



The assembly of the avian body plan: a 160-million-year long process

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ABSTRACT - *Birds are one of the most successful groups of vertebrates. The origin of birds from their reptilian ancestors is traditionally rooted near the Jurassic "Urvogel" Archaeopteryx, an approach that has contributed in defining the dichotomy between the "reptilian" (pre-Archaeopteryx) and "avian" (post-Archaeopteryx) phases of what is instead a single evolutionary continuum. A great and still ever increasing amount of evidence from the fossil record has filled the gaps between extinct dinosaurs, Mesozoic birds and modern avians, and led to the revision of the misleading dichotomy between pre- and post-Archaeopteryx stages in the evolution of bird biology. Herein, the progressive assembly of the modern avian body plan from the archosaurian ancestral condition is reviewed using a combination of phylogenetic methods. The stem lineage leading to modern birds is described using 38 internodes, which identify a series of progressively less inclusive ancestors of modern birds and their Mesozoic sister taxa. The 160-million-year long assembly of the avian bauplan is subdivided into three main stages on the basis of analyses of skeletal modularity, cladogenetic event timing, divergence rate inference and morphospace occupation. During the first phase ("Huxleyian stage": Early Triassic to Middle Jurassic), the earliest ancestors of birds acquired postcranial pneumatization, an obligate bipedal and digitigrade posture, the tridactyl hand and feather-like integument. The second phase ("Ostromian stage": second half of Jurassic) is characterised by a higher evolutionary rate, the loss of hypercarnivory, the enlargement of the braincase, the dramatic reduction of the caudofemoral module, and the development of true pennaceous feathers. The transition to powered flight was achieved only in the third phase ("Marshian stage": Cretaceous), with the re-organisation of both forelimb and tail as flight-adapted organs and the full acquisition of the modern bauplan. Restricting the investigation of the avian evolution to some Jurassic paravians or to the lineages crown-ward from Archaeopteryx ignores the evolutionary causes of over 60% of the features that define the avian body. The majority of the key elements forming the third phase are exaptations of novelties that took place under the different ecological and functional regimes of the Huxleyian and Ostromian stages, and cannot be properly interpreted without making reference to their original historical context.*

RIASSUNTO - [La costruzione del piano corporeo aviano: un processo lungo 160 milioni di anni] - *Gli uccelli sono uno dei gruppi di vertebrati di maggiore successo. L'origine degli uccelli dai loro antenati rettiliani è tradizionalmente ancorata intorno allo "Urvogel" giurassico Archaeopteryx; questo approccio ha consolidato la distinzione tra una fase "rettiliana" (precedente Archaeopteryx) ed una "aviana" (successiva ad Archaeopteryx) in quello che è invece un singolo continuum evolutivo. Una crescente quantità di evidenze dal registro fossilifero ha colmato le lacune esistenti tra i dinosauri non-aviani, gli uccelli mesozoici e quelli moderni, e ha portato alla revisione della fuorviante dicotomia tra fasi pre- e post-Archaeopteryx nell'evoluzione della biologia aviana. Il progressivo assemblaggio del moderno piano corporeo aviano è qui discusso usando una combinazione di metodi filogenetici. La linea filetica che conduce agli uccelli moderni è descritta da 38 internodi, che identificano una serie progressiva di antenati condivisi tra gli uccelli attuali e i loro sister group mesozoici. I 160 milioni di anni di durata della costruzione del bauplan aviano sono suddivisi in tre fasi principali sulla base di analisi della modularità scheletrica, della cronologia degli eventi cladogenetici, dei tassi di divergenza, e delle regioni del morfospazio occupate. Durante la prima fase (detta "huxleyana": dal Triassico Inferiore al Giurassico Medio), gli antenati degli uccelli svilupparono la pneumatizzazione postcraniale, una postura bipede obbligata e digitigrada, la mano tridattila e un tegumento simile al piumaggio. La seconda fase ("ostromiana": seconda metà del Giurassico) è caratterizzata da un più elevato tasso di evoluzione divergente, la perdita dell'ecologia ipercarnivora, l'espansione dell'endocranio, la drammatica riduzione del modulo caudofemorale, e lo sviluppo di piumaggio pennaceo. La transizione al volo battuto fu sviluppata solo nella terza fase ("marshiana": Cretacico), con la riorganizzazione dell'arto anteriore e della coda in organi adatti al volo, e la completa acquisizione del bauplan moderno. Restringere l'indagine sull'evoluzione aviana ad alcuni paraviani giurassici o alle linee successive ad Archaeopteryx significa ignorare la causa di oltre il 60% delle caratteristiche che definiscono il modello corporeo degli uccelli. La maggioranza degli elementi chiave che definiscono la moderna fase dell'evoluzione aviana sono exaptation di novità occorse sotto differenti regimi ecologico-funzionali nelle fasi huxleyana e ostromiana, e non possono essere propriamente interpretati senza fare riferimento al contesto storico della loro origine.*

INTRODUCTION

Plato had defined Man as an animal, biped and featherless, and was applauded. Diogenes plucked a fowl and brought it into the lecture-room with the words, "Behold Plato's man!"

(Diogenes Laërtius, in Hicks, 1925, p. 40)

While I appreciate their acceptance of my conclusions about the ancestral affinities of Archaeopteryx and later birds, I reject the assertion by Bakker & Galton that the avian radiation is merely an aerial exploitation of

basic dinosaurian physiology and structure, as well as their reasoning that birds should therefore be classified as dinosaurs. [...] I confess that I am unable to accept such theropods as Tyrannosaurus and Allosaurus as "birds", and therefore have little sympathy with this re-classification scheme either.

(John Ostrom, 1976, p. 172)

The birds (AVES Linnaeus, 1758) represent the most speciose lineage among the six forming the extant tetrapod vertebrates (the other lineages being amphibians, mammals, lepidosaurs, turtles, and crocodiles). Under

an evolutionary and phylogenetic framework, birds are diapsid amniotes and form the archosaurian clade with crocodiles and their relatives. Traditionally, the evolution of birds is anchored to *Archaeopteryx* Meyer, 1861, with the iconic “*Urvogel*” more or less explicitly assumed as “transitional step” between the reptilian and the avian grades (Ostrom, 1976). The use of *Archaeopteryx* as key point along the reptile-avian transition has aimed to conciliate the evolutionary paradigm with the traditional separation between reptiles and birds (which precedes the advent of taxonomy as a scientific discipline) that is followed in non-phylogenetic taxonomies (Hennig, 1975; Dupuis, 1984), and is established in the academic - and terminological - independence of herpetology and ornithology (Prum, 2002; Harris, 2004).

This typological framework is among the most consolidated in vertebrate zoology, and is still retained, more or less explicitly, in the recent scientific literature. This is evidenced by the common use of vernacular expressions including the negative adjective “non-avian” associated to clade names now known to include birds (e.g., “non-avian dinosaur”). Even after the recognition of the evolutionary continuity between the (other) dinosaurs and the extant birds (Ostrom, 1976; Gauthier & Padian, 1985), the former are often grouped in the artificial context of the “non-avian” grade, which is thus considered as an useful biological category (even if explicitly defined as non-monophyletic), qualitatively distinct from the birds (Fig. 1). In literature, the adjective “non-avian” is more frequently associated with the terms “theropods” and “maniraptorans” than to any other name of clades that include birds (pers. obs., Fig. 2). This shows that the typological (non-phylogenetic) concepts of “theropod” and “maniraptoran” (implicitly assumed in the “non-avian” categorisation) are more frequently-mentioned than those of other groups. Ironically, while “Theropoda” was erected over a century ago (Marsh, 1881) and was used for decades as a “strictly reptilian” group (i.e., not including birds), “Maniraptora” was explicitly erected in a phylogenetic systematic context as a bird-bearing clade (Gauthier, 1986)! This is further paradoxical, given the considerable amount of studies establishing the theropodan and maniraptoran nature of birds, published during the last four decades (e.g., Gauthier & Padian, 1985; Gauthier, 1986; Padian & Chiappe, 1998; Norell et al., 2001; Paul, 2002; Prum, 2002; Agnolín & Novas, 2013; Xu et al., 2014).

If “birds are maniraptoran theropods” is so vehemently remarked, why the paraphyletic “non-avian” subgroups of both Theropoda and Maniraptora are so frequently used? It must be remarked that paraphyletic groups represent arbitrary categories that do not correspond to biological phenomena (Gauthier & Padian, 1985), but may be retained as taxonomic tools due to their established explanatory value (Rieppel, 2005). At least for the members of Maniraptora, the analysis of the morphological disparity rejects an explanatory value for the use of the paraphyletic “non-avian maniraptoran” group, as it does not represent a coherent ecomorphological cluster distinct from that including *Archaeopteryx* and birds (Brusatte et al., 2014). This result for Maniraptora automatically invalidates any possible explanatory value also for “non-avian theropods”, because the latter category includes all

taxa included in the “non-avian maniraptorans” category (Gauthier, 1986; Prum, 2002). Thus, the persistent use in literature of some paraphyletic grades of the avian lineage (even if used as just vernacular terms) is not justified by epistemological reasons (e.g., Rieppel, 2005). This analysis of the vernacular taxonomy illuminates an implicit pre-Darwinian background, still persistent in the current age of phylogenetic systematics and feathered dinosaurs. Even if not rigorously defined as the technical taxonomic nomenclature, vernacular expressions are a form of taxonomy themselves, and thus they reflect (and consolidate) the theories on the structure of the world (Gould & Vrba, 1982). In this case, the persistent use of paraphyletic tools in avian evolutionary literature not only underestimates the evolutionary continuity between birds and those “groups” defined by the tools used, but inflates the evolutionary significance of those taxa, like *Archaeopteryx*, placed close to the arbitrary boundary between the two categories of “non-avian” and “avian”. Although the gradual evolutionary continuity between birds and other dinosaurs is probably well-consolidated among archosaur palaeontologists, the perception of the actual distance between the avian and “reptilian” body plans is more problematic among non-palaeontologists (see Prum, 2002).

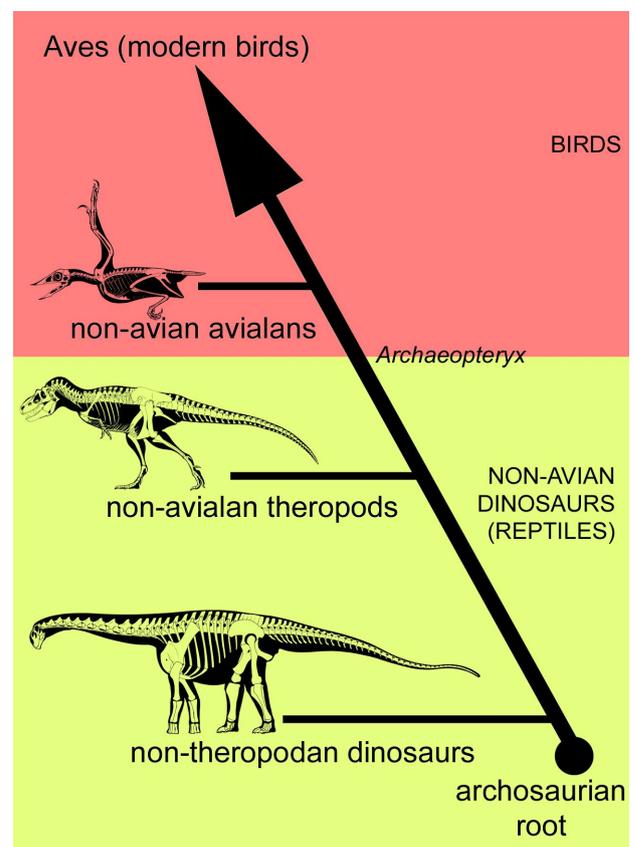


Fig. 1- The arbitrary boundary between birds and non-birds. The traditional representation of the avian evolution is a single linear transition from reptiles to birds, with *Archaeopteryx* as “origin” of the avian lineage. This misleading scenario is implicitly retained even under the phylogenetic paradigm: *Archaeopteryx* defines the boundary between birds and an arbitrary grade, the “non-avian reptiles/dinosaurs”. Skeletal reconstructions by Marco Auditore and Lukas Panzarin.

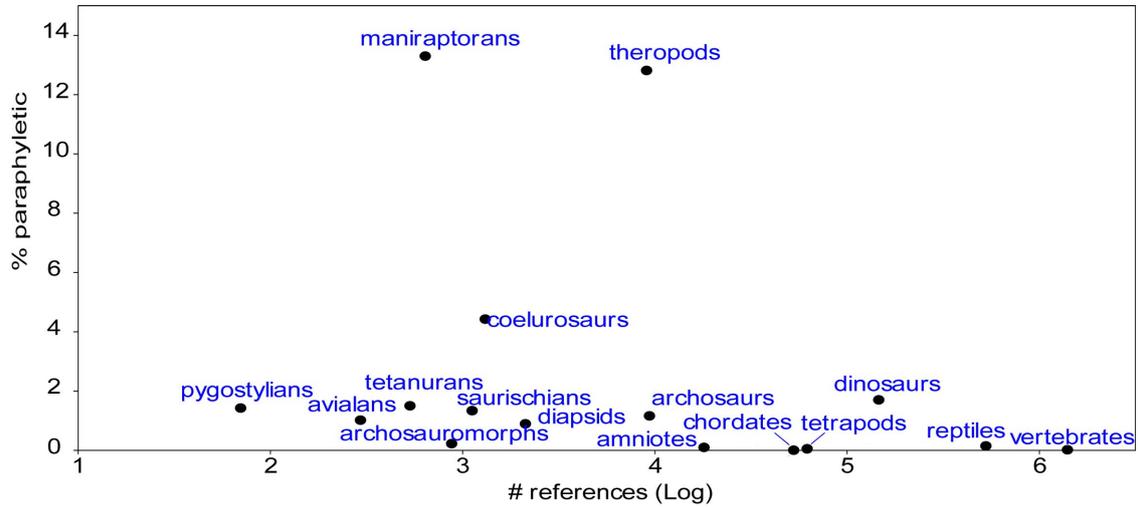


Fig. 2 - All clades are monophyletic, but some clades are more monophyletic than others. Frequency of association of the “non-avian” adjective with the most commonly-mentioned vernacular names of avian-including clades in technical publications (source, Google Scholar, retrieved 7 March, 2018). While this paraphyletic use is marginally frequent with most names (< 5% of mentions), it represents about 13% of the mentions of both “maniraptorans” and “theropods”.

The traditional division between herpetological (“pre-*Archaeopteryx*”) and ornithological (“post-*Archaeopteryx*”) parts of the avian evolution should be abandoned, as it is fundamentally misleading (e.g., Harris, 2004). An alternative approach, that follows the paradigm of the phylogenetic systematics, recognises the whole lineage stemming from the divergence of the birds and their closest living sister group (crocodiles) as the necessary setting for a complete interpretation of the bird biology. The history of the avian branch thus starts from the archosaurian root (i.e., the node defined by the last common ancestor of birds and crocodiles), and not from an arbitrary point defined around *Archaeopteryx*. This approach recognises that the most informative part of the avian branch of ARCHOSAURIA Cope, 1869, is the least inclusive group including all living birds (*AVES sensu stricto*: the avian crown group, Gauthier, 1986; but see Padian & Chiappe, 1998, for the use of a more inclusive definition for the name *AVES*). The much larger yet relatively less known part of the avian branch is formed by all fossil forms not included in *AVES s.s.* but closer to living birds than to the other living reptiles (the avian stem-group). Following this approach, the subset of the avian stem group formed by the series of branches that leads to the origin of the crown group forms the Avian Stem-Lineage (ASL). The series of evolutionary novelties gained along the ASL describes the progressive assembly of the avian body plan during over 160 million years, from the origin of archosaurs (Early-Middle Triassic; Nesbitt et al., 2017) to the root of the avian crown group (latest Cretaceous or earliest Palaeogene; Clarke et al., 2005; Lee et al., 2014a).

Although the close relationships between birds and dinosaurian archosaurs was first recognised in the late XIX Century (Huxley, 1868), for most of the XX Century this hypothesis received secondary attention, with dinosaurs and birds usually regarded as unrelated lineages of the archosaurian radiation, rooted by distinct “theodontians” of the Triassic (see historical review in Ostrom, 1976). The modern concept of the direct dinosaur-

bird relationships was introduced by Ostrom (1976), who demonstrated that among all fossil reptiles, the small-bodied theropod dinosaurs are those with the greatest morphological similarity with *Archaeopteryx*. Under that phylogenetic scenario, living birds are highly-modified theropod dinosaurs. Barsbold (1983) further elaborated the concept of a close evolutionary linkage between birds and theropod dinosaurs, suggesting that the different combinations of bird-like features present in the various groups of theropods demonstrate a general “ornithisation” trend among these taxa, which culminated in the particular lineage including *Archaeopteryx*. During the same decade, the distribution of the avian-like features among the reptiles was finally analysed through the application of the phylogenetic systematic methods, confirming Ostrom’s scenario (Gauthier, 1986). The “ornithisation” of Barsbold (1983) is thus a complex pattern that combines those avian synapomorphies distributed along the ASL with the numerous avian-like features independently gained by the sister-taxa of birds (Holtz, 2001). The dinosaurian heritage of birds was definitively supported by the discovery of feathers and feather-like integumentary structures among unambiguous dinosaurian taxa (Ji & Ji, 1996; Chen et al., 1998; Ji et al., 1998). During the last 25 years, a growing amount of discoveries has significantly filled both sides of the “reptile-bird discontinuity”. Along the crown-ward side, dozens of new Mesozoic birds have revealed some of the morphological, ecological and behavioural stages between the grade of *Archaeopteryx* and the modern birds; along the other side, several biological features, traditionally restricted to birds among living vertebrates, have been documented in many dinosaurian clades (see reviews in Makovicky & Zanno, 2011; Xu et al., 2014).

Among the first using the quantitative methods of phylogenetic systematics, Gauthier (1986) is one of the most influential studies attempting to reconstruct the affinities of birds among dinosaurs. The phylogenetic and taxonomic system introduced by Gauthier (1986) has inspired most of the theropod and stem-avian works of the last three decades. In particular, Gauthier (1986)

introduced a series of scions (i.e., monophyletic groups including the crown clade and a subset of the stem branches; Budd, 2001) or re-defined previous non-monophyletic groups as avian scions. For example, saurischians and theropods were re-defined as the pan-avian scions not including, respectively, ornithischians and sauropodomorphs; tetanurans and maniraptorans were introduced as the pan-avian scions excluding, respectively, ceratosaurians and ornithomimosaurs. During the last 30 years, dozens of analyses have progressively expanded the sampling and improved both completeness and resolution in the phylogenetic investigation of the stem avians (e.g., Sereno et al., 1996, 1998; Sereno, 1999; Holtz, 2000; Norell et al., 2001; Carrano et al., 2002; Rauhut, 2003; Holtz et al., 2004; Sereno et al., 2004; Makovicky et al., 2005; Carrano & Sampson, 2008; Smith et al., 2008; Xu et al., 2009; Benson et al., 2010; Carrano et al., 2012; Naish et al., 2012; Godefroit et al., 2013b; Brusatte et al., 2014; Lee et al., 2014b; Cau et al., 2017; Lefèvre et al., 2017). The present contribution focuses on the assembly of the body plan of birds along the whole ASL, and reconstructs the large-scale patterns during the “ornithisation”, here defined as the progressive accumulation of the features distinguishing living birds from the other living reptiles.

MATERIAL AND METHODS

The phylogenetic data set includes 132 operational taxonomic units scored for 1781 morphological character statements (Supplementary Online Material). Character statement definitions follow the recommendations in Sereno (2007) and Brazeau (2011), and were in their large majority modified versions of character statements used in previous studies on theropod phylogeny (see Cau et al., 2017, supplementary information, for the character list and source of definitions). Taxon sampling is based on a large-scale phylogenetic analysis of the pan-avian clade (Cau, in prep.) and includes representatives of all main pan-avian groups, each represented by two or more species/genus-level taxa. Although pterosaurs are usually placed among the basalmost members of the pan-avian clade (e.g., Nesbitt et al., 2017), the ancestral condition of these highly modified flying reptiles is problematic (Dalla Vecchia, 2013): pending a large-scale analysis of pterosaur relationships that accurately samples the Triassic disparity of the clade, they are provisionally excluded from the analysis of the ASL. Taxa included in this version of the analysis were chosen based on a balanced series of criteria, such as amount of skeletal completeness (preferring most complete taxa and those sampling poorly known anatomical regions instead of fragmentary taxa or those having character combinations redundant with other better preserved taxa), inferred phylogenetic position relative to other members of the same subclade (i.e., using a consensus among recently published phylogenies as reference, the earliest-diverging members were preferred over members of late-diverging subclades), and stratigraphic significance (preferring oldest taxa of a clade to the youngest members). The data set was analysed using maximum parsimony and Bayesian inference integrating stratigraphic information as tree

search strategies. Parsimony analyses were performed using TNT vers. 1.5 (Goloboff et al., 2008). Given the large size of the data set, the search strategy involved 100 “New Technology” search analyses using the default setting, followed by a series of “New Technology” search analyses exploring the tree islands found during the first round. Then, the analysis explored the tree islands recovered during the “New Technology” analysis rounds, using “Traditional Search” analysis and saving up to 99.999 shortest trees (default maximum storage in TNT). Nodal support was calculated saving all trees up to ten steps longer than the shortest topologies found and using the “Bremer Supports” function of TNT. Bayesian analysis integrated the morphological data used for the parsimony analysis with the absolute age (in million years before the present, Mya) of each terminal taxon. The combined morphological and stratigraphic data set was analysed following the inference method discussed by Lee et al. (2014a), using implementations discussed by Lee et al. (2014b) and the Fossilised Birth-Death tree model sampling ancestors (FBDSA) introduced by Gavryushkina et al. (2014). Bayesian inference analyses were performed in BEAST 2.4.4. (Drummond et al., 2012; Bouckaert et al., 2014), implemented with the packages for the analysis of morphological characters, using the model of Lewis (2001), and for sampling potential ancestors among the ingroup (Gavryushkina et al., 2014). Since the character matrix includes autapomorphies of the sampled taxa, the Lewis’s (2001) model was not conditioned to variable characters only. Stratigraphic information was taken from the literature, and converted to mean geochronological ages of the most inclusive known range of each taxon (see Lee et al., 2014b). In this analysis, rate variation across traits was modelled using the multi-gamma parameter (default model and unique implemented for the analysis of morphological data in BEAST 2). The rate variation across branches was modelled using the relaxed log-normal clock model, with the number of discrete rate categories that approximates the rate distribution set as $n-1$ (with n the number of branches), the mean clock rate using default setting, and not setting to normalise the average rate. Only root age constraint was enforced (the age of the last common ancestor of all included taxonomic units), conservatively set as a uniform range older than the age of the oldest included taxa and centred on the Permian-Triassic boundary (~ 252 Mya). The Bayesian analysis performed a run of 40 million generations, sampling every 1000 generations, with burnin set at 20%, and the Maximum Clade Credibility Tree (MCCT) was used as framework for phyletic reconstruction.

In all analyses, the Triassic archosauriform *Euparkeria* Broom, 1913, was used as root of the trees. A detailed description of the results and the diagnosis of all clades recovered is beyond the aim of this study: here, I will focus on the series of internodes along the lineage leading to the extant birds (represented in the data set by *Meleagris* Linnaeus, 1758), based on the strict consensus of all shortest trees found.

The strict consensus topology of the shortest trees found was used as framework for character transition optimisation. Only unambiguous synapomorphies inferred along the ASL internodes (the trajectory linking all pan-avian scions) were considered. Although alternative

options for ambiguous character optimisation are available (e.g., accelerated transformation optimisation, that minimises convergences and maximises reversals, or delayed transformation optimisation, that maximises convergences and minimises reversals) they may lead to spurious character combinations and an unbalanced distribution of character transition events along the evolutionary sequence. The morphological characters included in the analysis were grouped into six anatomical regions: skull (including mandible and dentition), presacral vertebral column (all vertebrae and ribs from atlas to the posteriormost dorsal vertebra, and gastralia), caudosacral vertebral column (all vertebrae and ribs from the first sacral vertebra to the distal end of tail), pectoral limb (pectoral girdle and forelimb, and including sternum and clavicles), pelvic limb (including pelvis and hindlimb) and integument (osteoderms and feathers). For each node along the ASL, the total number of inferred synapomorphies, and the particular number for each anatomical region, were counted and compared to the overall amount of changes along the entire lineage. The relative amount of characters gained for each anatomical region along the lineage was estimated and compared with the overall amount and those in the other anatomical regions. The resulted pattern formed the basis for a quantitative analysis of modular evolution during the avian body plan assemblage. Here, for “Ornithisation Grade” (OG) it is defined the % ratio between the amount of characters gained at a particular node of the ASL and the corresponding amount gained at the AVES node (the least inclusive node containing *Meleagris* in this analysis). The OG may refer to the whole skeleton (as a “whole OG”, OGw) or to a particular anatomical region (e.g., the skull OG, OGs). By definition, the OG of the extant bird clade (the crown group AVES) is 100, whereas that of ARCHOSAURIA (or of any other more inclusive bird-bearing clade) is 0. To avoid any misinterpretation of the Ornithisation Grade as a “ranking” of the pan-avian clades, note that the OG is exclusively a relative measurement of the internodes along the ASL, and is not a measure of “evolutionary level” for particular terminal branches of the avian total group (e.g., although the maniraptoriform node has a particular OG because it is part of the ASL, the terminal members of the same maniraptoriform node, that are not along the ASL [for example, the ornithomimids] cannot be scored for the OG).

The nodes of the “core topology” which is not biased by the search strategy used (i.e., those shared by both results of the parsimony-based and Bayesian-based analyses, see discussion in Madzia & Cau, 2017) define a chronologically progressive series of avian ancestors. For each of these ancestors, the cladogenetic age (the median age of the node inferred in the Bayesian analysis) and the character state combination at that node (using the parsimony-based topology) were inferred. The taxon-

character matrix of these ancestors was converted to an Euclidean distance matrix and subjected to Principal Coordinate Analysis (PCoA), in order to determine the distribution of the ancestors in the morphospace defined by the phylogenetically informative characters.

In this study, the name “AVES” refers to the avian crown-group, the least inclusive clade including the living species (for a discussion on the use and alternative definitions of the name “AVES”, see Gauthier, 1986); accordingly, the term “avian” refers exclusively to the modern birds. The taxonomic equivalent of the vernacular term “bird” is rarely defined explicitly (Padian & Chiappe, 1998). Here, the term is used conservatively for the taxa that result members of AVIALAE Gauthier, 1986.

A note on the meaning of “assembly of body plan”: although, under a typological paradigm, “plan” refers uniquely to a fixed set of features which is self-consistent, the Darwinian paradigm explicitly recognises the plan as the causal product of an assembly process. This means that the avian body plan refers to the actual set of features that describe the avians, and its assembly refers to the historical process that produced that set.

RESULTS

Of the 1781 characters included in the analysis, 1431 resulted phylogenetically informative for the taxon sample used. The phylogenetic analysis using TNT found 3072 shortest tree of 6790 steps each (Consistency Index excluding uninformative characters = 0.2181, Retention Index = 0.5634). The strict consensus of the 3072 shortest trees found is well resolved, and is used as framework for character evolution along the ASL (Figs 3-5). The result of the Bayesian analysis is broadly consistent with that of the parsimony analysis, and is visually summarised by the stratigraphically calibrated Maximum Clade Credibility Tree in Figs 6 and 7.

The sequence of character acquisitions along the ASL

The ASL is formed by a series of 38 internodes including the extant bird *Meleagris*, here listed progressively from the most inclusive node (Tab. 1). For each node, it is reported the whole OG value (approximate to the nearest integer), and the list of the unambiguous synapomorphies inferred.

NODE 1 (OGw = 2): (*Teleocrater* Nesbitt et al., 2017 + DINOSAURMORPHA Benton, 1985). The basalmost node along the ASL is defined by the last common ancestor of dinosauromorphs and aphanosaurians, represented here by *Teleocrater* (Nesbitt et al., 2017). This node is diagnosed by the following unambiguous synapomorphies: absence of the subnarial fenestra, the relatively more acute anterodorsal margin of maxilla, the relatively more extensive ventral margin of the antorbital fossa, the

Taxon name	Internal specifier	External specifier	Type
DRACOHORS (new)	<i>Megalosaurus bucklandii</i>	<i>Marasuchus lilloensis</i>	Branch based
MANIRAPTOROMORPHA (new)	<i>Vultur gryphus</i>	<i>Tyrannosaurus rex</i>	Branch based

Tab. 1 - Definitions of taxonomic terms introduced here.

extension of the supratemporal fossa onto the frontal, the steeply inclined scapular acromion, the relatively slender scapula, the relatively slender ischial shaft, and the absence of paramedian osteoderms.

NODE 2 (OGW = 3): DINOSAUMORPHA (LAGERPETIDAE Arcucci, 1986 + DINOSAURIFORMES Novas, 1992). Derived features shared by lagerpetids and dinosauriforms but absent in *Teleocrater* include a prominent supracetabular shelf in the ilium and the upturning of the preacetabular process (producing a concave dorsal margin of the ilium), the ventral expansion of the femoral head and the development of the anteromedial tuber in the femur. All these features document the earliest re-organisation of the hip-joint, from a primitive “reptile-like” sprawling posture toward a more “bird-like” parasagittal posture (Hutchinson, 2001a, b).

NODE 3 (OGW = 5): DINOSAURIFORMES (*Marasuchus* Sereno & Arcucci, 1994 + DRACOHORS new clade). Earliest dinosauriforms acquired additional muscle attachment sites in the lateral surface of the femoral head, absent in more basal pan-avians (a prominent trochanteric shelf and a distinct anterior trochanter), and a more “bird-like” foot, characterised by a distinct fossa in the distal end of tibia for accommodating the astragalus ascending process (indicating a more tight connection between the proximal elements of the mesotarsal ankle joint), a relatively more elongate metatarsus, and a relatively shorter fourth toe compared to the third (producing a more symmetrical foot).

NODE 4 (OGW = 7): DRACOHORS (new clade).

Etymology - From draco (Latin, dragon) and cohors (Latin, cohort, circle).

Definition - The most inclusive clade containing *Megalosaurus bucklandii* Mantell, 1827, but excluding *Marasuchus lilloensis* (Romer, 1971).

Remarks - Under all published topologies, DRACOHORS includes silesaurids and all taxa universally recognised as dinosaurs. Although the mutual relationships of the main dracohorsian subclades (silesaurids, herrerasaurs, sauropodomorphs, neotheropods and ornithischians) are controversial (e.g., Sereno, 1999; Langer & Benton, 2006; Langer et al., 2010; Baron et al., 2017), this lineage of dinosauriforms is universally recognised by all authors, and its monophyly has never been questioned by numerical analyses. Dracohorsian synapomorphies include the anterior tympanic recess, the axial epiphyses, the centrodiaepophyseal laminae in the presacral vertebrae, the relative size enlargement of the postacetabular process of ilium, the elongation of the pubis, the proximal sulcus and the reduction of the ligament tuber in the femoral head, and the further reduction in length of the fourth metatarsal and toe compared to the third.

The analyses using different search strategies confirm the recent re-evaluation of *Pisanosaurus* Casamiquela, 1967 among silesaurids and not as the basalmost ornithischian (Agnolín & Rozadilla, 2017).

NODE 5 (OGW = 11): DINOSAURIA Owen, 1842 (*Eodromaeus* Martinez et al., 2011, HERRERASAURIDAE Benedetto, 1973, SAUROPODOMORPHA Huene, 1932, ORNITHOSCELIDA Huxley, 1870). The analysis found an unresolved polytomy including all dracohorsians traditionally considered as “true” dinosaurs, but failed to resolve the relationships of herrerasaur-grade forms relative to sauropodomorphs and ornithoscelidans. In the Bayesian analysis, herrerasaurs are found as non-dinosaurian dracohorsians, although the support for this topology is relatively weak. The numerous synapomorphies supporting DINOSAURIA (containing herrerasaurs) include the narial fossa in the premaxilla, the posterolateral processes on nasal, the reduction in height of the postorbital process of jugal, the elongation of the dorsal quadratojugal process of jugal, the posterodorsal process of dentary, the posterior displacement of the axial neural spine, the elongation of the anterior postaxial cervical vertebrae, the humerus not longer than 60% of femur and with a distinction between head and deltopectoral crest, the straight dorsal margin of ilium (reversal to the plesiomorphic dinosauriform condition), the relative proximal placement of the obturator process of ischium, a sharp fourth trochanter, the reduction of the fibular facet on astragalus, and the loss of distal contact between metatarsal III and IV (suggesting a foot relatively broader than in other dinosauriforms).

NODE 6 (OGW = 15): ORNITHOSCELIDA (ORNITHISCHIA Seeley, 1887 + THEROPODA Marsh, 1881). This study supports the recent hypothesis of a neotheropod-ornithischian clade excluding sauropodomorphs and herrerasaur-grade dinosaurs (Baron et al., 2017). Ornithoscelidan synapomorphies (using the topology inferred by the Bayesian analysis, i.e., sauropodomorphs as sister-taxon of ORNITHOSCELIDA relative to *Eodromaeus* and herrerasaurs) are the interparietal median fusion, the ventral expansion of the pterygoid ramus of quadrate, the reduction of the anterior processes on cervical ribs, the increase of the number of sacral vertebrae to five, the gentle sloping of the acromial process relative to scapular dorsal margin (reversal to the plesiomorphic pan-avian condition), the elongation of the preacetabular process of ilium, the relative narrowing of the intrapubic space, the loss of the proximal sulcus of femoral head (reversal to the plesiomorphic dracohorsian condition), the extensive separation of the anterior trochanter from femoral shaft, the transversal expansion of the medial malleolus of tibia, the tight distal contact between fibula and tibia, the mediolateral constriction of the calcaneum with loss of the posterolateral process.

NODE 7 (OGW = 24): THEROPODA (COELOPHYSOIDEA [Nopcsa, 1928] + AVEROSTRA Paul, 2002). The ornithoscelidan hypothesis supported here excludes most Triassic dinosaurs, otherwise considered as basal theropods (e.g., HERRERASAURIDAE, see Sereno, 1999) from THEROPODA, and restricts the latter to the two neotheropod lineages, coelophysoids and averostrans. The numerous (neo)theropod synapomorphies include the medial subnarial foramen in premaxilla, the relatively narrow snout with subparallel maxillae in ventral view, the absence of a distinct rim along the margin of the antorbital fossa, a subvertical orientation of the lacrimal ventral

bar, the elongation of the postorbital process of jugal (reversal to the plesiomorphic dinosaurian condition), the posterior tympanic recess, the loss of the posterodorsal process of dentary (reversal to the plesiomorphic dinosaurian condition), the anteroventral foramen/notch in the splenial, the pleurocoels in the anterior presacral centra, the closely placed diapophyses and parapophyses in anterior and middle cervical vertebrae, the prezygodiapophyseal laminae in mid-cervical vertebrae, the elongation of the posterior cervical centra, the proximal caudal vertebrae with pre/postspinal laminae and hyposphene-hypantra, the proximal chevrons with anterior proximal processes, the fusion of the clavicles (furcula), the relative elongation of the deltopectoral crest, the loss of the fifth distal carpal, the reduction in length of metacarpal I, the anteroposteriorly elongate pubic peduncle of ilium, the distal cleft in the obturator process, the femoral head lacking the anteromedial tuber and bearing a deep ligamental sulcus, the mediolateral crest on femur, the tibia with a distinct cnemial crest and a cleft between the proximal condyles, the fibular crest of tibia reaching the proximal end of bone, the oblique ridge in the medial facet of proximal fibula, the astragalus with the anterior horizontal groove, the anterior platform and a posterior ascending process, the very short metatarsal I failing to contact the proximal end of the metatarsus, and the reduced first pedal ungual.

NODE 8 (OGW = 29): AVEROSTRA (CERATOSAURIA Marsh, 1884 + TETANURAE Gauthier, 1986). The members of AVEROSTRA differ from other ornithoscelidans in bearing premaxillary teeth with an asymmetrical cross section that is flatter lingually, a lacrimal posterodorsal recess, the X cranial nerve foramen in the occipital surface, a mediolaterally enlarged retroarticular process, a lateral surangular shelf, an enlarged axial intercentrum, axial pleurocoels, cervical pleurocoels inside fossae, the scapular blade not expanding distally, the absence of the ulnare and of distal carpals 3 and 4, a reduced ischial peduncle of ilium, the lateral margin of the femoral head that is squared in proximal view, a rounded medial condyle of femur, a flange-like anterior trochanter, a distinct cleft between the fibular condyle and the cnemial crest, a semilunate fossa at the base of the astragalar ascending process, and an anteriorly-restricted fibular face of astragalus.

NODE 9 (OGW = 32): TETANURAE (*Zuolong* Choiniere et al., 2010 + [*Chilesaurus* Novas et al., 2015 + NEOTETANURAE Sereno et al., 1994]). This analysis found *Zuolong* and the enigmatic *Chilesaurus* as the most basal members of the tetanuran lineage. *Zuolong* has been considered among the basal coelurosaurs, although on the basis of analyses relatively less-sampled among non-coelurosaurs, or rooted on allosauroids (e.g., Choiniere et al., 2010; Brusatte et al., 2014). The latter interpretation is supported by the Bayesian analysis, where *Zuolong* is recovered (although with weak support) among the basalmost coelurosaurs. A coelurosaurian placement for *Chilesaurus* is also supported in the Bayesian analysis. Tetanuran synapomorphies in the parsimony-based topology include the loss of the lacrimal shelf over the antorbital fossa, the contact between the lateral ridge

and the lateral condyle in the quadrate, the dorsoventral compression of the anterior cervical centra, the reduction of the supracetabular shelf covering the anterodorsal corner of acetabulum, the medial perforation of the pubic apron, a medially-directed femoral head, the reduction of the trochanteric shelf of femur, and an enlarged fibular trochlea of femur.

NODE 10 (OGW = 32): (*Chilesaurus* + NEOTETANURAE). The parsimony analysis confirms the basal tetanuran affinities of the enigmatic *Chilesaurus* and dismisses ornithischian relationships suggested by Baron & Barrett (2017). This node is diagnosed by two unambiguous synapomorphies: the extensor sulcus on femur and the absence (due to secondary loss) of the femoral mediolateral crest.

NODE 11 (OGW = 35): NEOTETANURAE (CARNOSAURIA Huene, 1914 + COELUROSAURIA Huene, 1914). In the parsimony-based scenario, neotetanuran synapomorphies absent in *Chilesaurus* and *Zuolong* are the anterior placement of the narial margin of premaxilla, anterior presacral vertebrae with convex anterior facet, ventral placement of metacarpal III relative to II, more gracile and elongate penultimate phalanges of first and second fingers, fossa on medial surface of proximal end of fibula, distal end of fibula placed anterior to tibia, more anterodistally-oriented condyles of astragalus, proximodistally longer ascending process of astragalus, relatively stouter metatarsal I, median constriction of proximal surface of metatarsal III.

NODE 12 (OGW = 36): COELUROSAURIA. The analysis recovered a series of “compsognathid-grade” forms along a paraphyletic series leading to TYRANNORAPTORA Sereno, 1999. *Aorun* Choiniere et al., 2013, resulted the basalmost coelurosaur (with the possible exception of *Chilesaurus* and *Zuolong*, see above). The basalmost node of COELUROSAURIA under this topology is supported unambiguously by four apomorphies: distinct posteroventral process of lacrimal, distal surface of pubic foot subrectangular, posterior part of pubic foot elongate, distal half of metatarsal IV shaft contacting metatarsal III.

NODE 13 (OGW = 38): (“compsognathid grade” + TYRANNORAPTORA). The parsimony analysis found a paraphyletic series of small-bodied coelurosaurs (“compsognathid-like” forms) as forming a pectinate series leading to tyrannoraptorans. On the contrary, these forms are united in a clade (Compsognathidae) in the topology found by the Bayesian analysis. Coelurosaurs with the exclusion of *Aorun* are diagnosed by the medially opened maxillary recess, the elongation of the cervical centra beyond the posterior level of the neural arch, fan-shaped dorsal neural spines, the fibular crest not reaching the proximal end of tibia (reversal to the plesiomorphic theropodan condition), and the absence of the anterior distal fossa in the tibia (reversal to the plesiomorphic dinosauriform condition).

NODE 14 (OGW = 39): (*Sinocalliopteryx* Ji et al., 2007 + TYRANNORAPTORA). This clade of coelurosaurs

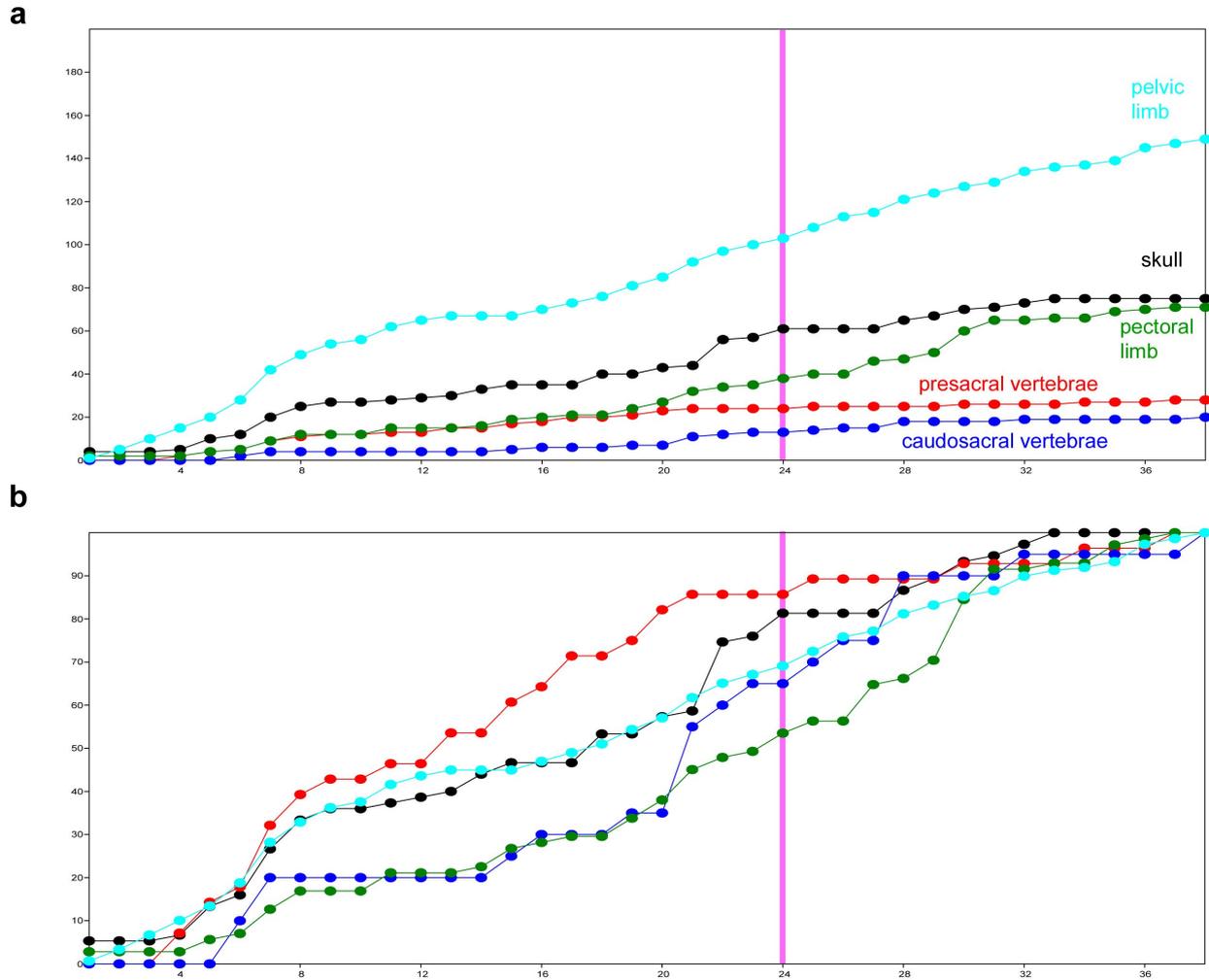


Fig. 5 - Modularity in the assembly of the avian body. Absolute (a) and relative (b) amount of change based on the unambiguous apomorphies reconstructed along the ASL. The pink vertical line at node 24 in both figures indicates the last common ancestor of *Archaeopteryx* and modern birds.

in caudal vertebrae (reversal to the plesiomorphic theropodan condition), a prominent dorsomedial process on the semilunate carpal, a convex ventral margin of the pubic foot, a subrectangular distal end of tibia, and a sulcus along the posterior margin of the proximal end of fibula.

NODE 17 (OGW = 45): (*Ornitholestes* + MANIRAPTORIFORMES). This clade of coelurosaurs is diagnosed by ventrally flexed cervical prezygapophyses, prominent anterior dorsal hypapophyses, a distinct pronator muscle scar on radius, proximal pubic shaft that is wider than deep, an enclosed pubic apron (reversal to the plesiomorphic tetanuran condition), and a reduced fourth trochanter.

NODE 18 (OGW = 47): MANIRAPTORIFORMES (ORNITHOMIMOSAURIA Barsbold, 1976 + MANIRAPTORA Gauthier, 1986). Maniraptoriforms differ from other tyrannoraptorans in having a relatively shallower snout, the shorter external naris (reversal to the plesiomorphic coelurosaurian condition), the anteroposteriorly shorter

ventral end of lacrimal, a well-defined orbital rim on frontal, the absence of distinct paradental laminae, a straight anterior margin of the pubic peduncle of ilium (reversal to the plesiomorphic coelurosaurian condition), and a reduced proximal surface of metatarsal III that is not constricted at mid-length (reversal to the plesiomorphic neotetanuran condition).

NODE 19 (OGW = 50): MANIRAPTORA (ALVAREZSAUROIDEA Bonaparte, 1991 + PENNARAPTORA Foth et al., 2014). The results of the parsimony and Bayesian analyses differ in the placement of therizinosaur relative to the other maniraptoriforms. In the parsimony analysis, therizinosaur are sister-taxon of the oviraptorosaurs, whereas in the Bayesian analysis they are the earliest diverging branch of Maniraptora. The maniraptoran clade is diagnosed by the elongate dorsal postzygapophyses, the shorter middle caudal prezygapophyses, the narrower coracoid facet on the scapular acromion, the proximodistal elongation of the ventral tuber of the humerus, the relative lateral extension of the semilunate carpal over metacarpal II,

the longitudinal reduction of the supracetabular crest, the reduction of the brevis shelf on ilium, the less convex shape of the ventral margin of pubic foot (reversal to the plesiomorphic maniraptoromorph condition), the enlargement of the proximal obturator notch in the ischium, and the absence of the ischial symphysis.

NODE 20 (OGW = 53): PENNARAPTORA (OVIRAPTOROSAURIA Barsbold, 1976 + PARAVES Sereno, 1997). Pennaraptora is a well-supported clade of maniraptorans, including paravians and oviraptorosaurs. Although the parsimony analysis recovered therizinosauroids among PENNARAPTORA (as sister-taxon of “core” oviraptorosaurs), another analysis using a larger taxon sample and the same character sample used here found therizinosauroids as sister-group of pennaraptorans (Cau et al., 2017). Among Pennaraptora, the parsimony and Bayesian analyses differ in the placement of the enigmatic scansoriopterygids, found, in the former, among basal avialans, whereas they are placed as the basalmost oviraptorosaurs in the Bayesian analysis.

Unambiguous synapomorphies of PENNARAPTORA (or of the pennaraptoran-therizinosauroid clade) include the reduction of the orbital margin of prefrontal (reversal to the plesiomorphic tyrannoraptoran condition), the ventral displacement of the base of the paroccipital processes relative to the occipital condyle, the development of the surangular lateral shelf (convergent with more basal averostrans), the short cervical neural spines, the pleurocoels extended back to the anterior dorsal vertebrae, the presence of a distinct median ridge on the ulnar cotyle, the laterally-bowed ulna, the presence of a distinct third distal carpal (reversal to the plesiomorphic averostran condition), the postacetabular blades that diverge posteriorly, the blade-like ischial shaft (reversal to the plesiomorphic dinosauriform condition), the absence of the ischial foot (reversal to the plesiomorphic dinosaurian condition), and barely-bowed metatarsal V.

NODE 21 (OGW = 59): PARAVES. This analysis found an unresolved polytomy at the paravian root, including *Fukuivenator* Azuma et al., 2016, two dromaeosaurid lineages and the troodontid-avialan clade. Exploration of the results shows that the unresolved polytomy is affected by the unstable position of *Fukuivenator* (found, alternatively, as a dromaeosaurid or as the basalmost paravian). A posteriori pruning of *Fukuivenator* confirms dromaeosaurid monophyly. The latter topology is used for character optimisation. An intriguing result of this analysis is the unenlagiine-halszkaraptorine sister-group relationships: although an analysis using the same character sample with a larger taxon sample among paravians does not support this hypothesis (Cau et al., 2017), these two dromaeosaurid subclades show adaptations related to a piscivorous diet (Gianechini et al., 2011; Cau et al., 2017). Paravian synapomorphies include relatively smaller infratemporal fenestra, carotid processes in cervical vertebrae, fusion of the sacral neural spines, elongation of the middle-caudal centra, loss of the middle-caudal neural spines, reduction of the number of caudal ribs, relatively lower scapular acromion, lateral orientation of the pectoral glenoid, medial deflection of

the posterior process of coracoid, inclusion of distal carpal 3 in the semilunate carpal, prominent flexor tubercles in the manual unguals, shallower cuppedicus fossa on ilium, development of the processus supratrochantericus on ilium, absence of the anterior process of the pubic foot, relatively shorter ischium, absence of the posteroventral process of the calcaneum, development of a posterolateral flange on metatarsal IV, relatively shorter second pedal digit, and development of pennaceous feathers on ulna and metatarsus.

NODE 22 (OGW = 65): AVERAPTORA Agnolín & Novas, 2013 (TROODONTIDAE Gilmore, 1924 + AVIALAE Gauthier, 1986). Troodontids, anchiornithids, and birds (eventually including scansoriopterygids, but see result of the Bayesian analysis) share a common ancestry excluding dromaeosaurids. The troodontid-avialan node is based on several apomorphies: premaxillary teeth with round to elliptical cross section, anterodorsally inclined lacrimal, a medially inset ventral ramus of lacrimal, vaulted frontals and parietals, reduced supratemporal fossae not extended onto the frontals, the absence of the squamosal-quadratojugal contact, a depressed crista interfenestralis in the middle ear, a dorsoventrally elongate foramen magnum, absence of the fossa housing cranial nerves X and XII, a posteriorly deepening lateral groove of dentary, a vestigial coronoid, marked reduction of middle caudal postzygapophyses, the absence of contact between scapular acromion and coracoid, the reduced bicipital scar in the deltopectoral crest, a relatively short ilium, a median dorsal process of ischium, a proximally narrowing femoral diaphysis, a more lateral placement of the iliofibularis tubercle on fibula, and prominent flexor tubercles in pedal unguals III and IV.

NODE 23 (OGW = 67): AVIALAE. In the parsimony analysis, the recently-established anchiornithid and scansoriopterygid groups result closer to birds than any “traditional” maniraptoran clade. The unresolved basal avialan tricotomy is unambiguously supported by relatively shortened nasals, a marked reduction in number and size of the proximal caudal neural spines, the humerus shaft subequal in thickness to the femur, the posteriorly concave ischium, a reduced cnemial crest, the penultimate phalanx in the third toe not shorter than the preceding phalanges.

NODE 24 (OGW = 70): (*Archaeopteryx* + more crownward avialans). *Archaeopteryx* is recovered as closer to modern birds than anchiornithids and scansoriopterygids. The “traditional” basal node of birds is supported by the posterior elongation of the nasal process of premaxilla, the participation of the maxilla in the margin of the external naris, the subvertical ventral ramus of lacrimal (reversal to the plesiomorphic averaptoran condition), the absence of the surangular lateral shelf, the anterior projection of the scapular acromion, the relatively more robust furcula, the presence of a lateral flange on the first phalanx of manual digit II, the pubic peduncle of ilium longer than the acetabulum, the posteriorly extended cuppedicus fossa, the first pedal ungual comparable in size to pedal unguals III and IV, and the absence of pennaceous feathers on metatarsus (reversal to the plesiomorphic paravian condition).

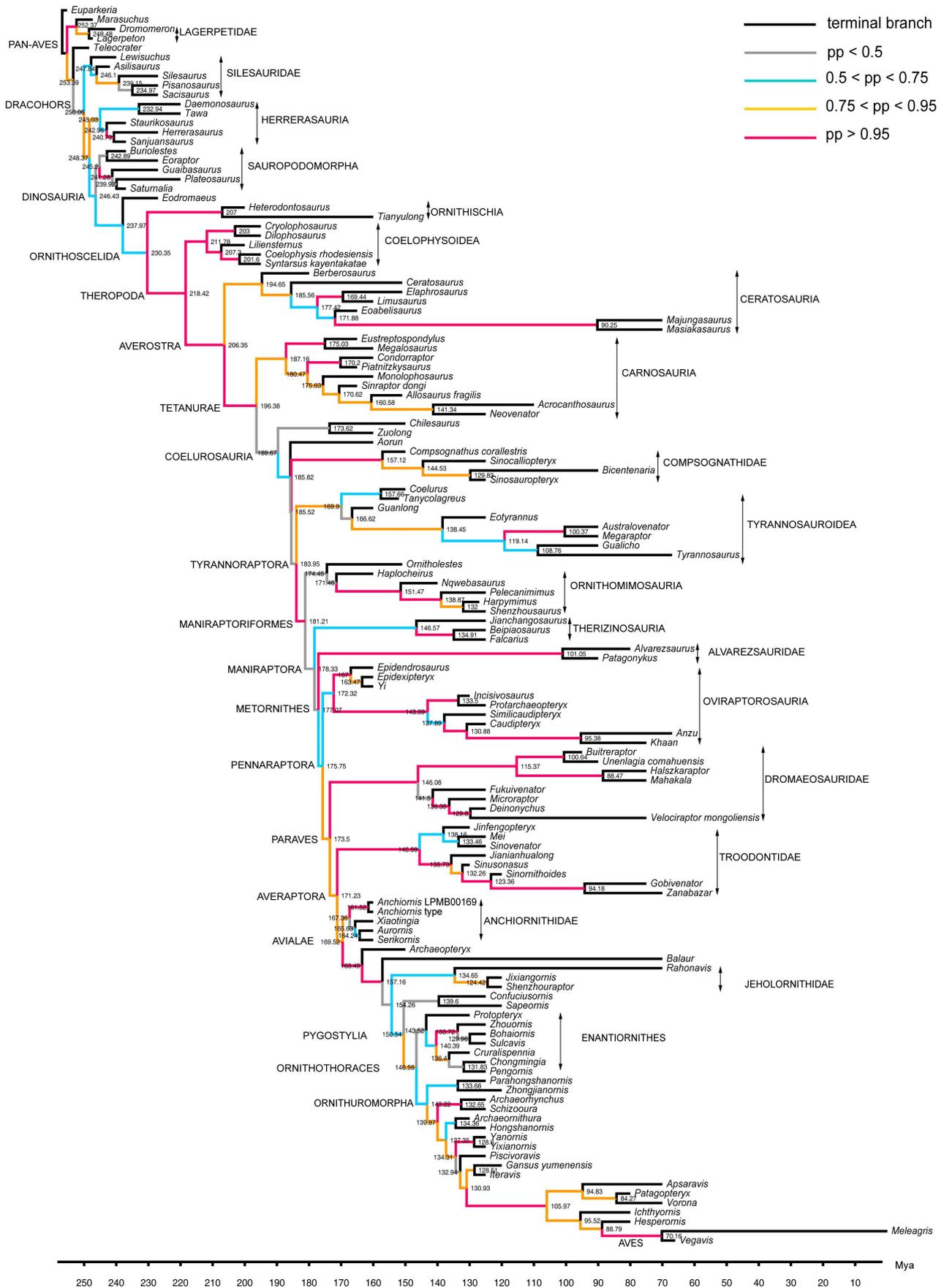


Fig. 6 - Maximum Clade Credibility resulted in the Bayesian analysis. Colour of branches according to posterior probability.

NODE 25 (OGW = 72): (*Rahonavis* Forster et al., 1998 + more crown-ward avialans). The enigmatic paravian *Rahonavis* is here recovered as a basal avialan, not related to unenlagiines (Makovicky et al., 2005). Supports for this placement are the lateral excavations and pneumatic foramina on the dorsal centra, the presence of six sacral vertebrae, the marked brachial scar in the ulna, the thickened anterior proximal ridge on ulna, the relative elongation of the ilium (reversal to the plesiomorphic paravian condition), the marked proximal compression of the pubic shaft, the posteriorly concave pubis, a straight ischium (reversal to the plesiomorphic averaptoran condition), the fusion between anterior and greater trochanters, and the relatively short metatarsus.

NODE 26 (OGW = 74): (*Balaur* Csiki et al., 2010 + more crown-ward avialans). Another enigmatic paravian, *Balaur*, is found as an avialan closer to short-tailed birds than *Archaeopteryx* (see discussion in Cau et al., 2015). This placement is based on the presence of seven sacral vertebrae, the reduction of the supracetabular crest on ilium, the marked posteroventral direction of the pubis, the presence of a lateral longitudinal ridge on ischium, the extension of the distal articular surface of the tibiotarsus along the posterior surface, and the proximal fusion of the metatarsals.

NODE 27 (OGW = 76): (JEHOLORNITHIDAE Zhou & Zhang, 2006 + PYGOSTYLIA Chatterjee, 1997). The long-tailed jeholornithids are the closest relatives of short-tailed avialans. This relationship is based on several derived features, including the absence of the subglenoid fossa of coracoid, the prominent humeral ectepicondyle, the ulna more robust than the tibiotarsus, the proximally expanded semilunate carpal, the relatively gracile first manual digit, the shortened penultimate phalanx in manual digit II (reversal to the plesiomorphic neotetanuran condition), the absence of the posterolateral flange on metatarsal IV (reversal to the plesiomorphic paravian condition), and the reduced dorsoventral expansion of the distal end of the first phalanx of the second toe (reversal to the plesiomorphic paravian condition).

NODE 28 (OGW = 80): PYGOSTYLIA. This clade includes all short-tailed birds, and is diagnosed by the relatively elongate preantorbital ramus of maxilla, the elongate posterodorsal process of lacrimal, acuminate dentary tip, widely-spaced dentition, markedly backturned posterior sacral ribs, short mid-caudal vertebrae, fusion of the distalmost caudal vertebrae, anteriorly-restricted humeral condyles, reduced pubic apron, obliteration of the suture between tibia and astragalar ascending process, distinctly ginglymoidal distal end of metatarsal II, pedal toes II and IV subequal in length (reversal to the plesiomorphic paravian condition), pedal ungual II not larger than pedal unguals III and IV (reversal to the plesiomorphic paravian condition), and the elongate penultimate phalanx in pedal digit IV.

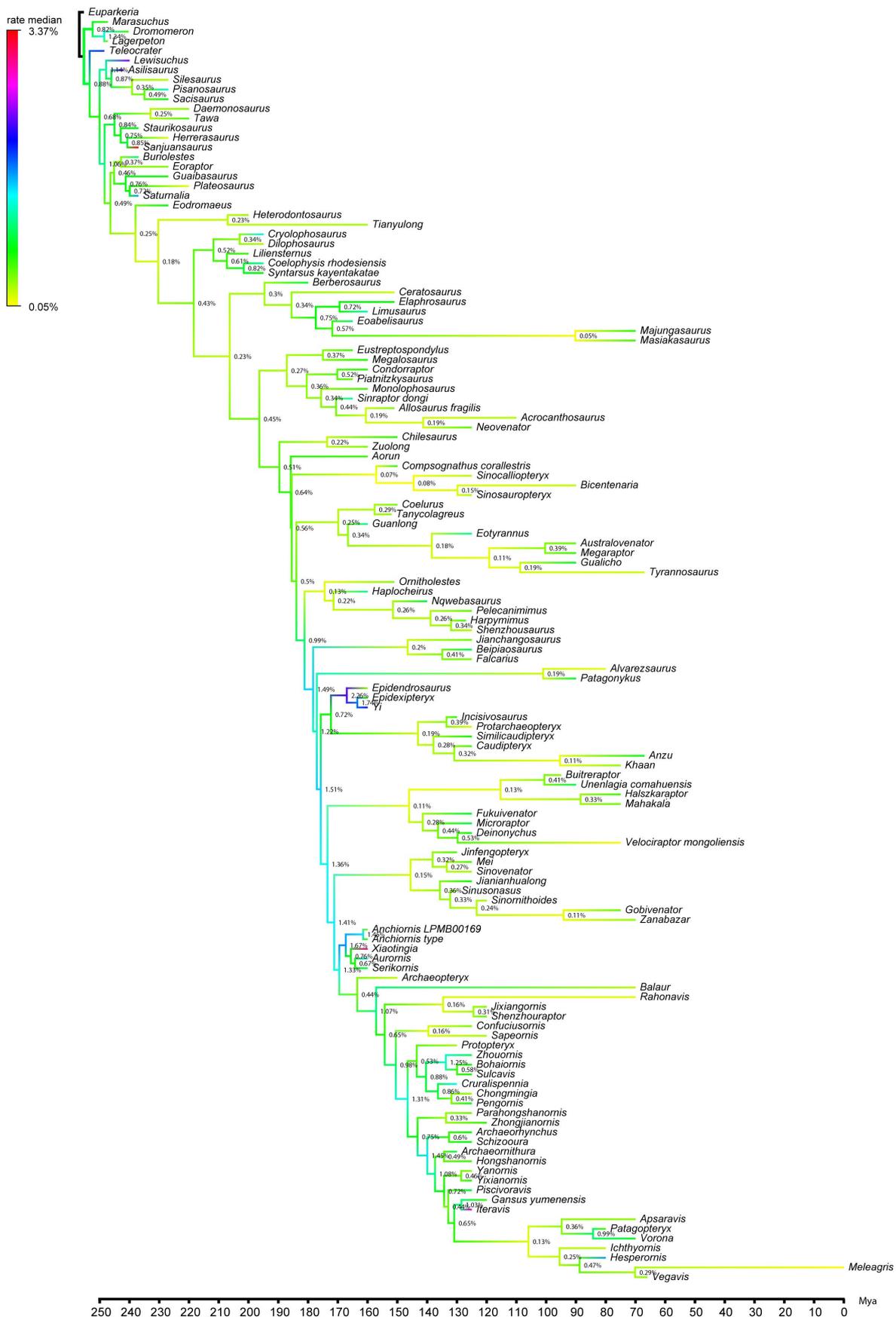
NODE 29 (OGW = 83): (*Confuciusornis* Hou et al., 1995 + ORNITHOTHORACES Chiappe & Calvo, 1994). Pygostylians with the exclusion of saepeornithids share an elongate premaxillary facet on the anteromedial margin

of nasal, the absence of the ascending process of jugal, a grooved lateral surface of furcula, a constricted coracoid neck, a well-developed bicipital tubercle on ulna, a narrow flexor fossa on distal femur, the enlarged distal end of metatarsal II, a well-developed musculus tibialis cranialis insertion tuber on metatarsal III.

NODE 30 (OGW = 88): ORNITHOTHORACES. Ornithothoracine birds include enantiornithines and ornithuromorphs. The phylogenetic placement of *Protopteryx* Zhang & Zhou, 2000, relative to other ornithothoracines is ambiguous in the parsimony analysis, being it found alternatively as the basalmost enantiornithine or as sister-taxon of ORNITHOTHORACES. The Bayesian analysis supports the former alternative. This clade is diagnosed by the shallow snout (reversal to the condition evolved in MANIRAPTORIFORMES), the rod-like suborbital bar of jugal, the upturned retroarticular process, less than 12 dorsal vertebrae, a narrow interclavicular angle, the carinate sternum, the dorsal placement of the scapular blades on the ribcage, a mobile scapulocoracoid joint, the straight/convex sternal margin of coracoid, the relatively distal placement of the scapular facet on coracoid, the absence of a distinct dorsomedial process of the semilunate carpal (reversal to the plesiomorphic maniraptoromorph condition), the fusion of metacarpal I with the semilunate carpal, the reduced second phalanx in the third manual digit, the distally narrowing penultimate phalanges on manual fingers, an anteroposteriorly short pubic peduncle of ilium (reversal to the plesiomorphic avialan condition), the comparable anterior projection of both tibiotarsal condyles, the elongate medial dorsal process on ischium, and the alula.

NODE 31 (OGW = 90): ORNITHUROMORPHA Chiappe et al., 1999. All avialans closer to extant birds than enantiornithines belong to the ornithuromorph clade. The analysis found an unresolved polytomy among basalmost ornithuromorphs and a clade comprising hongshanornithids and more crown-ward birds. The unambiguous synapomorphies of ORNITHUROMORPHA include the relatively enlarged premaxillary body, the loss of the hypocleidum, the relatively elongate sternum, a posteriorly extended sternal carina, the elongate posteromedial processes of sternum, reduced flexor processes on manual unguals (reversal to the plesiomorphic paravian condition), the absence of the median dorsal process of ischium (reversal to the plesiomorphic averaptoran condition), and a relatively short penultimate phalanx in pedal digit IV (reversal to the plesiomorphic pygostylian condition).

NODE 32 (OGW = 93): (HONGSHANORNITHIDAE O'Connor et al., 2010 + more crown-ward avialans). This clade of ornithuromorphs is diagnosed by the mentomeckelian ossification rostral to the dentary, the presence of teeth in the anterior end of dentary, the presence of nine sacral vertebrae, the ossification of the intercotylar eminence of the metatarsus, the latero-plantar displacement of distal end of metatarsal II relative to metatarsal III, the ventral placement of the proximal end of metatarsal III relative to metatarsals II and IV (convergently acquired by several coelurosaurian



lineages), the distal end of metatarsal I that does not reach the level of the distal end of metatarsal II, the fusion between metatarsal III and IV that defines the margins of the distal vascular foramen.

NODE 33 (OGw = 94): (YANORNITHIDAE Zhou & Zhang, 2001 + more crown-ward avialans). This clade is diagnosed by a relatively blunt anterior tip of the dentary (reversal to the plesiomorphic pygostylian condition), more than ten dentary teeth, a pair of fenestrae in the posterior end of the sternum, the presence of distinct plantar ridges on the distal tibiotarsal shaft, the distal fusion between metacarpals II and III.

NODE 34 (OGw = 95): (*Piscivoravis* Zhou et al., 2013 + more crown-ward avialans). Unambiguous synapomorphies of this clade are the heterocoelous condition in all cervical vertebrae, and the development of the extensor (patellar) sulcus on the distal end of the femur.

NODE 35 (OGw = 96): (*Gansus yumenensis* Hou & Liu, 1984, *Iteravis* Zhou et al., 2014, CARINATAE Merrem, 1813). The clade including all ornithuromorphs closer to modern birds than *Piscivoravis* is diagnosed by the first manual digit shorter than metacarpal II, the absence of a lateral sulcus on the clavicular rami (reversal to the plesiomorphic pygostylian condition), the unexpanded distal end of the posterolateral processes of sternum, the prominent and upturned lateral cnemial crest, and the relatively elongate first phalanx in the fourth pedal digit.

NODE 36 (OGw = 98): CARINATAE (*Ichthyornis* Marsh, 1872, PATAGOPTERYGIFORMES Agnolín & Martinelli, 2009, ORNITHURAE Haeckel, 1866). The clade of ornithuromorphs closer to (extant) avians than *Gansus*-like forms is diagnosed by the intermetacarpal process on metacarpal II, the posteroventral orientation of the pubic peduncle of ilium, the relatively enlarged ischial peduncle of ilium, the absence of the pubic symphysis, the presence of a distinct obturator flange on ischium, pedal digit IV subequal in length to pedal digit II, and the relatively small pedal ungual IV compared to pedal ungual III.

NODE 37 (OGw = 99): ORNITHURAE (*Hesperornis* Marsh, 1872 + AVES). Ornithurine birds are diagnosed by heterocoelous dorsal vertebrae, a relatively low deltopectoral crest on humerus, a marked anterior (ambiens) expansion in the proximal end of pubis, and a proximally projected femoral neck.

NODE 38 (OGw = 100): AVES (*Vegavis* Clarke et al., 2005 + *Meleagris*). Unambiguous synapomorphies of modern birds, here represented by the extant *Meleagris*, and also present in the Cretaceous *Vegavis* include eleven sacral vertebrae, the supratendineal bridge on distal tibiotarsus, and distinct sulci on the hypotarsus.

Tempo and mode in the Assembly of the Avian Body Plan

Using the strict consensus of the shortest trees found by the parsimony analysis, the sequence of character acquisition along the 38 nodes of the ASL includes 348 unambiguous morphological state transitions. This number of events represents the minimal value of the actual sequence of changes, as it is based solely on the unambiguously optimised apomorphies. Nevertheless, as stated above, I have refrained from including additional morphological transitions based on character optimisations (i.e., accelerated or delayed optimisations), because these approaches may spuriously include in the sequence some evolutionary events that instead occurred along other branches of the total avian group, not in the ASL, thus artificially inflating the actual amount of events in some parts of the sequence (see Figs 4-5). The amount of changes per internode ranges between 2 and 38, with a median value of 8. Among the 348 evolutionary events that minimally describe the assembly of the avian body plan, 75 (22% of the total) pertain to the skull, 28 (8% of the total) to the presacral vertebral column, 20 (6% of the total) to the caudosacral vertebral column, 71 (20% of the total) to the pectoral limb, 149 (43% of the total) to the pelvic limb, and five (1% of the total) to the integumentary system. The number of events inferred for the integumentary system is very small, and is not included in the analysis of the modular evolution. Among the 348 unambiguously optimised transitions, 32 events (9% of the whole sequence) are interpreted as reversals to the states lost in more inclusive nodes. The amount of reversals in the internodes is not related to the amount of changes (Spearman's rank, $S = 0.30$, $p = 0.06$). The amount of changes per node in each anatomical region is not correlated to that in other regions, with the possible exception of the caudosacral and pelvic limb regions couple, that shows a moderately positive correlation ($S = 0.42$, $p = 0.009$). The latter result may indicate that these two modules represent sub-units of a larger module.

The rate of character acquisition per node along the ASL is relatively uniform. The slope of the incremental curve plotting the total amount of changes gained does not show particular variations, with only the Ornithoscelida-Theropoda transition showing a higher increase relative to the rest of the lineage (Fig. 5a). Similar trends are evidenced comparing the change gain trends in the distinct anatomical regions. Yet, the incremental curves of the distinct regions show different slopes along the series, which may indicate a modular evolutionary pattern (Fig. 5b). Modularity in the evolution of the avian body plan is expressed here in term of heterogeneity in the OG values of the distinct anatomical regions, compared to the whole body OGw. In particular, the OG values of the different regions are similar along the first seven nodes of the ASL (from the tree root to the theropod root), they diverge between node 7 and node 21 (from the theropod root to the paravian root), then converge progressively, with a complete overlap along the terminal eight nodes (from the ornithuromorph node to the avian crown group). This

←
Fig. 7 - Tempo and mode of the ASL. Same tree as in Fig. 6, with colour of branches according to median rate of divergence (probability to observe one state transition per million year).

pattern is mostly influenced by the different trends in the caudosacral vertebral and pectoral limb regions relative to the other regions: for most of the central part of the series, these two regions show OG values consistently lower than those of the other regions.

The analysis of the *tempo* and mode of character evolution (i.e., inferring the timing of cladogenesis and estimating the rate of change along the geological time) using a topology based on parsimony analysis and estimating the rate of change along the geological time) using a topology based on parsimony analysis may be biased by the particular method used for the a posteriori stratigraphic calibration of the phylogenetic tree (see discussion in Lee et al., 2014a); accordingly, the discussion of the evolutionary dynamics is here based on the results of the Bayesian analysis, which simultaneously co-estimated relationships and timing of cladogenesis (Lee et al., 2014a, b; Figs 6-7). Although the topology resulted using the Bayesian inference does not completely fit the topology used for character optimisation (derived from the parsimony analysis), the most strongly robust areas in the two alternative topologies broadly overlap, and will be the focus of the discussion.

Using those nodes shared by the parsimony-based and Bayesian-based analyses, a minimum series of well-

supported avian ancestors is defined. The taxon-character matrix of these ancestors was converted to an Euclidean distance matrix and subjected to Principal Coordinate Analysis (PCoA). The first two Axes produced by the PCoA were used to describe the trajectory of the ASL in the morphospace during the Mesozoic. The 3-dimensional plot of the avian ancestors relative to the two first PCoA axes and the geological time identifies three distinct phases: the first, from the pan-avian root to the basalmost coelurosaurian nodes, with the lowest Axis 1 values, the second from the maniraptoromorph node to the ornithothoracine root, characterised by the progressive increase of both Axis 1 and 2 values, and the third phase, from the ornithuromorph ancestry to the origin of the crown group, showing a substantial decrease of the Axis 2 values (Fig. 8).

DISCUSSION

The investigation of bird origins has often focused on a few “key features” (e.g., feathers and the musculoskeletal adaptations to powered flight), and on those ecological scenarios that may drive the evolution of these features (e.g., the transition to flight from a ground-dwelling vs. an arboreal lifestyle; Ostrom, 1976; Padian & Chiappe, 1998; Dececchi & Larsson, 2013; Xu et al., 2014). This approach has emphasised the role of a subset of features and taxa over other factors, biasing our comprehension of the entire sequence of modifications leading to the modern avian *bauplan*. Such bias has been exacerbated by the contingent nature of the fossil record. For over a century, almost all discussions on bird ancestry have focused on *Archaeopteryx* alone. Even after the recognition of the dinosaurian ancestry of birds, most of the discussion on the evolutionary patterns related to avian ancestry has been defined around the iconic *Urvogel* and a limited set of “*Archaeopteryx*-like” taxa (i.e., deinonychosaurian theropods; e.g., Ostrom, 1976). The application of a less restrictive paradigm of bird evolution, including the whole stem lineage in the analysis of the avian-like novelties (e.g., Gatesy & Dial, 1996a, b; Hutchinson, 2001a, b; Dececchi & Larsson, 2013), has represented the most productive innovation in the study of bird evolution (Prum, 2002; Xu et al., 2014). From both phylogenetic and palaeontological perspectives, the particular lineage reconstructed here is one among the several evolutionary trajectories that form the Mesozoic history of the avian total group. What is significant from a biological and neontological perspective is that this lineage is the only one of that clade that survived the Cretaceous-Palaeogene boundary extinction event, and is still flourishing today. Although any particular subset of this lineage is shared with other Mesozoic pan-avians, the complete sequence reconstructed here leads exclusively to extant birds, and, retrospectively, it describes the unique sequence of evolutionary events that assembled the modern bird *bauplan*. It is therefore legit to “extract” that particular trajectory from the branching topology of the pan-avian clade and to discuss its properties as a linear, historical process, focusing on those elements pivotal in interpreting the modern avian biology.

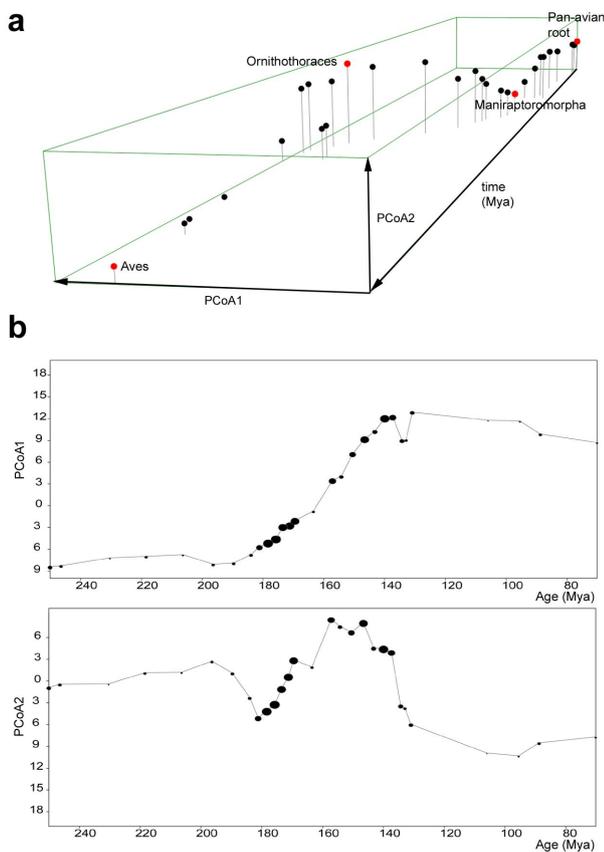


Fig. 8 - Morphospace distribution of the avian ancestors. Selected series of avian ancestors inferred by both parsimony and Bayesian analyses. In a), ancestors plotted according to inferred age of nodes and the first two axes of the PCoA of morphological disparity. In b), binary plots of the two first axes of the PCoA of morphological disparity. Bubble size proportional to divergence rate. Note that the ancestors are distributed along three relatively narrow regions.

The amount of character state transitions along the ASL is relatively uniform. In none of the internal branches the number of inferred novelties is unusually high, and this suggests that the character sample adequately describes the whole disparity in the taxonomic sample used. On the contrary, the evolutionary rate (amount of changes per million year per branch) inferred along the ASL is not homogeneous. In particular, the analysis inferred two main

phases when the rate of morphological divergence along the ASL is significantly higher than the background rate of the whole tree (i.e., higher than in 95% of all branches in all sampled trees, a rate estimated in this analysis as > 4.78% of changes per million year): along the basalmost internodes of the stem lineage (from the pan-avian root to the node DINOSAURIA) and in most of the coelurosaurian internodes of the avian stem, with the exclusion of the least

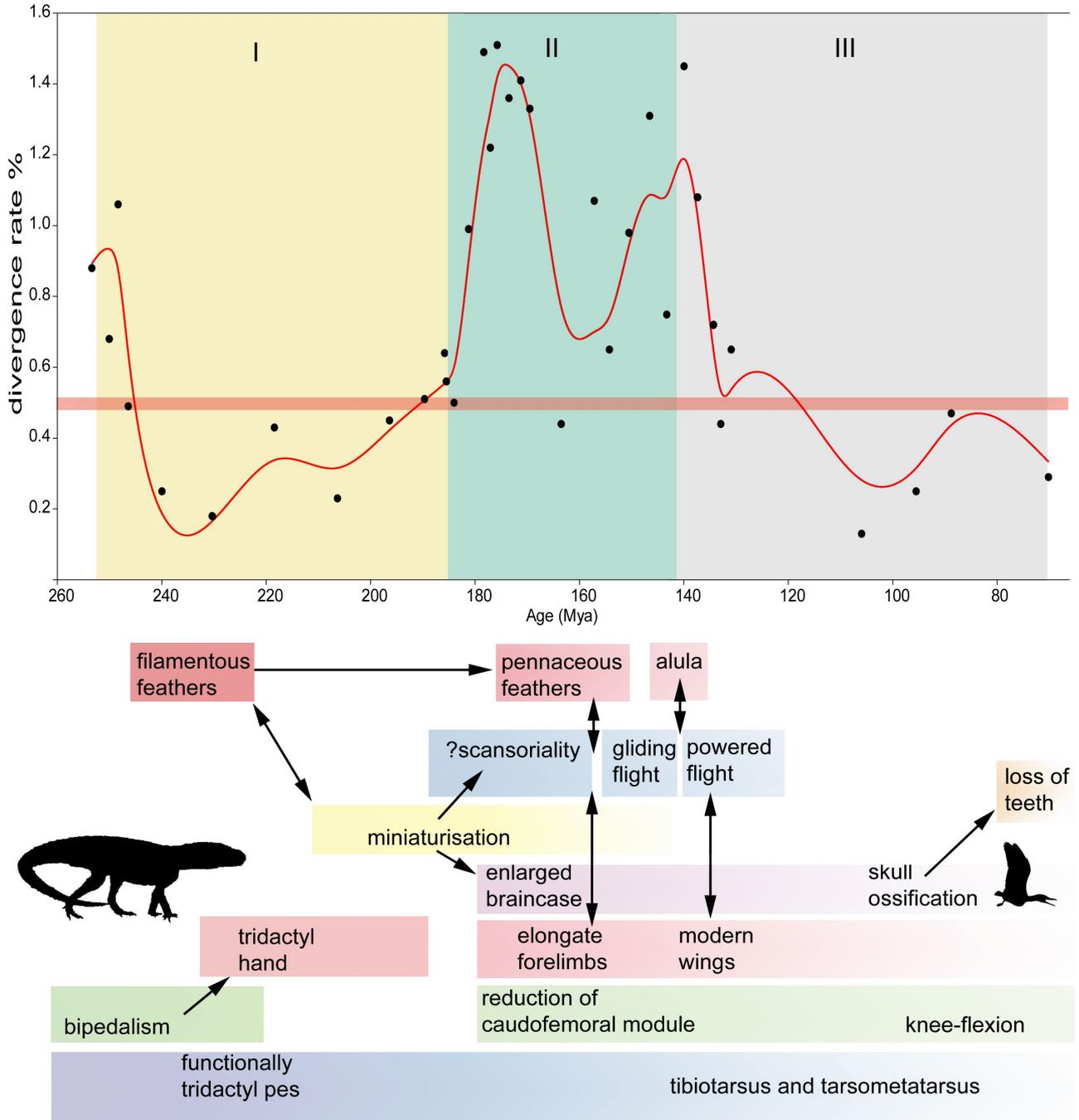


Fig. 9 - The three main phases in the assembly of the avian body plan. Above, plot of the avian ancestors relative to the rate of morphological divergence and cladogenetic median age, both inferred by the Bayesian analysis. Horizontal red bar indicates upper limit of background rate of divergence from all branches of all sampled trees (4.87%). Roman numbers indicate the phases. Below, historical series indicating the origin and evolution of the main features of the avian *bauplan* documented in the fossil record. Single-headed arrows indicate possible causal relationships, double-headed arrows denote possible co-evolving features. Silhouettes based on artworks by Davide Bonadonna and Lukas Panzarin.

inclusive nodes including, respectively, *Archaeopteryx* and *Piscivoravis*, and the scion including the four most crown-ward nodes (Fig. 9). An unusually high rate of divergence along part of the ASL was obtained in the analysis of Lee et al. (2014b), although that analysis found the highest values among the basal tetanuran internodes. It should be remarked that in their analysis, Lee et al. (2014b) enforced the age of the neotetanuran node at about 175 Mya, and that such constraint may have biased (inflating) the divergence rates among the branches that radiated from the enforced node. In the current analysis, only the age of the root of the tree was enforced. In this analysis, the age of the root of the tree was constrained as not older than the Permian-Triassic boundary: this age setting may explain the higher values inferred along the basalmost nodes. No age constraints were enforced for the tetanuran branches; thus the high evolutionary rate inferred along the coelurosaurian internodes of the avian stem is interpreted as a genuine evolutionary phenomenon.

Morphospace occupation along the ASL further supports a non-homogeneous evolutionary history of the bird ancestors. As described above, the trajectory linking the avian ancestors along the space defined by the two first axes resulted in the PCoA shows two most significant transitions in morphospace occupation. The first transition occurred among the ancestral coelurosaurs toward the maniraptoromorph origin, while the second transition occurred at the origin of the ornithothoracines. These transitions in morphospace occupation closely match the two most significant variations in the evolutionary rates inferred in the Bayesian analysis (i.e., the first among basal coelurosaurs and the other among basal ornithothoracines). Once combined, the results of these analyses define three distinct phases along the ASL evolutionary trajectory, each phase characterised by significant differences in feeding ecologies, locomotory modules and rates of morphological divergence.

Pan-avian phase I: the Huxleyian stage (~ 245-185 Mya)

The last common ancestor of birds and crocodiles was probably a predator with ziphodont dentition, a quadrupedal semi-erect posture, and a scaly integument including osteoderms, as in most Triassic archosauriforms (Nesbitt et al., 2017): these have to be assumed as the main features of the ancestral body plan at the beginning of the avian history. The first phase of the assembly of the avian body plan spans about 60 million years, from the Early Triassic to the Middle Jurassic. This phase, here named “Huxleyian” in honor of Thomas Henry Huxley (1825-1895), includes the pan-avian series leading to the last common ancestor of the maniraptoromorph theropods. About 40-45% of the key avian features, still shared by modern birds, were acquired during this phase. In the integumentary system, the osteoderms of the ancestral archosaurs were lost relatively early among the basalmost pan-avians. The simplest form of filamentous appendages was acquired before the origin of the last ornithoscelidan common ancestor (Godefroit et al., 2014), and then elaborated among the earliest coelurosaurian ancestors in basally branching feather-like structures (Ji et al., 1998, 2007). During this phase, the presacral vertebral series is progressively pneumatized by diverticula of the respiratory system, following a pattern that is repeated

during the ontogeny of living birds (King, 1957). In the tail skeleton, bird ancestors acquired a distinct “transition point”, abruptly marking the regionalisation between a proximal and more mobile region and a distal and more rigid region: this morphology also characterises, to an extreme level, the tail of modern birds. In the locomotory system, the most distinctive bird adaptation among living tetrapods (obligate bipedalism) is acquired during this phase (Hutchinson, 2001a, b). Both hindlimb and pelvis progressively developed an erect parasagittal posture and a digitigrade and functionally-tridactyl pes before the origin of the last common ancestor of all theropods. The acquisition of a fully bipedal stance in these hypercarnivorous forms allowed the hand to evolve a grasping function: this predatory function selected the medialmost three fingers and led to the progressive reduction and then complete loss of manual fingers IV and V: at the end of this stage the tridactyl hand, another key feature of the birds among modern vertebrates, had acquired its fundamental structure.

Pan-avian phase II: the Ostromian stage (~ 185-145 Mya)

The second main phase in the evolution of the avian body plan spans 40 million years, during the second half of the Jurassic. This phase, here named “Ostromian” in honor of John Harnold Ostrom (1928-2005), includes all avian ancestors from the origin of maniraptoromorphs to the last common ancestor of the pygostylian birds. This shorter phase is characterised by a significantly higher rate of morphological divergence than in the rest of the ASL, and a dramatic increase in the number of avian-like features acquired (OG raises from 40 to 90) corresponding to about half of the whole set of apomorphies evolved during the assembly of the bird body. The most significant trend observed during the whole phase, and presumably started at the end of the previous phase, is a sustained body miniaturisation which drove the accumulation of pedomorphic features (Lee et al., 2014b). It is particularly intriguing that many of the most successful theropod clades of the Cretaceous (i.e., ornithomimosaurs, alvarezsauroids, oviraptorosaurs, dromaeosaurids and troodontids) are sister taxa of subsets of the lineage evolved during the Ostromian stage. All these lineages are inferred to originate during the Middle Jurassic (Lee et al., 2014b). This relatively rapid morphological radiation may be explained as the result of the “exploration” of novel ecological regions, previously not occupied by theropods (Zanno & Makovicky, 2011; Lautenschlager et al., 2013; Lautenschlager, 2014). In particular, most of the avian ancestors along the Ostromian stage are inferred to lack the majority of the mandibular and tooth features related to hypercarnivory and macrophagy, and instead widespread among non-maniraptoriform theropods (Zanno & Makovicky, 2011). This supports the hypothesis that the ancestral hypercarnivorous ecology of most archosaurs, retained during the Huxleyian stage, was replaced in this second phase by an omnivorous ecology. Furthermore, both encephalisation ratios and braincase anatomy support an expansion and re-organisation of the central nervous system during the Ostromian stage (Currie, 1985; Larsson et al., 2000; Balanoff et al., 2013). In the appendicular system, a sustained elongation of the forelimb is documented along the entire phase, being it

particularly dramatic in the terminal internodes, when the forelimb exceeds the hindlimb in both length and robustness (Dececchi & Larsson, 2013). It has been shown that this trend was driven by allometric effects related to body miniaturisation (Dececchi & Larsson, 2013; Lee et al., 2014b). In the hindlimb, the most important trend observed during this phase is the progressive reduction of the hindlimb retractor muscles, which represent the main locomotory module in all limbed (non-avian) reptiles (Gatesy & Dial, 1996a; Hutchinson, 2001a, b). This trend culminated in the extreme reduction of the size of the tail at the end of this phase, reduced to a very short element at the root of pygostilians (Chiappe et al., 1999). Although often remarked as a key element of the avian flight apparatus, the pygostyle is merely the extreme stage of a general trend widespread among most coelurosaurs: stiffening the distal half of the tail (Gatesy & Dial, 1996a). The multiple evolution of pygostyle-like structures among the non-volant maniraptoriforms and the absence of modern rectrices in basalmost pygostilians (Wang & O'Connor, 2017) suggest that the origin of the pygostyle in the last phase of the Ostromian series was merely a by-product of tail reduction, not related to flight adaptations. Thus, one possible explanation of the dramatic atrophy of the caudofemoral musculature at the end of the Ostromian stage may be non-adaptive: the combination of allometric and structural factors in a miniaturised theropod with a stiffened tail end. It is particularly intriguing that the most impressive reduction in the size of the pelvis bones (in particular, in the area of the postacetabular part of the ilium and the length of the ischium) is observed in anchiornithids and some basal avialans (Godefroit et al., 2013a, b; Lefèvre et al., 2017): these theropods probably had, compared to body size, the smallest surface areas for the origin of the retractor hindlimb muscles among all dinosaurs (Hutchinson, 2001a, b), a peculiar condition that requires further scrutiny.

What factors drove the modular re-organisation of the appendicular system? While allometry may explain the first phase of forelimb elongation (Dececchi & Larsson, 2013), the significantly enlarged forelimb and the ossified sternum present in the last three internodes of the Ostromian stage appear as unambiguously related to the acquisition of some flight adaptation (Padian & Chiappe, 1998; Chiappe et al., 1999). The precise optimisation of these features along the sequence is complicated by the problematic combination of features differentiating jeholornithids, sapeornithids and confuciusornithids (Zhou & Zhang, 2006). Although an arboreal ecology in the early internodes of the Ostromian stage is not supported by morphometric analysis (Dececchi & Larsson, 2011), it may have played an important role at the end of this stage (among the internodes more crownward than those shared with *Archaeopteryx* and *Balaur*). Body size miniaturisation and reduction of the hindlimb retractor muscles may indicate that during the last part of the Ostromian stage, the avian ancestors adapted to more densely vegetated ecotones, including arboreal settings, that did not require the cursorial adaptations widespread along most of the preceding internodes. This scenario is supported by the unambiguous scansorial adaptations acquired in the final part of this phase (e.g., the opposable hallux; Chiappe et al., 1999). Both the overall reduction in

adult body size and the possible exploration of scansorial/arboreal ecologies during this phase co-evolved with (or co-opted) a progressive elaboration of the plumage. During the Ostromian stage, the avian ancestors acquired and then elaborated the pennaceous feathers (Ji et al., 1998; Prum, 1999; Lefèvre et al., 2017). It is useful to compare feather complexity and distribution, on one side, and locomotory adaptations, on the other side, along the series of the avian ancestors inferred in this phase. Based on the known distribution of the pennaceous plumage among the maniraptorans, this novel type of feather appeared initially only on the distal end of the forelimb and on the distal end of the tail in cursorial/ground-dwelling forms (Ji et al., 1998; Zelenitsky et al., 2012). Distinct lines of evidence suggest that sexual selection and reproductive functions may have driven the origin of the pennaceous structures in the forelimb and tail (Zelenitsky et al., 2012; Persons et al., 2014). A more extensive distribution of pennaceous feathers, along the whole forearm, most of the tail, and the hindlimb, is inferred exclusively in more crown-ward avian ancestors (among the paravians), characterised by a smaller adult body size, a relative reduction of the hindlimb musculature, and incipient scansorial adaptations (e.g., unguals in both fore- and hindlimb showing a marked falciform shape, and relatively longer forelimbs). Assuming that these small-bodied theropods were able, even incipiently, to exploit arboreal environments, the selection of plumage elaboration due to its passive aerodynamic function (i.e., parachuting) cannot be ruled out. This stage may precede the evolution of a fully-developed wing with asymmetric feathers, inferred in the last nodes of this phase (Chiappe, 1995; Chiappe et al., 1999; Zhou & Zhang, 2006). Following this scenario, the progressive adult size miniaturisation, the elaboration of sexually-related features with aerodynamic effects, and then the acquisition of scansorial habits, all co-evolved through a positive feedback along the avialan internodes of the Ostromian stage.

The lineage leading exclusively to *Archaeopteryx* is the sister-taxon of one of the internodes along the Ostromian stage. Thus, the evolutionary point traditionally considered the boundary between birds and “non-birds” is placed along the Ostromian stage. Yet, the internode represented by the last common ancestor of *Archaeopteryx* and birds (node that is often used to identify the “ancestral bird”) does not show any significant divergence in morphospace occupation, compared to the adjacent nodes along the ASL. Its historical meaning aside, once analysed using a large-scale morphological and taxonomic sampling, *Archaeopteryx* does not mark any peculiar evolutionary shift toward the origin of modern birds or the evolution of flight. Furthermore, the first unambiguous flight-related adaptations are inferred along the last nodes of the Ostromian stage, after the divergence of *Archaeopteryx*-grade avialans (Padian & Chiappe, 1998; Dececchi & Larsson, 2011). The actual flight abilities of those basal avialans with unambiguous flight-adaptations (e.g., *Jeholornis*, *Sapeornis*, *confuciusornithids*; Padian & Chiappe, 1998; Chiappe et al., 1999; Senter, 2006; Zhou & Zhang, 2006) are controversial. It should be remarked that even if potentially adapted to scansorial or arboreal ecologies,

the most advanced members of the Ostromian stage (at the root of Pygostylia) lack unambiguous features indicating the acquisition of flapping, powered flight (Senter, 2006). Although the ongoing debate on the basal avialans has focused on their actual flight capabilities (Padian & Chiappe, 1998; Senter, 2006; Dececchi & Larsson, 2011, 2013), all alternative scenarios agree in considering the last node of the Ostromian stage as represented by miniaturised theropods (body mass < 1 kg; Lee et al., 2014b) with an omnivorous ecology and a series of appendicular and integumentary adaptations for successfully exploiting, for the first time among dinosaurs, the arboreal environment.

Pan-avian phase III: the Marshian stage (~ 145-85 Mya)

The last main phase in the assembly of the avian body plan is exclusively Cretaceous in age, and spans from the origin of ornithothoracines to the last common ancestor of all living birds (inferred to be mid- or Late Cretaceous in age; Lee et al., 2014a). This phase is named “Marshian”, honoring Othniel Charles Marsh (1831-1899) who first described Cretaceous birds and provided the first systematic review of their diversity (Marsh, 1872, 1880). During about 60 million years, the bird ancestors acquired 10-15% of the features that define the modern avian *bauplan*. This relatively smaller amount of apomorphies, compared in particular to the evolutionary transformation occurred during the shorter Ostromian stage, is also expressed by the significantly lower rate of divergence inferred for most of this phase in the Bayesian analysis. In particular, during the first 10 million years of this phase, the rate of morphological evolution is inferred to drop from the high values estimated during the Ostromian stage to values comparable to the background rate of the rest of the tree (Fig. 9). Morphospace occupation in this phase mirrors the trend in the divergence rates, showing that the avian ancestors along the most basal ornithuromorph nodes were subjected to a remarkable shift along the second main axis inferred in the PCoA.

The two most significant trends inferred during the Marshian phase are the evolution of powered flight (in particular, during the earliest part of this phase), and a general simplification of the skeleton due to loss or fusion of elements. The largest majority of the musculoskeletal adaptations to flapping flight evolved at the very beginning of this phase, once the avian ancestors had acquired the full set of adaptations allowing them, for the first time, to exploit the arboreal environments (Chiappe & Calvo, 1994; Chiappe, 1995; Zhang & Zhou, 2000). These include, among others, the expansion of the sternum and the development of a midline keel, the radical transformation of the coracoid in a strut-like bar, the re-location of the scapulae on the dorsal surface of the ribcage, paralleling the dorsal vertebral series, the ossification of the carpometacarpal elements, the simplification of the manual phalanges with loss of any predatory or grasping function in the hand, and the development of the alula (Chiappe & Calvo, 1994; Chiappe, 1995; Padian & Chiappe, 1998; Zhang & Zhou, 2000; Clarke & Norell, 2002). In the first part of this radiation, the atrophied tail was inherited relatively unmodified from the last part of the previous phase,

and lacked any apparent flight-related function (Wang & O'Connor, 2017): later, among the ornithuromorphs, the tail is co-opted to its modern function, as a third locomotory module that is independent from the musculoskeletal system of the hindlimb (Gatesy & Dial, 1996b).

The other most significant trend occurred during the Cretaceous phase is the general co-ossification or loss of many skeletal elements, in particular in the skull (including the complete loss of dentition), in the thoraco-sacral vertebrae, and in the metapodial elements (formation of the carpometacarpus and tarsometatarsus) (Padian & Chiappe, 1998; Clarke & Chiappe, 2001; Clarke & Norell, 2002; Clarke, 2004). Although a causal relationships between skeletal simplification, fusion of appendicular elements and evolution of powered flight cannot be ruled out, the fusion of previously-distinct elements is reported also in non-volant theropod lineages (e.g., Carrano & Sampson, 2008; Cau et al., 2015). It is intriguing that a driven trend in cranial simplification is documented along the mammalian stem lineage, and may represent a general trend in tetrapod evolution (Sidor, 2001).

Innovation, reduction and exaptation

Several key features that characterise the modern avian *bauplan* are modification of innovations that evolved before the Marshian phase. These exaptations (Gould & Vrba, 1982) originated and then were fixed under the Huxleyian and Ostromian stages, presumably under ecological and functional regimes different from those exploited for the actual functions. For example, although the tail was part of the locomotory module in the ancestral pan-avians, there is not unambiguous evidence that the shortened tail of the earliest pygostylians (at the end of the Ostromian stage) retained some locomotory function: later, during the Marshian phase, this organ was co-opted to a novel locomotory module, among the ornithuromorphs (Gatesy & Dial, 1996a; Wang & O'Connor, 2017). The peculiar metacarpo-phalangeal articulation that provides mobility to the alular feathers is the exaptation of the hyper-extendable articulation (related to a predatory use of the forelimb) acquired during the earliest internodes of the Huxleyian stage, after the evolution of the fully-bipedal posture (Galton, 1971; Zhang & Zhou, 2000; Senter & Robins, 2006). The first toe lost any significant locomotory function relatively early during the Huxleyian stage, when the toes acquired a symmetrical and a functionally-tridactyl configuration related to development of the fully-erect posture: in that state of “latency” for over 60 million years, the hallux was then subjected to a limited set of changes in order to acquire a novel function, grasping related to arboreality, during the last internodes of the Ostromian stage (Galton, 1971; Middleton, 2001; Hattori, 2016). Finally, feathers probably evolved as structures with no aerodynamic function along the early internodes of the Huxleyian stage (Godefroit et al., 2014), were then elaborated as complex appendages probably under a sexual selection regime along the earliest internodes of the Ostromian phase (Zelenitsky et al., 2012), and then co-opted as aerodynamically-functional organs at the end of the same phase (Padian & Chiappe, 1998).

CONCLUSION

The evolution of the avian body plan is a 160-million-year long macroevolutionary process that cannot be reduced to the branching off of the avialan lineage in the mid-Jurassic, and could not be resolved exclusively to the acquisition of powered flight. The assembly of the avian *bauplan* was a hierarchically-diversified process, and different levels of biological organisation are described by different patterns and regimes. At the lowest complexity scale, that of the morphological features usually targeted by phylogenetic analyses, the ornithisation was a gradual and probably stochastic process, as evidenced by the overall uniformity in the amount of novelties gained during the assembly of each module. Body size reduction is a large-scale macroevolutionary trend that is inferred along a significant part of the ASL: this process ignited and drove several innovations related to paedomorphosis and heterochrony, progressively gained along the Ostromian stage. A by-product of miniaturisation, allometric scaling in the different modules, played a pivotal role in producing non-adaptive novelties, subsequently co-opted as exaptations in later internodes. At a higher scale, that of the whole character combinations that define each ancestor along the stem lineage, the ornithisation was a more heterogeneous pattern, as indicated by the significant raise and drop in the rate of divergence during the Middle Jurassic-earliest Cretaceous interval. Such rate heterogeneity is paralleled by the trajectory linking the series of ancestors in the morphospace analysis. Both patterns support a tripartite sequence for the avian history, into the Huxleyian, Ostromian and Marshian stages: these phases define three distinct macroevolutionary regimes explored by the ASL during its history.

Phylogenetic taxonomy aims to describe evolutionary *events* (the origin of taxa), and thus must be strictly monophyletic (Gauthier & Padian, 1985). The terminology introduced here does not conflict with the phylogenetic taxonomy of the avian branch, because it describes the ordered stages of a *process* (i.e., the assembly of an avian body plan). This tripartite subdivision of the avian evolution is novel in its formulation, and is based on the explicit rejection of a privileged explicative role to some particular taxa (e.g., *Archaeopteryx*, or basal paravians) or set of morphological features (e.g., feathers, or flight-adapted forelimbs). This alternative paradigm could not be properly recognised until we look at bird evolution under the traditional dichotomy between “birds/avians/avialans” vs. “non-birds/avians/avialans”, anchored for over a century to *Archaeopteryx* and recently fixed to the arbitrary root of the clade Avialae. The importance of *Archaeopteryx* in our understanding of bird evolution is mainly a historical contingency because no significant morphological disparity differentiates it from “non-avian dinosaurs”. While it is now widely recognised that *Archaeopteryx* is not the “missing link” between two biological “classes”, its historical role of “first bird” has been fixed through taxonomic definitions that anchored the “bird clade” to the Jurassic *Urvogel*. Yet, bird evolution is more than just fixing the phyletic position of a clade name, and focusing on the evolutionary events placed around the “*Archaeopteryx* node” inflates the importance of a few internodes over the rest of the assembly process.

Distinct lines of evidence have shown that the debate on the ecomorphology of the “*Archaeopteryx* grade” is not just overrated, it is probably misleading. Placed along the Ostromian stage of the bird evolution, the node defined by the last common ancestor of *Archaeopteryx* and avians was not a “key discontinuity” in what is indeed a longer and more complex branching continuum. More significant ecomorphological transitions occurred in distinct moments, before and after the *Archaeopteryx*-bearing internode of the ornithisation. As a couple of examples, both obligate bipedalism and feathers, the most distinctive features that unambiguously differentiate birds from the other living amniotes, are key innovations of the Huxleyian stage and evolved under a regime distinct from that of early avialans. The powered flight, the most significant adaptation of living birds, was acquired during the Marshian phase, in a context different to that at the origin of the *Archaeopteryx*-like forms.

Being it the framework of the “reptile-to-bird” transition, the pan-avian (avemetatarsalian) radiation has been polarised into two opposite narrations. One, focusing on bird ancestry, has oversimplified the complex pattern among the lineages not leading to birds, that have been reduced to a series of steps along the avian body assembly. The other, focusing almost exclusively on “non-avian dinosaurs”, has implicitly perpetuated the use of arbitrary grades based on paraphyletic groups, and has inflated the differences between birds and the other pan-avians. The terminology introduced here is explicitly - and exclusively - devoted to bird ancestry (i.e., to the process that assembled the avian *bauplan*), but, at the same time, it avoids to use the same systematic terminology that refers to branches not involved in the avian body assembly. Such terminological distinction prevents the various sister taxa of birds to be inappropriately mentioned as examples of “stages” along the avian body assembly (e.g., eudromaeosaurs mentioned as examples of the “proto-bird” *bauplan*).

The recognition of a hierarchical structure linking the various factors involved in bird evolution reinforces, at the lowest anatomical scale, the unity and continuity between the “reptilian” and “avian” body plans, and, at the highest ecological and functional scale, helps in identifying and interpreting the complex concert of historical factors that shaped this unique and successful *bauplan*.

SUPPLEMENTARY ONLINE MATERIAL

All the Supplementary data of this work are available on the BSPI website at <http://paleoitalia.org/archives/bollettino-spi/>

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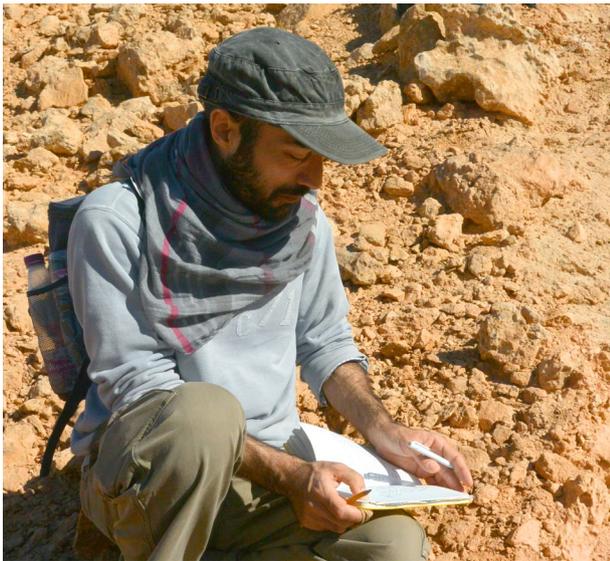
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