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RESEARCH PAPER

'Dinosaur-bird' macroevolution, locomotor modules and the origins of flight

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Abstract

The dinosaurian origin of birds is one of the best documented events that palaeontology has contributed to the understanding of deep time evolution. This transition has been studied on multiple fossils using numerous multidisciplinary resources, including systematics, taxonomic, anatomical, morphological, biomechanical and molecular approaches. However, whereas deep time origins and phylogenetic relationships are robust, important nuances of this transition's dynamics remain controversial. In particular, the fossil record of several maniraptoran groups clearly shows that aerial locomotion was developed before an 'avialization' (i.e., before the first divergence towards avialans), thus earlier than presumed. Although aspects as important as miniaturization and the acquisition of several anatomical and morphological modifications are key factors determining such evolutionary transition, understanding this macroevolutionary trend also involves to seize the evolution of developmental systems, which requires assessing the morphological expression of integration and modularity of the locomotor apparatus throughout time. This is so because, as it happened in other flying vertebrate taxa such as pterosaurs and bats, the transformation of the maniraptoran forelimbs into flying locomotor modules must not only have involved a gradual anatomical transformation, but also a complete developmental re-patterning of the integration scheme between them and the hindlimbs. Here, we review the most relevant aspects of limb morphological transformation during the so-called 'dinosaur-bird' transition to stress the importance of assessing the role of modularity and morphological integration in such macroevolutionary transition, which ultimately involves the origins of flight in dinosaurs.

Keywords Aves · Dinosauria · Limbs · Modularity · Morphological integration · Flight

Macroevolución 'dinosaurio-ave', módulos locomotores y el origen del vuelo

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Resumen
El origen de las aves a partir de los dinosaurios es uno de los eventos mejor documentados por la paleontología y que más ha ayudado a la comprensión de la evolución en el tiempo profundo. Esta transición ha sido estudiada a partir de múltiples fósiles y ha utilizado recursos multidisciplinares, incluyendo sistemática, taxonomía, anatomía, morfología, biomecánica y aproximaciones moleculares. Sin embargo, mientras que sus orígenes y sus relaciones filogenéticas son robustas, hay importantes matices en esta transición aún controvertidos. En particular, el registro fósil de varios grupos de manirraptores muestra claramente que la locomoción aérea se desarrolló antes que la 'avialización' (i.e., antes de la primera divergencia hacia las aves). Aspectos tan importantes como la miniaturización y la adquisición de varias modificaciones anatómicas y morfológicas fueron clave en la determinación de dicha transición, pero entender esta tendencia macroevolutiva implica también comprender la evolución de los sistemas de desarrollo. Esto requiere investigar la expresión morfológica de la integración y la modularidad del aparato locomotor a lo largo del tiempo. Como ocurre en otros vertebrados voladores como los pterosaurios o los murciélagos, la transformación de las extremidades anteriores en módulos locomotores voladores no implica solamente una transformación anatómica gradual, sino también una redistribución durante el desarrollo del esquema de integración que comparten con las extremidades posteriores. En este trabajo revisamos los aspectos más relevantes de la transformación morfológica de las extremidades durante la transición 'dinosaurio-ave', enfatizando la importancia de investigar el rol de la modularidad y la integración morfológica en dicha transición, la cual implicó finalmente el origen del vuelo en dinosaurios.

Palabras clave Aves · Dinosauria · Extremidades · Modularidad · Integración Morfológica · Vuelo

1 Introduction

Birds (i.e. crown-group Avialae) represent one of the most abundant, diverse, and globally distributed vertebrate clades (Jetz et al., 2012). They belong to a lineage of bipedal dinosaurs that originated during the mid-Jurassic, the maniraptoran theropods (Gauthier, 1986; Fig. 1), and many of the features uniquely assumed to be avian, such as the elongated arms and hands and extensively feathered bodies, were already present in the Mesozoic maniraptoran radiations (Brusatte et al., 2015; Qiang et al., 1998; Xu et al., 1999). During the Mesozoic, different maniraptoran dinosaur lineages protagonized a radiation (Benson et al., 2014) yielding major clades such as therizinosaurs, alvarezsaurs, oviraptorosaurs and paravians. At the origin, most of these dinosaurs were mid-sized cursorial and bipedal predators (Benson, 2018; Brusatte et al., 2014; Lee et al., 2014). In this context, birds belong to Paraves (Sereno, 1997), a clade with mid to small-sized maniraptorans including the dromaeosaurids, troodontids, and emblematic fossils such as *Archaeopteryx*. A subsequent radiation along the Mesozoic involved the pygostylian avialans (Padian & Chiappe, 1998; Fig. 1), a clade encompassing the enantiornithine and ornithuromorphan birds (O'Connor et al., 2011). Some of the latter diverged into the crown group birds (i.e. Neornithes), during the late Cretaceous, and survived the K-Pg extinction giving rise to the first great early-Cenozoic radiation of the so-called 'modern' birds (Field et al., 2020; Jarvis et al., 2014; Ksepka et al., 2017; Prum et al., 2015). The second Cenozoic radiation was that of the birds sensu stricto, the passerines, during the Oligocene (Oliveros et al., 2019). Both Cenozoic radiations shaped the current avian diversity across an increasing range of avian ecomorphotypes (i.e. terrestrial, arboreal, aquatic, extremely aerial, etc.).

The origins of aerial locomotion and the development of powered flight in birds has been traditionally viewed as a process that involved two iconic avian features: the acquisition of feathers and the anatomical transformation of the appendicular skeleton. However, now a days this view has changed dramatically with the discovery of hundreds of exquisitely preserved fossils, especially from the Lower Cretaceous of China (Meng & Chiappe, 2016). Such, interest of palaeobiological scientist has focused on hypotheses that incorporate different perspectives from developmental biology, physiology, biomechanics, and life-history theory (see e.g., Balanoff et al., 2013; Knoll, 2018; Marugán-Lobón et al., 2011; O'Connor et al., 2012). Whereas feathers have also become a typical feature of non-avialan dinosaurs and a classic example of evolutionary exaptation (Gould & Vrba, 1982), the transformation of the forelimbs with grasping hands into flying skeletal wings remain the quintessential picture of the avian *bauplan*. However, proximate causes remain poorly understood.

Here, we review the most relevant events of limb evolution across the so-called dinosaur-bird transition, paying special attention to how such transformation has been interpreted in relation to the origins of flight. We further address the meaning and the importance of analyzing both the disparity and the integration/modularity tandem within such macroevolutionary trend, discussing why such approaches require a fine-tuned shape analytical tools to address this question in macroevolution. Finally, we propose a protocol as example of how to address these questions in macroevolutionary transitions.

2 Materials and methods

The present review compiles and summarizes a series of original research articles that have assessed the evolution of maniraptoran limbs across the 'dinosaur-bird' transition, and how such structures have been interpreted in light of adaptations to the emergence of flight as a new locomotion behaviour. Such scope encompasses studies that tackle the issue differently, namely: (1) using quantitative proxies (traditional morphometrics) to address the main trends of evolutionary variation of the limbs across theropod macroevolution, (2) using traditional taxonomic descriptions that stress ubiquitous features of limb anatomical evolution that can be related to changes in locomotion (i.e., flight as opposed to terrestrial locomotion), and (3) theoretical and empirical assessments of morphological integration and modularity of the limbs from different conceptual proxies (morphological, functional, developmental, etc.).

Here, we illustrate the main evolutionary trends of the 'dinosaur-bird' transition on an informal phylogenetic hypothesis of the theropod clade Coelurosauria (Fig. 1), where the clade Maniraptora is rooted, from mid Jurassic to the present, encompassing all the grades as well as the most relevant taxa. The phylogenetic hypothesis was reconstructed with Mesquite v.3.40 (Maddison & Maddison, 2011) and is based on the topologies of Pei et al. (2020). The resulting tree was calibrated with the R package 'paleotree' (Bapst, 2012), following the 'minimun branch length' option (mbl) in 'bin_timePaleoPhy' function to scale branches using dates of first and last appearance for each taxon from 'fossilworks' database (www.fossilworks.org).

Finally, we succinctly discuss whether morphological integration (Olson & Miller, 1958) and its nuanced conceptual version of modularity (Klingenberg, 2008) can contribute to unveil which processes were involved in the transformation of the maniraptoran limbs and the origins of flight. This discussion lays its foundations on the operational possibilities opened by the One-dimensional Procrustes Analysis (OPA), a new morphometric tool that was recently proposed by Nebreda et al. (2020), to combine shape (morphological data) on articulated structures, with phylogenetic, ecomorphological and morphofunctional data. Such tool allows exploiting the accessibility of longitudinal measurements by transforming them into Procrustes coordinates, which can be submitted to multivariate statistics, for testing hypotheses of shape disparity and morphological integration and modularity between different structures that are constituted by an articulated unit (e.g. hands, wings, or legs).

3 Results and discussion

3.1 Limb evolution in the 'dinosaur-bird' transition

Before the rise of the so-called 'modern' birds, there were different trends characterizing theropod dinosaur evolution (Fig. 1). For instance, several stem lineages such as alvarezsaurs, troodontids and dromaeosaurids tended to body size miniaturization early in the splitting of each lineage. Within this trend the pygostylians attained the smallest body sizes, comparable to those presented by extant birds (Benson et al., 2017; Lee et al., 2014; Novas et al., 2012; Puttick et al., 2014; Turner et al., 2007). Body size decrease was followed by high evolutionary rates of anatomical and morphological change, especially in the limbs (Benson & Choiniere, 2013; Brusatte et al., 2014; O'Connor et al., 2011). Interestingly, during such trend towards miniaturization, forelimb elongation occurred mostly as a negative allometric trend anatomically characterizing the non-avialan maniraptoran lineages. Thereafter, during the avialan cladogenesis forelimb allometric scaling relationships shifted to positive (Dececchi & Larsson, 2013), thus implying that important growth shifts preceded the pygostylian radiations, decoupling and re-assembling forelimb length to body size.

Limb morphological transformation is a milestone of the 'dinosaur-bird' transition, indeed. Yet, to fully understand how the limbs evolved it is necessary to map their disparity, namely, to study the breadth of morphological variation, or the range of forms through geological time (Raup, 1966). In theory, biological form is not distributed homogeneously through morphospace, and exploring the factors that potentially have biased such distribution is the key to understand their evolution. Tackling morphological evolution under the conceptual framework of morphospace involves a quantitative parameterization, that translates biological forms into a multidimensional space (i.e., Morphospace; McGhee, 1999). This, in fact, is why previous aims to understand limb evolution in the 'dinosaur-bird' transition have been quantitative, rather than qualitative. Such approaches have focused on exploring disparity according to limb proportional variation, using ternary diagrams to construct morphospaces. These convenient depictions represent a triangular scatter-plot diagram that allows mapping the combined variation of three proportions of a structure as a whole, across three geometrically semi-independent dimensions. Accordingly, using these methods Middleton and Gatesy (2000) observed that forelimb long-bone proportions (humerus, ulna and carpometacarpus) were not significantly different between non-avialan theropods and basal avialans, entailing, in turn, that limb disparity increased during the neornithine radiation.

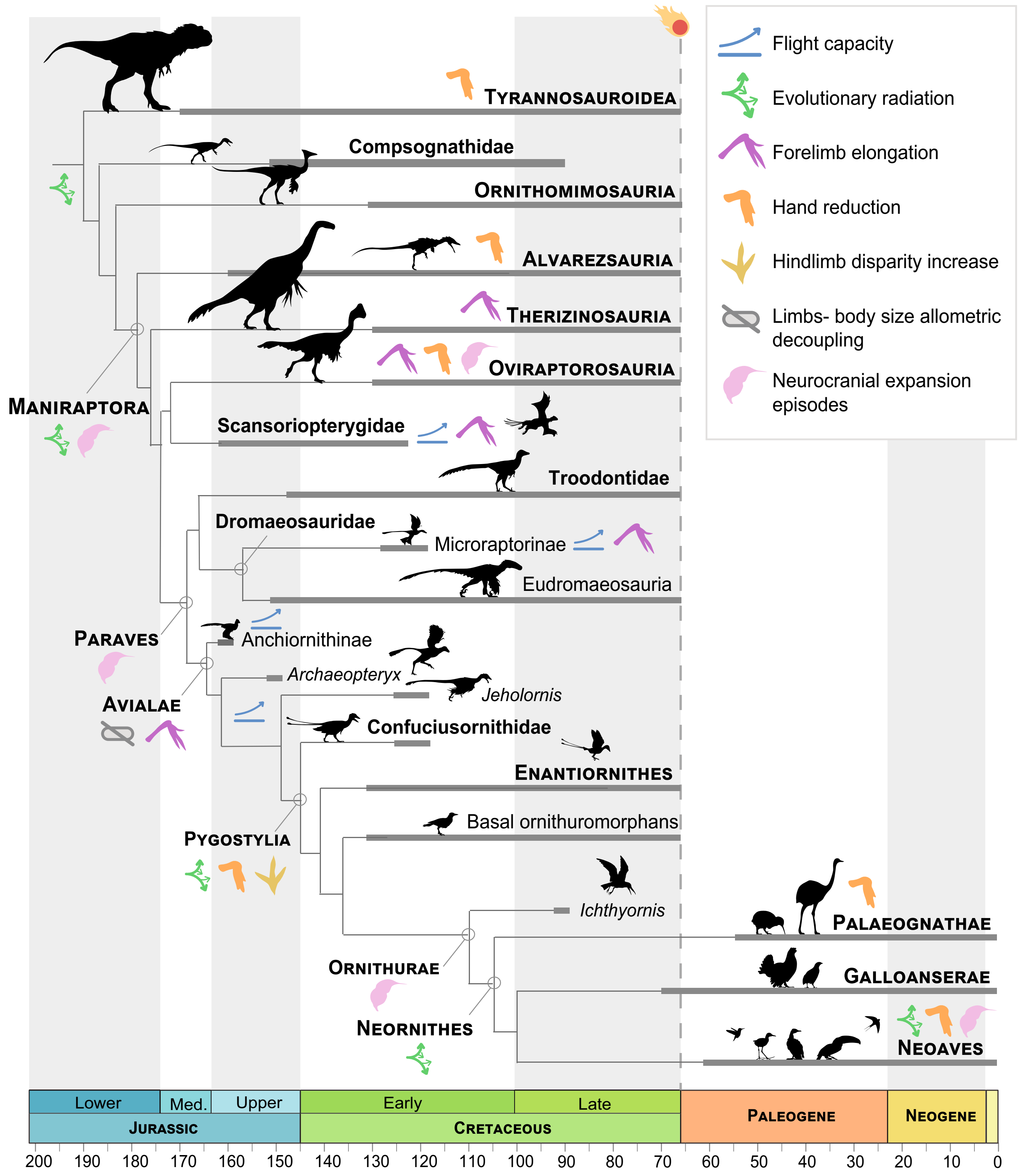

Fig. 1 Coelurosaur phylogeny showing the 'dinosaur-bird' transition between the Lower Jurassic and the present. Grey bars represent the period of existence of the different clades, based on its first and last appearance. Coloured symbols show macroevolutionary events related to each lineage (legend at the top right shows the meaning of each symbol). Flight capacity is based on Pei et al. (2020) and Dececchi et al. (2020). Evolutionary radiations are based on Benson et al. (2014) and Puttick et al. (2014). Forelimb, hindlimb and hand evolutionary dynamics are based on Benson and Choiniere (2013), Dececchi and Larsson (2013) and Nebreda et al. (2020). Finally, neurocranial expansion episodes are based on Walsh et al. (2016), Fabbri et al. (2017), Balanoff et al. (2018) and Beyrand et al. (2019). The dashed line marks the K-Pg boundary. Silhouettes are not to the same scale but try to represent the trend toward miniaturization along the Mesozoic

To explain this evolutionary trend, the authors hypothesized that intrinsic mechanisms (e.g., proximate causes such as developmental pathways, constructional demands) along with morpho-functional biomechanics (e.g., limb folding and their inertia, and spatial access) could be the potential factors underlying such patterns of limb variation and evolution. Interestingly, Gatesy and Middleton (1997) had previously found a relevant increase on disparity of the hindlimb proportions in Neornithes, compared to their non-avialan theropod ancestors, arguably related to build a functional wing, a uniquely dedicated locomotor structure. Furthermore, the authors compellingly argued that such specialization decoupled the legs as a functionally separate module. Similar results on the evolution of theropod limb proportions have substantiated such observations (Benson & Choiniere, 2013; Dececchi & Larsson, 2009), stressing that hindlimb disparity increase was a key innovation both in the late Cretaceous, bolstering the pygostylian radiation, and later, in the early Cenozoic, that of the neornithines. However, what was left unscored was the possible variational interdependence between forelimbs and hindlimbs during their evolutionary repatterning (i.e., their evolutionary transition into modules).

During the transition towards crown birds, in the Mesozoic, the anatomical evolution of the manus (the hand), represents the most drastic change as a module of the forelimb (Fig. 1), as it involved the reduction, fusion and/or loss of phalangeal elements and digits (Nebreda et al., 2020). This transformation draws a gradual transition from a more typically 'dinosaurian' grasping structure, present in the early-diverging maniraptorans and paravians, to a more avian-like (largely fused and reduced) hand in the enantiornithines and ornithuromorphans, within crown-group birds polarizing this transition. Nebreda et al. (2020) addressed this morphological transformation quantitatively using One-dimensional Procrustes Analysis (OPA) shape analytical tools, showing that this general trend involved an unexpected decrease in hand proportional disparity that was attained by decoupling the ancestral (plesiomorphic) patterning of hand growth allometry. Furthermore, the authors argued that such allometric shift was not only driven by flight evolution, as it seemingly involved their own autapomorphic evolutionary pathways.

Moreover, crown birds are not the only lineage among the coelurosaurian history in which the hand underwent an important reduction and loss of elements (Fig. 1). Tyrannosauroids (Benson & Choiniere, 2013), alvarezsaurs (Choiniere et al., 2010; Xu et al., 2011, 2018), heyuannine oviraptorosaurs (Funston et al., 2020) and some dromaeosaurids (Brusatte et al., 2013) tend to reduce their hand's elements and to lose different digits independently. Furthermore, a bizarrely extreme elongation of different digits has also occurred in scansoriopterygids (Wang et al., 2019; Xu et al., 2015), some therizinosaurs, oviraptorosaurs and dromaeosaurs (Funston et al., 2020; Nebreda et al., 2020), reinforcing the view of hand modularity driven by non-strictly locomotor demands.

More and more evidences support the classic view that morphological evolution reflects the evolution of developmental pathways (Waddington, 1975). Several hypotheses have been proposed to explain the morphogenetic pathways underlying digit variation and/or loss in theropod dinosaurs, but all of them remain highly controversial (Bever et al., 2011; Stewart et al., 2019; Tamura et al., 2011; Vargas & Wagner, 2009; Wang et al., 2011; Xu et al., 2009; Young et al., 2011). The 'frame shift' hypothesis (Wagner & Gauthier, 1999), one of the most accepted ones, proposes that digits with I-II-III identity are expressed into the embryological positions 2, 3 and 4. More recently, it has been shown that along with a huge evolutionary dynamism in digital gene expression, especially regarding digit identity and position, only digit I shifts into a different spatial expression (Stewart et al., 2019). Thus, although the mechanisms of digit development surely hold the key to address evolutionary modularity of the hand within the forelimb, more research is needed on large-scale variation across clades (Nebreda et al., 2020). Although the evolutionary patterning and diversity of limb morphology is clearly influenced by selective pressures (functional demands), it is also underlined by conserved morphogenetic pathways (Duboc & Logan, 2011; Young, 2013; Young & Hallgrímsson, 2005), and the use of embryos from different bird species have yielded important insight on these macroevolutionary issues (Bakker et al., 2013; Botelho et al., 2016, 2017; Tickle, 2004).

3.2 Multiple origins of dinosaur flight

Most of the macroevolutionary trends across the 'dinosaur-bird' transition have been hypothesized in relation to the origin of flight, largely forecasting that forelimb structure evolved as an adaptation to such new way of locomotion. Thus, traditionally it has been supposed that the refinement of flight from archetypical bipedal theropod dinosaurs took place progressively by fine-tuning the avian *bauplan* under such selective pressure. However, the fossil record suggests that flight was probably more widespread than originally thought before avian origins (Fig. 1). The astonishing wealth of fossil discoveries in the past decades have increased our knowledge about the origins of flight in maniraptoran dinosaurs and how different groups (not only birds) exploited this new locomotion behaviour (Brusatte, 2017; Dececchi et al., 2020; Pei et al., 2020). According to this new evidence, it is unquestionable that non-avialan maniraptoran theropods already possessed features that were once thought to be unique to modern flying birds, such as feathers, asymmetrical feathers building wings, and air-filled bones that lightened body mass, among other anatomical traits.

One of such examples of flight ability that stroke the scientific community was the hypothesis of a 'four-winged' dromaeosaurid *Microraptor* (Xu et al., 2003), a non-avialan dinosaur that was postulated to be able to perform gliding (Dyke et al., 2013). Moreover, Han et al. (2014) hypothesized that *Changyuraptor*, another microraptorine, was able to perform active aerial locomotion using long-feathered hindlimbs and the tail. The Upper-Jurassic *Anchiornis* also possessed forelimbs and hindlimbs sufficiently feathered as if it also was a 'four-winged' paravian (Hu et al., 2009). This is the reason why it has been proposed as a potential aerial performer that reached such capacity independently from avialan ancestry (Pei et al., 2020). Further, some members of the bizarre paravian Jurassic clade Scansoriopterygidae, with genus such as *Yi* and *Ambopteryx*, possessed extra novel elements in their hands that supported a characteristic membranous patagium along their extremely elongated hands, similarly to the building of the wing in pterosaurs or bats, allegedly qualifying them for a potential flying performance (Wang et al., 2019; Xu et al., 2015). Nevertheless, recent evidence suggests that these small non-avialan maniraptorans were not able to perform powered flight or flapping-based aerial locomotion, being limited to be arboreal gliders and, therefore, showing a completely different pattern of aerial performance compared to any crown birds (Dececchi et al., 2020). Thus, the fossil record reveals that increased anatomical variation and its expression as morphological disparity is linked to multiple origins of different flying capacities in Maniraptora. This is especially noticeable in Paraves, suggesting that experimentation and complexity of aerial performance was taking place in parallel across several clades of mid to small-sized maniraptoran dinosaurs during the upper Jurassic and the early Cretaceous.

3.3 Functional modularity and morphological integration

Anatomical structures can be interpreted as modules—partitions—that build up the whole. Although there are several definitions, modules are often considered subregions that are semi-autonomous; namely, highly integrated within themselves and only weakly linked to others (Klingenberg, 2008). Importantly, although functional modules do not always map onto morphological and/or developmental modules (Klingenberg, 2014), integration and modularity offer the conceptual scaffold to link morphology, genetics, and evolution into a coherent research agenda (Goswami & Polly, 2010). Furthermore, the developmental and the morphological identity of modules are features that evolve and affect evolvability, which is why studying them represents an important part of the palaeobiological research agenda.

Gatesy and Dial (1996) took a big step into understanding the transition towards avian locomotion, proposing the 'locomotor modules' hypothesis. Under this model, the transition from one to three modules took place within bipedal and terrestrial non-avialan theropods (Fig. 1), initially departing from the presence of a unique locomotor module consisting of the hindlimb plus the tail, functioning together as a unit during terrestrial locomotion. Birds later innovated by developing the wings as a separate module that was functionally adhered to flight, while dramatically reducing the tail into a short pygostyle. Such transformations decoupled the terrestrially cursorial unit into two different subregions (hindlimbs and tail). Functionally, the reduced tail would match up with the wings during flight performance, thus releasing the legs. Accordingly, Gatesy and Dial (1996) explained the origin of aerial locomotion across the 'dinosaur-bird' transition as a product of such 'modularity', namely, as the emergence of a new association between separate and functionally different anatomical regions (i.e. modules). Furthermore, the observed increase of limb proportional disparity, and especially that of the hindlimbs, had its theoretical foundations in functional specialization (Gatesy & Middleton, 1997). According to this view, the evolved modularity between wings and legs could be considered key to the broad diversity of avian aerial lifestyles and hindlimb ecomorphologies (Zeffer et al., 2003). It is interesting to note that such functional modularity not only coincided with the anatomical transformation of the wings and the tail, but also with the allometric decoupling of forelimb and body sizes (Dececchi & Larsson, 2013), as well as the macroevolutionary transformation of the manus that took place across the 'dinosaur-bird' transition (Nebreda et al., 2020).

Function seems to be a meaningful factor in the evolution of modules, especially in structures constrained by their use and effectiveness (Dullemeijer, 1980). Functional dissociations like those in the limbs during the 'dinosaur-bird' transition stem from evolutionary anatomical change, and available models suggest that they could be a source of disparity. In this sense, primate evolution is a good example too, as it has been shown that the decoupling of the evolutionary ways in which each limb relates to its function selectively facilitated the evolvability of the limbs through development (Young et al., 2010). Thus, limbs with distinct functions and locomotor performance may evolve relatively more independently, namely, as modules. For that reason, it is very important to clarify the type of modules that one is dealing with when studying macroevolutionary patterns (see Wagner et al., 2007), especially since functional, morphological and developmental modules might not always coincide (Klingenberg, 2014). In effect, current theory allows separating the modules that can be defined by function from those that have a morphological (hence developmental) sense, as well as anatomical or morphometrically variational, because the

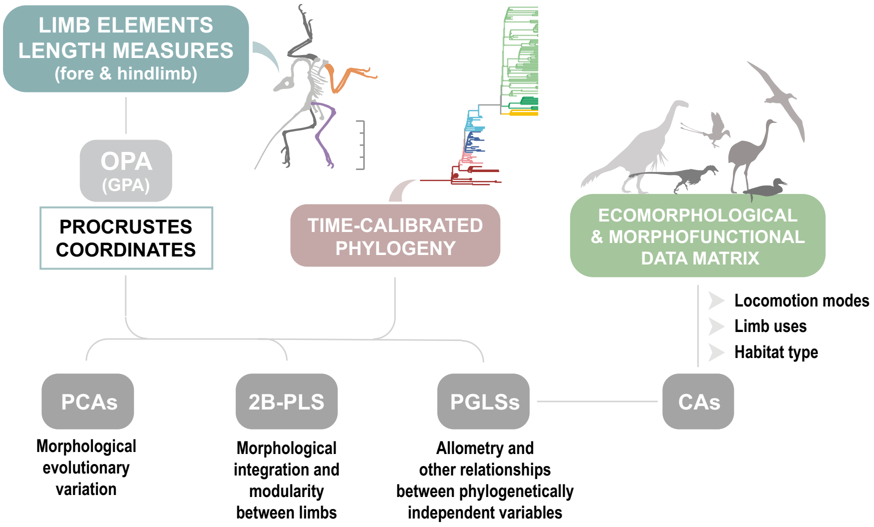

Fig. 2 Proposed protocol as example to assess morphological integration and modularity on an important evolutionary transformation, the limb evolution during 'dinosaur-bird' transition, combining morphological, phylogenetical, ecomorphological and morphofunctional data. This protocol is based on Procrustes analyses (OPA methodology) and geometrics morphometrics tools applied in Nebreda et al. (2020). *OPA* One-dimensional Procrustes Analysis, *GPA* Generalized Procrustes Analysis, *PCA* Principal Component Analysis, *2B-PLS* Two-Blocks Partial Least Squares, *PGLS* Phylogenetic Generalized Least Squares, *CA* Correspondence Analysis

nature of variation, selective pressures and constraints are different. The terrestrial locomotor module of non-avialan theropods (i.e. hindlimb and tail), as proposed by Gatesy and Middleton (1997), is a good example of functional module, because both structures evolved to act as a whole to perform the same function, but they varied and evolved independently. On the contrary, a variational module is featured by elements that vary together and relatively independent of other elements (Wagner et al., 2007). However, two subparts could act as relatively independent functional modules even if they show strong statistical integration. Thus, different types of modules could lead to different evolutionary tendencies (Klingenberg, 2014), an aspect that remains intriguing for evolutionary theory.

Functional relationships involving anatomical and morphological transformation during the 'dinosaur-bird' transition are reasonably well documented. However, factors involved in such a long-term macroevolutionary trend are not only functional, but deeply developmentally regulated (Erwin, 2000; Gilbert et al., 1996; Jablonski, 2020; Xu et al., 2014). Thus, the underlying mechanisms involved in the transformation of a new functional module (evolutionary innovation), such as theropod wings, remain poorly understood. Developmental patterning not only could be assumed to be a cause of anatomical change, but also the underlying mechanism that was either limiting (integration) or alleviating (modularity) the necessary constraints related to the emergence of different functions (i.e., locomotion). Arguably, the fact that the limbs are serially homologous structures sharing a deeply conservative morphogenetic pathway (Capdevila & Belmonte, 2000; Zeller et al., 2009) strongly suggests that important features of the avian transition could be better understood under the conceptual framework of morphological integration and modularity. Operationally, this issue could be tackled in a similar way to that proposed in Nebreda et al. (2020), adapting shape analytical methods to all the available qualitative and quantitative resources (morphological, phylogenetic, morphofunctional, and ecomorphological data) (Fig. 2). Looking into the evolutionary relationships between locomotor structures, as well as into their morphological variation and covariation, is a powerful way to understand disparity patterns across deep time and how modularity and integration may have contributed via innovation, hence to the origins of flight (Fig. 2).

4 Conclusions

The origin of flight is clearly one of the most studied changes in locomotion across the history of dinosaurian groups, even across the history of tetrapods. Thus, limb evolution in maniraptoran dinosaurs is key to understand the 'dinosaur-bird' transition, as it represented a complete re-patterning of the main structures involve in flight. The topic of the origin of flight has provided several lines of palaeobiological research aimed in understanding the major factors involved in the evolution of the limbs, and in our comprehension of how modern birds arose from ancestral theropod dinosaurs. However, much is still unknown about the proximate and ultimate causes of these macroevolutionary trends. Addressing morphological integration and modularity between limbs is one of the ways of tackling such issue and hypothesizing how developmental pathways underlie such evolutionary trends. Furthermore, these concepts could also help to address important insight on aerial performance before the origin of birds. In reviewing limb evolution in the 'dinosaur-bird' transition we show that optimised morphometric tools such as the OPA open new avenues of research on limb morphological evolution.

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