyly of successively less inclusive subgroups of the avian total-group (Fig. 4, Figs S2-S3 of the SOM): e.g., Dinosauria, Saurischia, Theropoda, Averostra, Tetanurae, Neotetanurae, Coelurosauria, Maniraptoriformes, Maniraptora, Paraves and Avialae (Cau, 2018). Most of the "wilcards" are taxa known uniquely for immature semaphoronts and thus could not be directly compared to the majority of OTUs (which are known uniquely for mature semaphoronts): yet, despite being reconstructed in several equally-parsimonious alternative placements, exploration of the shortest trees shows that each of these "unstable" OTUs keeps being consistently placed in a restricted section of the topology (a grade), and does not impact the large-scale topology and the relationships among the main branches (Fig. 4). Relevant relationships supported by the analysis are the placement in Dinosauria of the "silesaurids" as a paraphyletic series of early-branching ornithischians (Müller & Garcia, 2020), the placement of Herrerasauria in Theropoda, the coelophysoid-grade neotheropods forming a paraphyletic series leading to Averostra, the noasaurid-grade abelisauroids forming a paraphyletic series leading to the abelisaurids, the sister group relationship between *Elaphrosaurus* and the "bahariasaurids" in Abelisauroidea, the tetanuran placement of *Chilesaurus* (Novas et al., 2015), the exclusion of Megalosauroidea from Neotetanurae (Carrano et al., 2012), the placement of Megaraptora in Tyrannosauroidea (Fig. 4, see also figure in SOM 2), the sister group relationship between ornithomimosaurs and therizinosauroids, the troodontid-grade paravians forming a paraphyletic series leading to Avialae, the anchiornithid-grade avialans forming a paraphyletic series leading to Scansoriopterygidae, and the referral of the enigmatic giant avialan *Gargantuavis* (Buffetaut & Loleuff, 1998; Mayr et al., 2019) to Enantiornithes (Fig. 4; see also figure in SOM 3).

The most significant difference between the topology reconstructed by the test explicitly biased by the semaphoront coding artifacts and the new analysis based on the OPS protocol is the placement of the taxa currently known uniquely for immature semaphoronts. Using the traditional method biased by semaphoront coding artifacts, the two taxa *Bagaraatan* (recoded following Słowiak et al., 2024) and *Raptorex* (Carr, 2023) resulted, respectively, a non-tyrannosaurid tyrannosauroid more basal than *Dryptosaurus*, and a member of the spurious "nursery group" including all immature tyrannosaurid morphs and distinct from the "mature Tyrannosauridae" cluster (Fig. 3). Using the OPS protocol, both taxa are instead
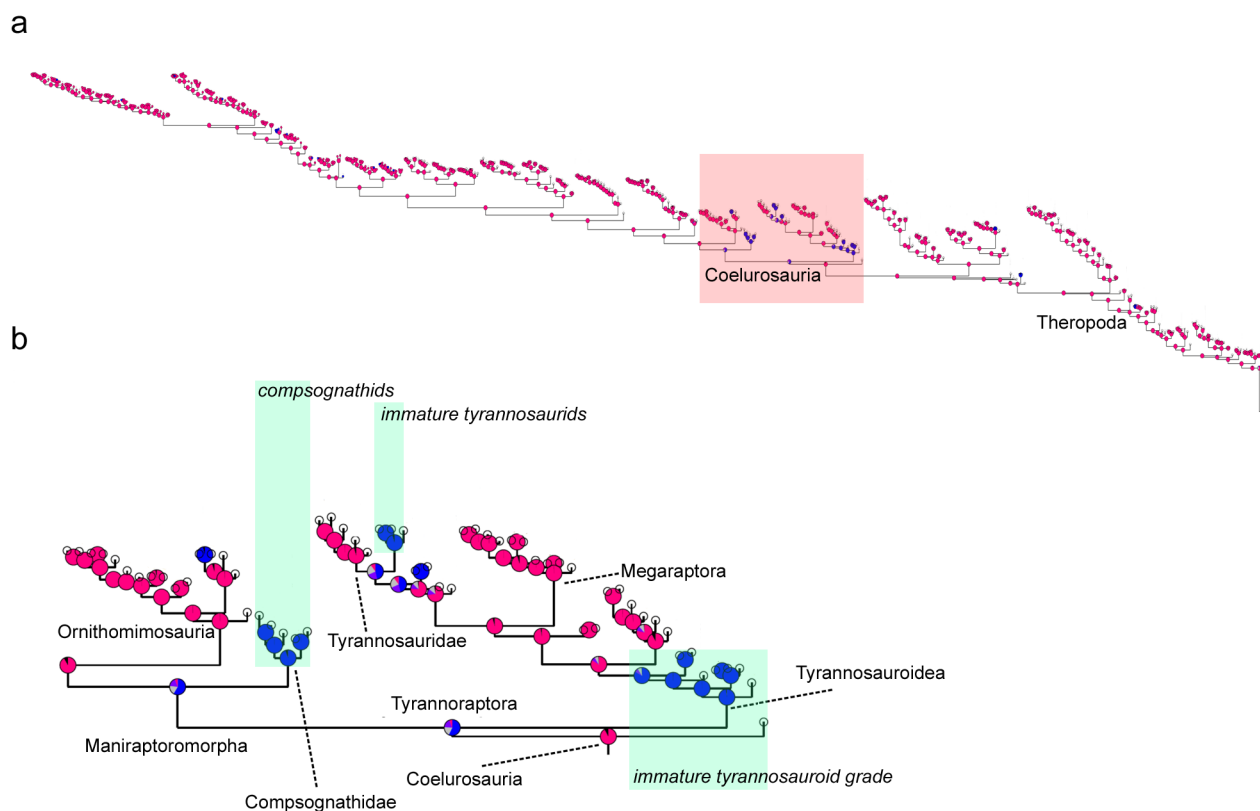
a

b

Fig. 3 - Semaphoront coding test. a) Bayesian inference of maturity state at nodes using the agreement subtree produced by the phylogenetic test based on the explicit semaphoront coding. Pink area is enlarged in (b). Colors at nodes indicate posterior probability of maturity state (blue, immature; pink, mature; violet, uncertain state). A higher resolution version of this image is shown in SOM 1. b) Detail of (a) showing the earliest diverging branches of Coelurosauria. Note that: Compsognathidae is inferred to be diagnosed by immature morphologies, the analysis reconstructed a spurious "young tyrannosaurid" clade and a "nursery grade" at tyrannosauroid base. Clade names in normal font, "nursery groups" in italics.

reconstructed as genuine tyrannosaurids bracketed by *Gorgosaurus* and *Tyrannosaurus* (both taxa coded for both immature and mature semaphoronts; Carr, 2020; Voris et al., 2021), i.e., as members of Tyrannosaurinae (Fig. 4).

The compsognathid-like OTUs have been reconstructed among several branches of Tetanurae (Fig. 4). In particular, *Xunmenglong* resulted among the earliest-diverging branches of the clade. Both *Compsognathus* specimens, *Scipionyx* and *Sciurumimus* resulted members of Megalosauroidea, with *Scipionyx* closer to spinosaurids than the other "compsognathids". *Juravenator* has been reconstructed among several alternative placements in Allosauroidea. Three Jehol Biota "compsognathids" (*Huaxiagnathus*, *Sinocalliopteryx* and *Sinosauropteryx*) and *Mirischia* have been placed along the basalmost branches of Coelurosauria. Another, yet unnamed Jehol Biota "compsognathid" (NGMC 2124, originally referred to *Sinosauropteryx*), has been placed among the earliest branches of Tyrannosauroidea.

A few other OTUs usually placed in Coelurosauria and known uniquely for immature semaphoronts have been placed outside that clade: *Aorun*, considered as an early-diverging coelurosaur or as an early-diverging alvarezsauroid (Choiniere et al., 2013; Xu et al., 2018) is reconstructed as an early-diverging member of Allosauroidea. The fragmentary holotype of the purported coelurosaur *Nedcolbertia* (Kirkland et al., 1998) is also

reconstructed among early-diverging allosauroids. Note that other taxa known for immature semaphoronts have been confirmed in Coelurosauria (e.g., *Nqwebasaurus* in Ornithomimosauria, *Haplocheirus* in Alvarezsauroidea), dismissing a metholodogical artifact biasing the results against placement in the latter clade.

Theropod guild analysis

The hypothesis that the RSC metric is biased by sampling artifacts is rejected because the median of the RSC in each class is significantly distinct from that of the corresponding class in the sample of 500 randomly-generated communities (Mann-Whitney U test for distribution around equal median, $p < 0.0026$). The PCA of the theropod communities based on their RSC values distinctly segregates them based on size class distribution and reveals a faunal pattern in shaping the community structure (Fig. 5). The seven size classes have a variable effect on the distribution of the communities. The two smallest size classes most significantly affect the distribution of the communities in the second quadrant of the distribution. The third and fourth size classes most significantly affect the distribution of the communities in the first quadrant of the distribution. The largest three size classes most significantly affect the distribution of the communities in the fourth quadrant. The amount of coelurosaurian taxa ("coelurosaurian ratio") in the
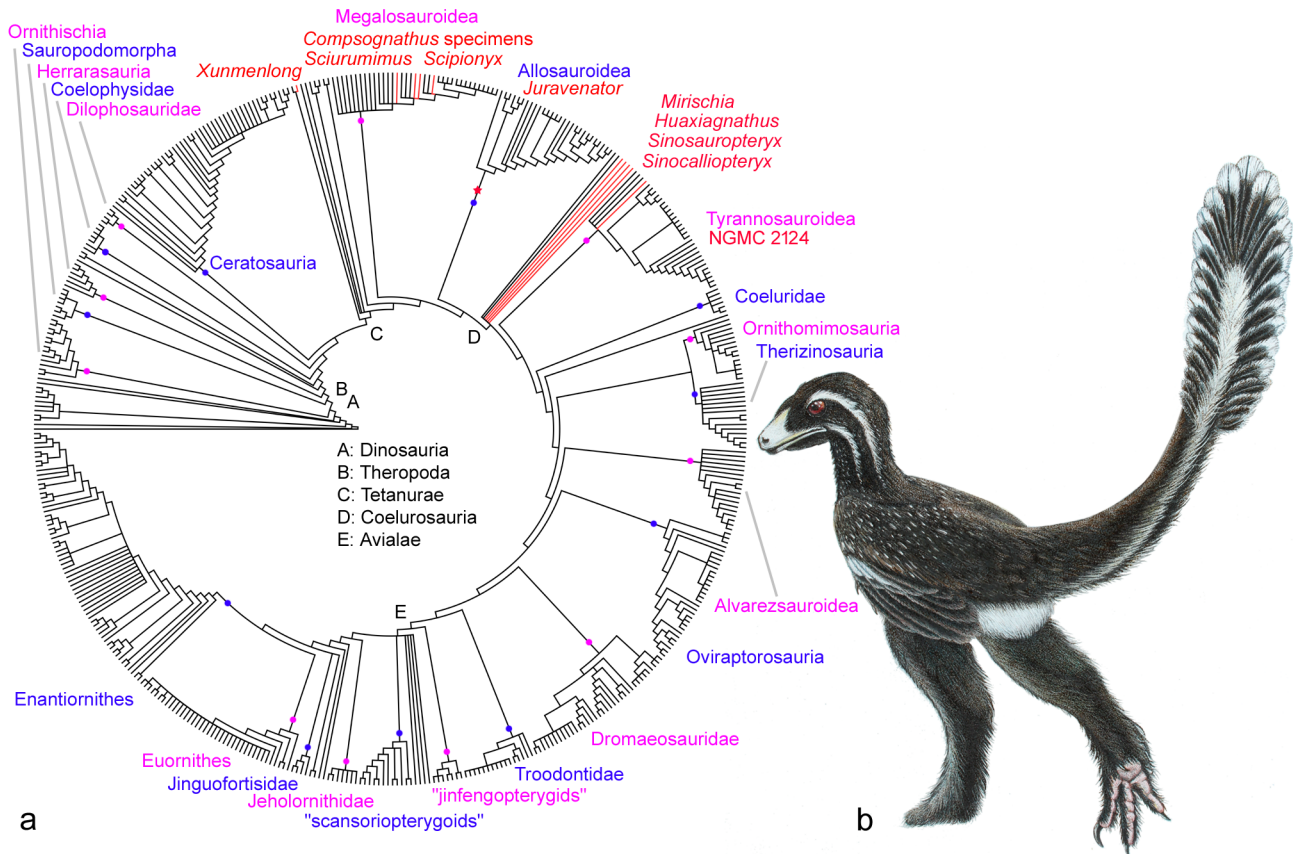
Fig. 4 - a) Reduced strict consensus of the shortest trees found by the phylogenetic analysis using the OSP protocol. Details of the topology shown in SOM 2-3. Key clades indicated by colored nodes. The "compsognathids" indicated by the red branches. The red star in Allosauroidea indicates that *Juravenator* is reconstructed among several alternative placements in that clade. b) Reconstruction of hypothetical earliest bird based on character state optimization at node E (artwork by Loana Riboli).

community is higher among the communities clustered in the second and third quadrants of the distribution. The majority of the tyrannosaur-dominated communities ("tyrannies") is concentrated in the area bracketed by the concave corner described by the biplots of the two smallest and the two largest size classes, with the notable exception of the two pre-Campanian communities (Fig. 5, pink stars; see Holtz, 2021). The triumvirates (sensu Sereno & Brusatte, 2008) are clustered in the fourth quadrant.

The distribution of the small- and middle- size classes among the tyrannies is significantly different from those among the other communities (Fig. 6a), with the tyrannies showing a higher contribution by the smallest classes and the other communities having a higher contribution by the middle-size classes. No significant difference results in the contribution of the large classes among the two groups. The total number of occupied size classes is significantly smaller among the tyrannies than in the other groups (Kruskal-Wallis test for equal medians; H [χ^2]: 7983; Hc [tie corrected]: 8038; $p = 0.0046$; Fig. 6b).

DISCUSSION

Compsognathidae is a "nursery group"

The Implicit Semaphoront Coding test applied to Theropoda showed that this coding artifact produces topologies clustering most of the OTUs based on immature semaphoronts in branches placed close to the root of Coelurosauria (Fig. 3a). In particular (Fig. 3b), the analysis produced a spurious "nursery group" clustering the immature semaphoronts of the tyrannosaurids in a clade distinct from that including their corresponding mature semaphoronts, as expected by analyses using explicit semaphoront coding strategies (Sharma et al., 2017). Analogous "nursery nodes" are reconstructed among Ornithomimosauria and Spinosauridae and based on immature semaphoronts. Furthermore, the earliest diverging nodes of Tyrannosauroidea are reconstructed as being diagnosed by a speciose cluster of immature specimens. Another clade reconstructed as a nursery group and diagnosed by immature morphologies includes the two specimens of *Compsognathus* and other taxa coded from immature semaphoronts (e.g., *Juravenator*, *Scipionyx*): since this clade is, by definition, Compsognathidae (Holtz et al., 2004), the test indicates that the latter cannot be distinguished from spurious clustering due to ontogeny-biased coding artifacts.

The hypotheses tested here stem from the identification of all known compsognathid specimens as immature semaphoronts, regardless to the actual adult size of the species they belong to. A combination of criteria for assessing the ontogenetic stage in fossil vertebrates (Griffin et al., 2021) supports this hypothesis. The
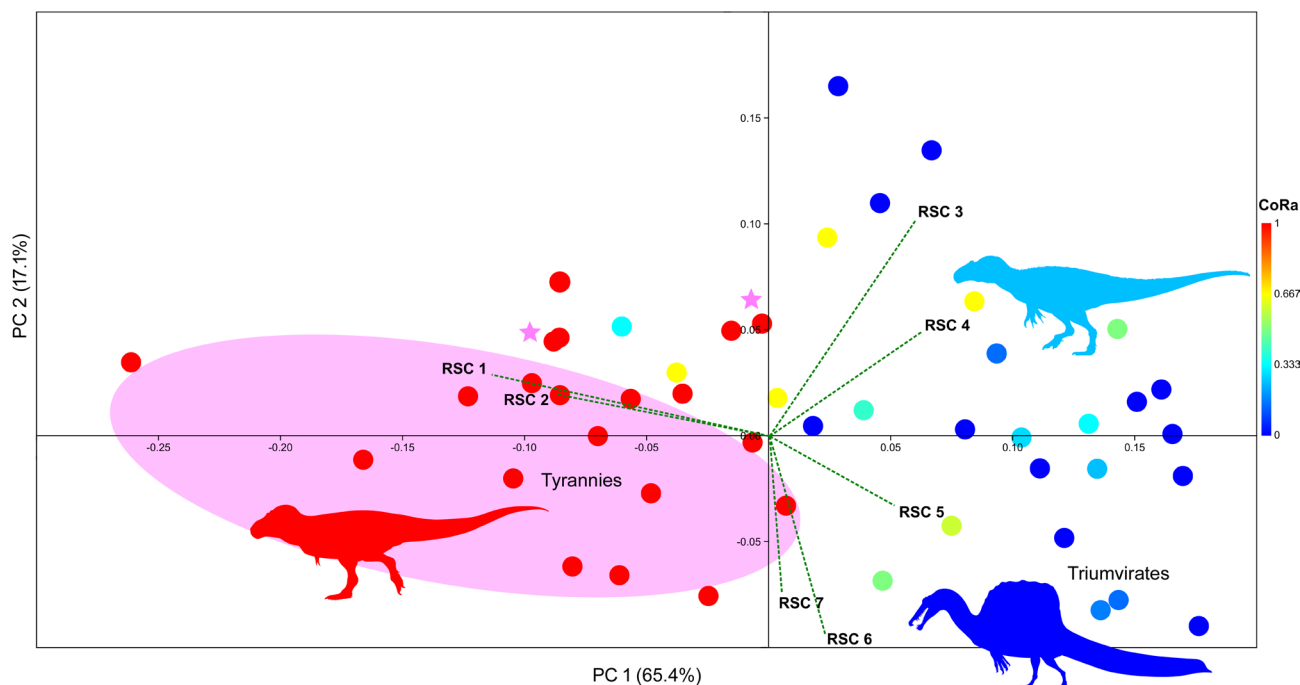
Fig. 5 - Clade-specificity of the size class structure in the main Jurassic and Cretaceous theropod communities. PCA of the RSC values calculated for each community. Community color based on the Coelurosaurian Ratio (CoRa). Biplot of the RSC axes in green. Pink ellipse marks the range of the Campanian-Maastrichtian tyrannies. Pre-Campanian tyrannies marked by the pink stars. Silhouettes from PhyloPic. org (details in Acknowledgements).

body size range of the compsognathids overlaps with that inferred for immature (hatchling and juvenile) individuals of large-bodied theropods (e.g., *Allosaurus*; Rauhut & Fechner, 2005; Carpenter, 2010). Several lines of evidence indicate that the holotypes of *Juravenator*, *Scipionyx, Sciurumimus* and *Xunmenglong* are very immature individuals (Göhlich & Chiappe, 2006; Dal Sasso & Maganuco, 2011; Rauhut et al., 2012; Xing et al., 2019). Both specimens of *Compsognathus* show proportions in the skull and orbit (i.e., round orbit with rostrocaudal diameter about 1/4 of skull length, skull subequal to or longer than femur) and incomplete fusion among the sacral centra which support an immature stage of development (Ostrom, 1978; Peyer, 2006). The specimens of *Sinosauropteryx prima* show skull and orbit proportions, and bone texture typical of immature stages (Currie & Chen, 2001). The largest *Sinosauropteryx* specimen was considered by Currie & Chen (2001) as a reproductively-active "young adult" because it bears two ovoid structures in the belly region, adjacent to the gastralia, interpreted as eggs by those authors. Yet, such "eggs" are topographically more congruent with the intestine tracts (Dal Sasso & Maganuco, 2011; Wang et al., 2022), and gut contents or ingested stones are reported in the same region in other compsognathids (e.g., Hwang et al., 2004; Xing et al., 2012), dismissing the hypothesis that the elements in *Sinosauropteryx* are eggs. Although the ontogenetic stage of the specimens of *Huaxiagnathus* is stated to be unclear (Hwang et al., 2004), the proportions of skull and orbit, and the lack of neurocentral fusion along all vertebral series indicate an immature stage. The unfused contact between ilia and sacral vertebrae, and the incomplete degree of ossification of the obturator fenestrae in the holotype of *Mirischia* (Naish et al., 2004) support

an immature stage of development in this specimen. In the largest known compsognathid, the holotype of *Sinocalliopteryx gigas* (Ji et al., 2007), the skull is longer than the femur, the braincase is completely disarticulated, and all elements in both pectoral and pelvic girdles are separated: all these features indicate an immature stage of development. It is noteworthy that the peculiar tooth morphology shared by all compsognathids was suggested to be a juvenile condition widespread among theropods (Makovicky, pers. obs. in Peyer, 2006), and that the "hook-like" projections of the dorsal neural spines, typical of compsognathids, represent an immature stage of vertebral development (Wilson et al., 2016). In conclusion, none of the compsognathid taxa is based on skeletally mature individuals (Cau, 2021).

Although a few features shared by all compsognathids cannot be interpreted as ontogeny-related, they are homoplastic or size-related conditions with little taxonomic significance: the "hair-like" morphology of the cervical ribs is likely an allometrically-controlled feature shared by taxa with elongate cervical ribs, and is observed in other small-bodied theropods (e.g., *Anchiornis*, pers. obs., 2015); the "fan-shaped" dorsal neural spines are widespread among small-bodied theropods and not unique to compsognathids (e.g., abelisauroids, ornithomimosaurs, troodontids; Xu et al., 2002; Ji et al., 2003; Baiano et al., 2020).

The impact of implicit semaphoront coding artifacts in the published phylogenies of Theropoda is likely beyond the status of the compsognathids, since several analyses so far published have included OTUs based only on immature semaphoronts (e.g., *Dilong, Dubreuillosaurus*, *Epidendrosaurus*, *Eustreptospondylus*, *Huinculsaurus*, *Microvenator, Tanycolagreus*).

The Ontogenetic State Partitioning here introduced is a coding protocol epistemologically superior to previously used coding methods because: 1) by equally sampling the phylogenetic significance of both immature and mature states of all features, it does not violate semaphoront equality (Hennig, 1966); 2) it prevents alternative ontogenetic stages to be erroneously coded as alternative apomorphy-states of the same feature; 3) it does not exclude available information (which is instead an implicit consequence of any "contingent coding"); 4) it does not support spurious clusterings due to ontogeny-biased artifacts (the "nursery groups").

Under the OPS protocol, immature and mature features are considered as distinct partitions, biologically segregated by the irreversibility of the individual ontogenetic process: the homologous features of one partition could not be mixed with those of the other to support "ontogenetic chimeras" diagnosing spurious nodes. All placements of the OTUs coded uniquely from one stage (like the "compsognathids" for the immature stage, or the majority of the other OTUs for the mature stage) are based uniquely on the features shared with other OTUs also coded for (but not necessarily only for) the same stage.

The most relevant differences between the results based on the two coding protocols are the alternative placements of the "immature tyrannosaurids" and of the "compsognathids". The robust ontogenetic data available for the tyrannosaurids (Carr, 2020; Voris et al., 2021) dismisses the validity of the "nursery clade" resulted in the semaphoront coding test which clustered the immature tyrannosaurid semaphoronts outside the clade formed by the mature semaphoronts (Fig. 3), and suggests that the phylogenetic placement of the tyrannosauroids is strongly affected by coding artifacts amplified by the estreme ontogenetic and size disparities in that group. In particular, the placement of *Bagaraatan* and *Raptorex*, both reconstructed by the semaphoront coding test outside Tyrannosauridae, is suggested to be the effect of such method bias. It is noteworthy that recently published analyses, even acknowledging the problematic effect of coding the immature morphology of these two OTUs, have produced topologies similar to that biased by semaphoront coding (e.g., compare figs 23 and 24 in Słowiak et al., 2024, with Fig. 3). On the contrary, the new analysis based on the OSP protocol places both taxa nested among late-diverging tyrannosaurids (i.e., in Tyrannosaurinae): this topology is more in agreement with the rich Asian end-Cretaceous record of the clade, dominated by tyrannosaurines and lacking early-diverging tyrannosauroids (Carr, 2023; Słowiak et al., 2024).

The results of the analysis based on the OSP protocol revise the phylogenetic affinities and the status of the compsognathid-like theropods. The "compsognathids" are reconstructed in various positions among Tetanurae and do not form a monophyletic group nested among early-diverging coelurosaurs, corroborating and expanding the hypotheses originally suggested by Rauhut et al. (2012) and Cau (2021). Although a non-coelurosaurian status for some of these taxa was suggested previously (e.g., Rauhut et al., 2012; Cau, 2021), even those phylogenetic scenarios were variably affected by implicit forms of semaphoront coding. Despite the holotype of *Scipionyx*

shows similarities with the adult morphology of some coelurosaurs (Dal Sasso & Maganuco, 2011) or of some allosauroids (Cau, 2021), both relationships were diagnosed by combining the immature morphology of one taxon with the mature morphology of the other, and are here rejected: the analysis using ontogenetic partitioning found a closer relationships between the Italian theropod and the immature morphology of the spinosaurids (described by Lakin & Longrich, 2019). *Scipionyx* is thus interpreted as a spinosaurid taxon, and its morphology provides information on the juvenile condition of the latter clade. Analogous conclusions could be argumented for the other "compsognathids": *Compsognathus* and *Sciurumimus* shed light on the immature condition of the non-spinosaurid megalosauroids, *Juravenator* illustrates the early juvenile condition of the allosauroids, and the yet unnamed taxon NGMC 2124 shows an immature semaphoront of the early-diverging tyrannosauroids. The interpretation of other "compsognathids" (e.g., *Sinosauropteryx*, *Sinocalliopteryx*) is more controversial, because the analysis did cluster them at the root of Coelurosauria but not directly associated to any other taxon known for mature semaphoronts. They could indicate a yet unknown lineage of early-diverging coelurosaurs whose adult forms are unreported, or might turn being referred to an already known group once additional evidence of the immature semaphoronts of the latter is found.

Exploration of the results shows that the phylogenetic significance of the immature character statements in supporting the reconstructed topologies is proportional to their sampling in the data matrix: contrary to the nodes reconstructed by the previously-used coding methods (e.g., "contingent coding"), under the OSP protocol the immature features are not reconstructed as spurious alternative states of the mature features, but as distinct synapomorphies. Each node is simultaneously diagnosed by two sets of character states (the immature and mature states which diagnose the ontogenetic transitions at that node), which are not mixed together and thus cannot produce "ontogenetic chimaeras". Since this approach prevents the reconstruction of spurious nursery groups, the aprioristic exclusion of the immature morphotypes from the data set is no more justified.

The phylogenetic results of the analysis using the OSP protocol have several macroevolutionary implications for both Theropoda (in general) and the avian ancestry (in particular). In all shortest trees found, the genus *Compsognathus* is nested in an unresolved polytomy with *Megalosaurus*, *Torvosaurus* and the spinosaurid branch: if confirmed by future iterations of this data set, the name Compsognathidae Cope, 1871, could thus be a junior synonym of Megalosauridae Huxley, 1869, and should be abandoned. Other small bodied "unspecialized" theropods, currently considered "primitive" coelurosaurs (e.g., Naish, 2002), might result immature semaphoronts of large-bodied taxa: a re-analysis of their ontogenetic and taxonomic status is thus suggested. One key phase in the evolution of the bird ancestors is defined by early-branching coelurosaurs, and includes the "compsognathids" (e.g., Novas et al., 2012; Brusatte et al., 2014; Cau, 2018). In particular, the phyletic sequence involving the transition from the earliest tetanurans (i.e., mid- to large-bodied forms with a strictly carnivorous
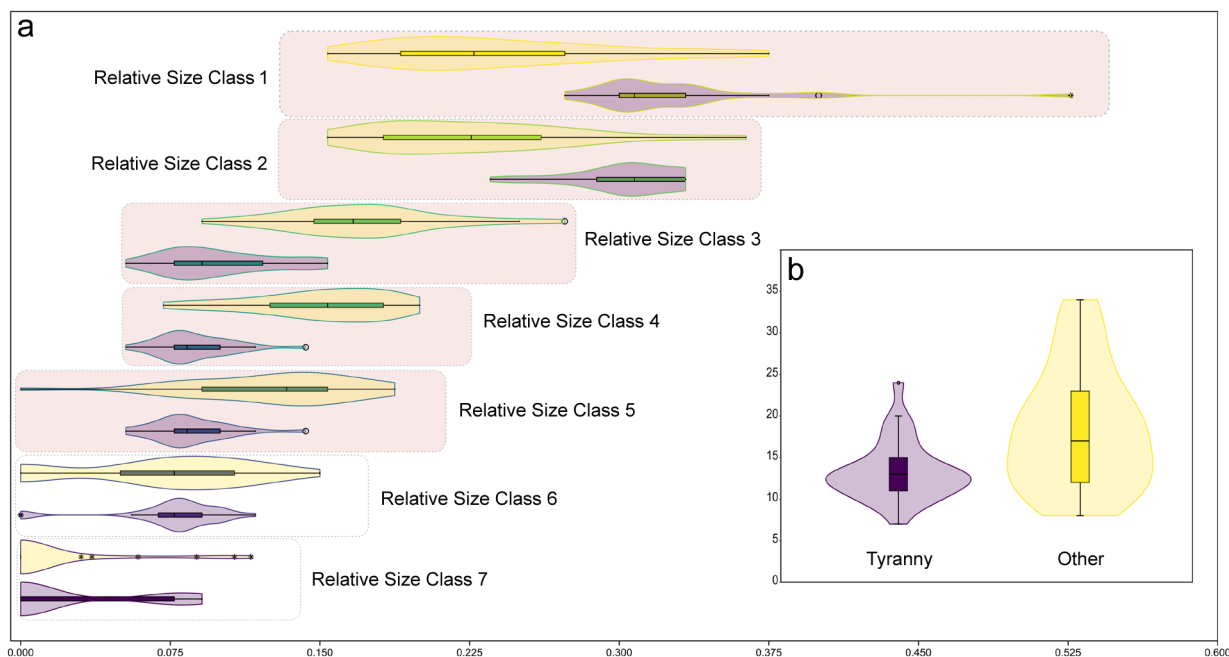
Fig. 6 - Comparison between the structures of the tyrannies and the other theropod communities. a) Distribution of the RSC values among the seven size classes between tyrannies and the other communities. Statistically significant differences marked by the pink areas. In the small size classes, the RSC values are significantly higher in the tyrannies. In the middle size classes, the RSC values are significantly higher in the other communities. There is no significant difference among the groups in the large size classes. b) Distribution of the total number of size classes among the theropod communities. The number of classes in the tyrannies is significantly lower than in the other communities.

diet, lack of true pennaceous feathers, more "reptile-like" brain organization, and relatively short forelimbs) to the maniraptoriforms (i.e., mid- to small-bodied forms with an omnivorous diet, true pennaceous feathers, more "bird-like" brain organization, and relatively longer forelimbs) is usually represented by a series of "compsognathid-like" forms (Holtz et al., 2004). Removing the latter from the avian stem lineage recalibrates the tempo and mode of the body miniaturization which is linked to the occurrence of many bird-like novelties (Lee et al., 2014). Furthermore, the lack of a "compsognathid grade" along the evolution of the avian body plan reconciliates the phylogeny with the embryological sequence observed in living birds (Griffin et al., 2022).

A unified framework for theropod macroevolution

The re-evaluation of the "compsognathids" as immature semaphoronts of non-maniraptoriform tetanurans significantly impacts our interpretation of theropod macroevolution beyond the mere phylogenetics, and extends to the ecological levels. Each compsognathid species could potentially be synonym of another contemporary mid- to large-bodied theropod species found in the same unit and clustered in the same phylogenetic grade. Thus, the taxonomic diversity of the communities including compsognathid species has to be revised and might turn being simplified. This revision might extend to other communities including non-compsognathid taxa currently known uniquely for immature semaphoronts. For example, the tyrannosauroid *Dilong* from the Yixian Formation is currently coded uniquely from immature specimens (Xu et al., 2006).

The OSP analysis found several equally-parsimonious placements for *Dilong* among Tyrannosauroidea (SOM 2). One of these alternative placements is as sister taxon of another Yixian Formation tyrannosauroid, the large-bodied *Yutyrannus*, whose hypodigm currently lacks specimens of the same size classes of the *Dilong* material: if such relationships is confirmed, it might support the two taxa as being synonyms (with *Dilong* being the valid name and its type material expressing the less mature morphology). Analogous revisions might involve the Morrison Formation tyrannosauroids *Stokesosaurus* and *Tanycolagreus*, and the Huincul Formation abelisauroids *Huinculsaurus* and *Ilokelesia.*

The recognition that non-avian theropods were precocial or hyper-precocial at birth (e.g., Varricchio et al., 2002; Dal Sasso & Maganuco, 2011) and that in several cases they went through two-three orders of magnitude size during ontogeny, implies that the ecological roles of their immature stages were radically different from those of the immature semaphoronts of modern-day species of carnivorous birds or mammals (Holtz, 2021). Despite being removed from the systematic and taxonomic lists, from a palaeoecological perspective the "compsognathid" (meant as size class and morphotype) keeps having an ecological role, which is re-attributed to the early growth stages of some large-bodied tetanuran. So far, the discussion on the ecological roles of the immature stages of large theropods has focused on tyrannosaurids, which have been suggested to be ecologically segregated from their mature conspecifics (Holtz, 2021). The "compsognathids" could illuminate on the ecological plasticity experienced by other large-bodied taxa during their life cycles.

The high diversity in gut contents among the "compsognathids" (see above) supports an efficient and generalist carnivorous role for all tetanurans since their earliest growth stages. A special note deserves the gut content of the *Scipionyx* holotype, which includes both fish and terrestrial reptiles (Dal Sasso & Maganuco, 2011): the same feeding diversity is reported uniquely in spinosaurids among large-bodied theropods (Hone & Holtz, 2021), and independently corroborates the novel phylogenetic relationships suggested for the Italian theropod with that clade of penecontemporary tetanurans. Assuming the *Scipionyx* specimen as an immature member of Spinosauridae, suggests that the latter group did not experience a dramatic shift in prey preference along the ontogeny, yet it was characterised by extreme specialization of the craniomandibular morphology (Hone & Holtz, 2021). An extreme semaphoront disparity, in particular in the craniofacial morphology, which led to higher ecomorphological specialization in the adults, could thus be a general pattern among large theropods, not restricted to the tyrannosaurids (Carr, 2020). The generalist body plan shared by the immature morphs usually classified among the "compsognathids" might help explaining the significant impact of homoplasy in theropod phylogenetic reconstructions (e.g., Carrano et al., 2012), and might provide an ontogenetic source for calibrating character state polarity.

The analysis of the guild structure integrating the ontogenetic disparity helps identifying different patterns shaping the theropod communities (Figs 5 and 6). The relatively uniform "compsognathid" morphotype shared by the small-sized (immature) stages of most tetanurans contrasts with the higher diversity and broader ecological disparity expressed at the same size classes by the maniraptoriforms (e.g., Zanno & Makovicky, 2011). On the contrary, the non-maniraptoriforms expressed a higher disparity among the large- to giant-sized classes (Holtz et al., 2004; Holtz, 2021). A distinct distribution of the size classes among the coelurosaur-dominated communities compared to the other faunas is thus expected. Holtz (2021) demonstrated structural differences between the tyrannosaurid-dominated communities (here named "tyrannies") and the other theropod faunas. The analysis performed here confirms and expands that scenario. Even taking into account the contribution by the immature stages, the "mid-Cretaceous" triumvirates (sensu Sereno & Brusatte, 2008) represent an extreme version of the pattern shared by the communities lacking coelurosaurs, and are characterized by a relatively depauperate contribution by the small size classes (Fig. 5). The limited ecomorphological segregation among the immature semaphoronts of the sympatric non-coelurosaurian theropods might had acted as a strong interspecific selective regime which favored the evolution of larger body size and more extreme niche partitioning among the adult forms of the same communities. The tyrannies differ from the other communities in the more important contribution by the small size classes simultaneously combined with the depauperate contribution by the mid-sized classes (Fig. 5). Yet, the tyrannies cluster close to the other coelurosaur-dominated communities, and emerged as a particular version of the same pattern (Fig. 5). Contrary to the expectation, the tyrannies do not differ from the other communities with giant taxa in the contribution by the large size classes: their peculiar structure is mainly due to a re-modulated contribution between the small- and mid-sized classes (Fig. 6a). Given that the tyrannies have a number of occupied size classes significantly smaller then in other communities (Fig. 6b), the emergence of the tyrannosaurid-dominated faunas (and the evolution of the "niche assimilation" sensu Holtz, 2021) should be explained focusing on the peculiarities of the non-tyrannosaurid component of these communities. The hypothesis suggested here is that the tyranny-like structure resulted by the combination of two factors, a historical contingency which freed the large-sized niches (i.e., the demise of the non-coelurosaurian theropods in Laurasia around the Cenomanian-Turonian boundary; Zanno & Makovicky, 2013) and a mix of biological constraints which precluded the occupation of such niches by the non-tyrannosaurids (i.e., the acquisition of a bird-like bauplan among the maniraptoriforms). The first hypothesis is confirmed by the community structure of the oldest (pre-Campanian) tyrannies, which does not differ from those of the other coelurosaur-dominated faunas (Fig. 5, pink stars): the "typical" structure of the tyrannies was thus acquired only after the Cenomanian-Turonian, following the demise of the non-coelurosaurian component (Zanno & Makovicky, 2013). The second hypothesis assumes that a combination of biological novelties prevented the maniraptoriforms to compete with the tyrannosauroids in the occupation of the predatory guilds of large size. Among Maniraptoriformes, size classes 6 and 7 are known to be occupied only by a small number of non-maniraptoran taxa, none of which is interpreted as hypercarnivorous (e.g. *Therizinosaurus*; Senter & James, 2010; Zanno & Makovicky, 2011; *Deinocheirus*; Lee et al., 2014; note that the phylogenetic analysis used in this study supports therizinosauroids as non-maniraptorans and sister taxa of the ornithomimosaurs). Among maniraptorans, only a few oviraptorosaurs are known to reach size class 6 (e.g., *Gigantoraptor*; Xu et al., 2007; Tanaka et al., 2018), whereas no paravian is known at size classes higher than 5 (Holtz, 2021; Sues et al., 2022). This pattern constrasts with the large number of non-maniraptoran lineages which successfully occupied the largest size classes (Paul, 1988; Sereno & Brusatte, 2008; Carrano et al., 2012; Holtz, 2021), and suggests a combination of clade-specific factors negatively biasing maniraptoran diversification at giant body size. This scenario is supported by several morphological and physiological features, gradually acquired along the avian stem lineage (Cau, 2018), which were co-opted by (and led to) body miniaturisation in the closest relatives of Avialae (Lee et al., 2014). Bird-like features uniquely acquired by the maniraptorans among theropods and that could be interpreted as less adaptive at the largest size classes include reproductive and nesting constraints related to the evolution of an avian-like incubation behaviour (see Tanaka et al., 2018), the re-organization of the musculoskeletal system toward a more "knee-based" locomotory model (Hutchinson, 2001a, b) with loss of the peculiar biomechanical adaptations acquired by the large-bodied macropredatory averostrans (see Allen et al., 2021), and the acquisition of a more bird-like endothermic termophysiology (Li et al., 2014) which is known to enforce a decrease in maximum body

size among terrestrial vertebrates (Burness et al., 2001). Lacking all these biological constraints, early Late Cretaceous tyrannosauroids (e.g., *Alectrosaurus*; see Holtz, 2021) outcompeted the sympatric maniraptoran predators of similar size (e.g., *Achillobator*; see Holtz, 2021) in the occupation of the largest size classes freed after the demise of the allosauroids.

The "mid-Cretaceous" extinction of the non-coelurosaurian theropods in Asiamerica has been so far discussed focusing on the taxonomic turn-over at the largest size classes (i.e., between allosauroids and tyrannosauroids; e.g., Bakker et al., 1992; Zanno & Makovicky, 2013). Yet, the recognition that the "compsognathids" are immature semaphoronts of many tetanuran groups (including the allosauroids) implies that the extinction of Allosauroidea also impacted the ecological relationships among the small-size guilds to which the "compsognathids" are usually referred (Holtz, 2021). Fossil evidence supports trophic interactions between "compsognathid-like" forms and maniraptorans, with possible predation of the first over the latter (Xing et al., 2012): this suggests that the "full impact" of the allosauroid extinction at the beginning of the Late Cretaceous (Zanno & Makovicky, 2013) likely extended to the maniraptoriforms. In analogy with the coeval tyrannosaurid success, the significant adaptive radiation of the maniraptorans in Asiamerica during the second half of the Cretaceous (e.g., Holtz, 1994; Zanno & Makovicky, 2011) might had been the consequence of the novel ecological regime which followed the extinction of all non-coelurosaurian theropods.

Although the evolution of the Cenozoic birds is traditionally analysed separately from their Mesozoic relatives (both avialans and non-avialan theropods), there is not biological justification for considering their evolution radically distinct from the rest of Theropoda, and may be incorporated in the general theory here defined. Could the large-scale macroevolution of birds after the K-Pg boundary mass extinction be interpreted as a direct expression of the same patterns recognised among the Mesozoic theropods? In particular, modern birds show the combination of biological constraints which prevented the maniraptorans to compete with the tyrannosauroids in the occupation of the large-size guilds (Tanaka et al., 2018; Allen et al., 2021). Accordingly, it is predicted that birds cannot evolve giant taxa and thus have diversified mainly into the smallest size classes: this prediction perfectly fits the Cenozoic fossil record of birds and the modern avifaunas. Furthermore, the paedomorphic nature of the avian bauplan compared to other theropod morphotypes (Bhullar et al., 2012) implies that the among-semaphoront disparity in birds is less dramatic than in the non-avian lineages: under the paradigm here defined, this predicts a limited potential for the avian faunas to diversify into communities analogous to triumvirates or tyrannies, leaving potential ecospace available for other sympatric clades of predatory tetrapods (e.g., mammals, crocodylomorphs): this second prediction is also in agreement with the Cenozoic fossil record. Even today, by means of their avian branch, dinosaurs keep being a very speciose and ecologically diverse group of tetrapods, and their numerical success has not been affected by the end-Cretaceous mass extinction. Yet, the Cenozoic history of birds is usually depicted as a radical discontinuity from the Mesozoic "reign of the reptiles". Under the paradigm here discussed, we can instead re-evaluate the Cenozoic history of Dinosauria as a coherent continuation of patterns already established in the Mesozoic. Accordingly, the Cenozoic part of dinosaur history is a "planet-scale version" of the theropod communities seen in Asiamerica during the second half of the Late Cretaceous: a coelurosaur-only fauna originated after an extinction event which bottlenecked the body models by removing those best planned to diversify at the largest size classes. The explosive radiation of small-bodied forms and the evolution of only a few ground-dwelling hypercarnivorous lineages during the Cenozoic, none of which above size class 5 (e.g., Alvarenga & Höfling, 2003), is the coherent expression of the maniraptoran bauplan inherited by the living dinosaurs.

CONCLUSIONS

Compsognathidae is a "nursery group", a spurious taxonomic cluster due to the implicit semaphoront coding bias which has affected most of the theropod phylogenetic analyses so far published. Once the coding artifacts are removed, and the character sampling is not biased against immature features, the "compsognathids" are reconstructed as juvenile semaphoronts of non-maniraptoriform tetanurans. Contrary to the notion that immature morphologies are source of "phylogenetic noise", the amount of phylogenetic significance of the immature characters is proportional to their sampling, as expected by the total evidence approach advocated by phylogenetic systematics: further investigation of the growth series and on the diversity among immature stages would significantly impact the resolution of controversial areas of the theropod phylogeny. The coding protocol introduced here is explicitly designed to be quickly applied to published data matrices and does not require time-consuming recoding of already-coded OTUs: applications to other clades characterized by a significant semaphoront disparity (e.g., hadrosaurids, ceratopsids) might help solving their phylogenetic structure.

The "compsognathid body plan" represents the generalized immature condition of megalosauroids, allosauroids and early-diverging coelurosaurs, with the notable exception of tyrannosaurids: this implies that in the theropod communities dominated by non-coelurosaurs (e.g., the "triumvirates") the ecological diversity among the smallest size classes was less marked than among the large-sized classes. An opposite trend is documented in the coelurosaur-dominated faunas (like the "tyrannies"), suggesting a clade-specific pattern in the structure of the predatory theropod communities. The origin of the Asiamerican tyrannies of the Late Cretaceous and the evolution of the tyrannosaurid "niche assimilation" could be explained by a combination of historical contingencies (the extinction of the non-coelurosaurian tetanurans in Laurasia) and bauplan constraints which penalized the maniraptoriforms in the occupation of the hypercarnivorous niches of large body size.

The general theory here defined could help explaining why the great success of birds in the Cenozoic did not

replicate many community structures expressed by their Mesozoic relatives.

Thomas Huxley was so concerned by the peculiar morphology of *Compsognathus* to consider it as representing a group close to yet distinct from the dinosaurians known at his time. Although the interpretation proposed by Huxley to explain such distinction is now considered inaccurate, his concern was well-grounded: what distinguishes *Compsognathus* from *Iguanodon* and *Megalosaurus* is real but is not phylogenetic, it is ontogenetic.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-631/

Captions of supplementary figures
SOM 1 - Higher resolution version of Fig. 3a. Semaphoront coding test. Bayesian inference of maturity state at nodes using the agreement subtree produced by the phylogenetic test based on the explicit semaphoront coding. Blue: immature morphology. Pink: mature morphology. Violet: mixed semaphoront morphologies.
SOM 2 - Non-maniraptoromorph section of the reduced strict consensus of the shortest trees reconstructed by the phylogenetic analysis using the novel coding protocol (maniraptoromorph section in SOM 3). Letters at branches indicate the "wildcard" OTUs pruned from topology. Black silhouettes indicate the placement of the "compsognathids" (names in bold) among the branches of Tetanurae. Silhouettes from PhyloPic.org (details in Acknowledgements). Abbreviations: a, *Austrocheirus*; b, *Bicentenaria*; c, *Chuandongocoelurus*; d, *Dahalokely*; e, *Dracoraptor*; f, *Flexomornis*; g, *Kelmayisaurus*; h, *Maip*; i, *Microvenator*; j, *Moros*; k, *Shanag*; l, *Tyrannomimus*; m, *Erectopus superbus*; n, MCF PVPH 320; o, *Dilong*; p, *Eosinopteryx*; q, *Huinculsaurus*; r, *Juravenator*; s, *Ligabueino*; t, *Ningyuansaurus*; u, *Santanaraptor*; v, *Xunmenglong*; w, OPH 2211.
SOM 3 - Maniraptoromorph section of the reduced strict consensus of the shortest trees reconstructed by the phylogenetic analysis using the novel coding protocol (non-maniraptoromorph section in SOM 2). Letters at branches indicate the "wildcard" OTUs pruned from topology. Abbreviations: a, *Austrocheirus*; b, *Bicentenaria*; c, *Chuandongocoelurus*; d, *Dahalokely*; e, *Dracoraptor*; f, *Flexomornis*; g, *Kelmayisaurus*; h, *Maip*; i, *Microvenator*; j, *Moros*; k, *Shanag*; l, *Tyrannomimus*; m, *Erectopus superbus*; n, MCF PVPH 320; o, *Dilong*; p, *Eosinopteryx*; q, *Huinculsaurus*; r, *Juravenator*; s, *Ligabueino*; t, *Ningyuansaurus*; u, *Santanaraptor*; v, *Xunmenglong*; w, OPH 2211.

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