Chapter 5
Discussion

Present analysis invites to review previous hypotheses regarding the acquisition of evolutionary novelties towards the line to birds, especially those of appendicular skeleton and integumentary structures.

5.1 Evolution of Feathers and Wings Among Basal Paravians

Recently Hu et al. (2009) and Witmer (2009) interpreted that the four-winged condition evolved in the common paravian ancestor, because these authors accepted *Microraptor*, *Anchiornis,* and *Pedopenna* as basal members of Dromaeosauridae, Troodontidae and Avialae, respectively (Fig. 5.1). However, in the context of the phylogeny defended here, the development of hindlimb wings (producing a four-winged pattern) did not occur at the base of Paraves, but at the base of Averaptora: *Microraptor* exhibits well-developed hindlimb wings, with 14 pennaceous feathers attached to the metatarsals (Xu et al. 2003), a condition that is also seen in *Anchiornis* (Hu et al. 2009), as well as in the basal avialan *Pedopenna* (Xu and Zhang 2005). The presence of very long feathers in the femur of *Xiaotingia* also suggests a tetrapterygian condition for this genus (Xu et al. 2011a). However, a trend towards the reduction of hindwings occurred among avialans: in *Anchiornis*, although the hindwings are extensive, the metatarsal feathers have symmetrical vanes, condition that is usually considered as indicative of non-aerodynamical functions (Feduccia 1996). In the basal avialan *Pedopenna*, the vanes of distal metatarsal feathers are also symmetrical, but they are proportionally smaller and weaker than in *Microraptor* and *Anchiornis* (Xu and Zhang 2005). In *Archaeopteryx*, the metatarsal feathers are still present, although strongly reduced and not attached to the metatarsus (Christiansen and Bonde 2004; Hone et al. 2010). Leg feathers have been also confirmed in *Confuciusornis*, *Longipteryx* and other enantiornithes (Zhang and Zhou 2004), although they are extremely reduced in size. In non-enantiornithine ornithothoracine birds the leg feathers are totally absent (Zhou and Zhang 2006). Instead, they are replaced by pedal scales, which may be secondarily derived structures diagnostic of Ornithothoraces (Hu

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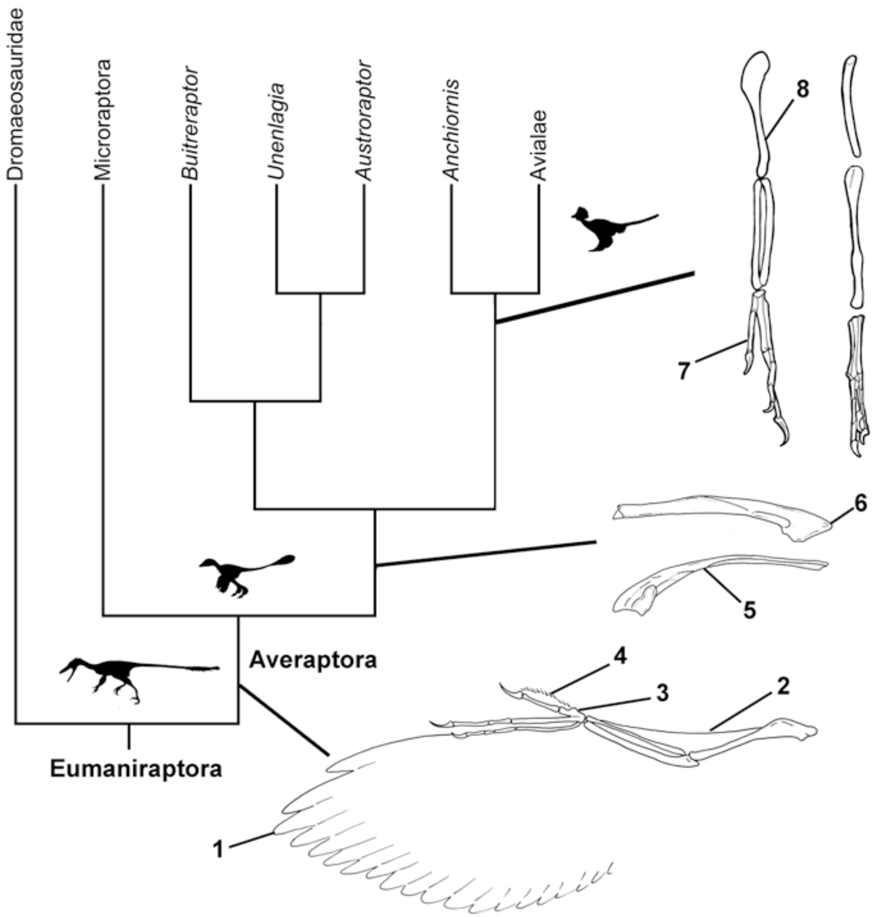

Fig. 5.1 Diagram of eumaniraptoran phylogenetic relationships showing main anatomical adquisitions related to flight. Forewing of *Microraptor gui* showing main characters allowing a powewerful flight: *1* asymmetrical remiges; *2* propatagial tendons; *3* expanded extensor process on metacarpal I; *4* alula. Scapula of *Unenlagia comahuensis*; *5* twisted scapular blade; *6* subtriangular and pointed acromion. Left fore and hindlimb of *Archaeopteryx lithographica*; *7* extremely elongate manus; *8* very robust and elongate humerus (much more robust and larger than femur)

et al. 2009). In sum, available information indicates that hindwings were progresively reduced and lost in the line to birds, as previously advocated by Xu and Zhang (2005).

In relation with the previous topic, a similar trend in the reduction in the number of secondary remiges manifest in the forelimbs: it is 12 in basal maniraptorans (e.g., the oviraptorosaurian *Similicaudipteryx*; Xu et al. 2010), a number that is similar to that in *Anchiornis* and *Archaeopteryx* for which 12 or probably 13 secondary remiges have been reported (Hu et al. 2009; Christiansen and Bonde 2004). In more derived birds, the number of remiges is even lower, with 10 remiges proposed for *Rahonavis* (Forster et al. 1998), and less than 10 remiges in Enantiornithes (e.g., 8 in *Eoalulavis*; Sanz et al. 1996). In modern birds the number of remiges is highly variable, although the presence of 10 secondary remiges appears to be the more widespread condition among living birds (Feduccia 1996).

However, certain dromaeosaurids (e.g., *Velociraptor*) and *Microraptor* seem to depart from this trend towards the reduction in the number of remiges: 14 secondary remiges are attached to the ulna in *Velociraptor* (Turner et al. 2007b), and in *Microraptor* at least 18 of these feathers have been counted (Chatterjee and Templin 2007). Taken alone the number of secondary remiges, the presence of more than 14 of these feathers seem to represent a derived condition shared by *Microraptor* and *Velociraptor*, but this alternative needs to be confirmed with additional specimens preserving the feather covering.

A puzzling situation for microraptorians is that two different kinds of feathers are present in the best known members of this group: simple, branched feather-like structures are documented in the 150 cm long *Sinornithosaurus milleni*, and considerably more complex, pennaceous feathers exhibited by *Microraptor gui*, which surpass 77 cm in length (Xu et al. 1999, 2000, 2003; Xu and Guo 2009). Character presence or absence of remiges has been coded in the present matrix, but the lack of information for most of the studied taxa precludes recognition of a pattern. Moreover, recent analysis indicate that the two-dimensional preservation of specimens during fossilization makes the identification of different kind of feather difficult due to overlapping feather structures in vivo (Foth 2011).

In regards with the Scansoriopterygidae, Zhang et al. (2008) have explained the absence of pennaceous feathers in these coelurosaurs as a consequence of a secondary loss of flight capabilities. However, in the present phylogeny, Scansoriopterygidae are located far from Avialae, and the absence of modern-like feathers is better interpreted as primary rather than to the result of a secondary reversal.

5.2 Osteological and Integumental Modifications Related to the Origin of Flight

Novas and Puerta (1997) suggested that most relevant differences in the line of theropods to birds have to do with changes in skeletal proportions (see also Xu et al. 2011a). In this regard, *Anchiornis* exhibits forelimb proportions that are more derived than those of *Microraptor*, thus closely resembling the condition present in basal birds (e.g., *Archaeopteryx*, *Jeholornis*) (Fig. 5.1). For example, in *Anchiornis* the humerus is longer than the femur, and its transverse with equals that of the latter bone; forelimb lenght in *Anchiornis* is 80 % of hindlimb length, and its elongate hand represents about 130 % of femoral length (Xu et al. 2008). This set of modifications in the forelimbs may reflect improved flying capabilities in avialans.

Several other features related with the acquisition of flying control (e.g., alula, protopatagium, automatic control of forearms, development of muscles that flex the forearms) have developed early in the evolution of averaptorans, and they are reviewed in light of the present phylogeny (Fig. 5.1).

The propatagium is an integumentary structure that fills the space in front of the flexed wing, being considered as a very important condition for flight control (Paul 2002); in addition, the ligamentum propatagiale may also support the distal portion of the wing against drag (Vasquez 1994). Several authors (see Paul 2002) proposed that the propatagium constituted a diagnostic trait of derived birds (i.e. Ornithurae). Although the fossil record of propatagium is still patchy, presence of this soft structure has been recently documented in *Microraptor* (see Xu et al. 2003), *Anchiornis* (see Hu et al. 2009), *Archaeopteryx* (Martin and Lim 2005), and Enantiornithes (e.g., *Noguerornis*; Chiappe and Lacasa Ruiz 2002). Moreover, all known averaptorans (e.g. *Sinornithosaurus*, *Anchiornis, Jeholornis, Confuciusornis*) show a well-developed extensor process on the carpometacarpus (Paul 2002), an osteological correlate of the insertion site of propatagial tendons (Vasquez 1994). Presence of extensor process on carpometacarpus may indicate that most averaptorans possesed a well-developed propatagium, and that this modern wing design and control already evolved in the common ancestor of Averaptora (Fig. 5.1).

As Vasquez (1992, 1994) pointed out, the modern avian wrist possesses the ability to synchronize flexion of extension of the elbow and wrist joints automatically. This kind of automatic mechanism of the wing is widely accepted (see Vasquez 1994) as an indispensable requirement for the powered and well-controlled flight seen in all modern birds. Vasquez (1994) indicates two main osteological features as indicative of automatic wing coordination: the presence of a groove at the distal-dorsal surface of ulna, and a well developed extensor process on metacarpal I for the insertion of the M. extensor metacarpi radialis (Campbell 2008). The presence of a relatively well-developed extensor process on metacarpal I is corroborated in *Sinornithosaurus, Microraptor*, *Anchiornis,* and *Archaeopteryx* (Paul 2002; Campbell 2008; Xu et al. 2008), suggesting that the presence of an automatic mechanism for flight may be traced back to the base of Averaptora (Fig. 5.1).

Other modifications documented in early averaptorans regards with the development and orientation of the acrocoracoidal process. This process (also named "biceps tubercle" in non-avian theropods; Ostrom 1976) serves as site for insertion of the M. biceps brachii, the chief flexor of the avian forearm (Sereno 2004; Jasinoski et al. 2006). In basal eumaniraptorans (e.g., *Deinonychus*, *Bambiraptor, Sinornithoides*; Ostrom 1969; Burnham et al. 2000; Currie and Zhiming 2001) the acrocoracoidal process is small and rounded. In basal averaptorans (*Sinornithosaurus, Microraptor*; Xu 2002; Xu et al. 2003), however, the acrocoracoid process is bigger and more laterally projected, being caudally connected with a sharp and acute ridge that runs along the lateral coracoidal surface (Xu 2002) (Fig. 5.2). The unenlagiid *Buitreraptor* shows a larger and craniolaterally projected acrocoracoidal process, conditions that *Buitreraptor* shares with *Archaeopteryx* and more derived birds (Paul 2002; Makovicky et al. 2005).

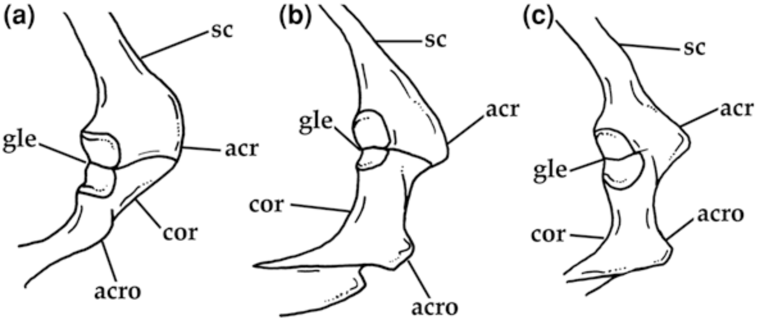

Fig. 5.2 Scapulocoracoids of selected paravian theropods in right lateral view. **a** *Bambiraptor feinbergi*. **b** *Buitreraptor gonzalezorum*. **c** *Archaeopteryx lithographica*. **a**, **c**, modified from Paul (2002); **b** modified from Makovicky et al. (2005). Not to scale

In sum, averaptorans shows the acquisition of two functionally significant sites for muscle attachment (i.e., the acrocoracoidal process and the extensor process on metacarpal I) which are present in the avian wing, suggesting that the ability of flapping flight was already developed at the base of Averaptora.

The set of modifications described above in averaptorans are in concert with a remodeling in the pectoral girdle, which had important consequences in the arc of motion of the forelimbs. The presence of a laterodorsally oriented glenoid cavity on the scapulocoracoid in derived birds (i.e. Ornithurae; Senter 2006) is considered as an unambiguous prerequisite for flapping flight (Fig. 5.1). Novas and Puerta (1997) indicated that the external surface of the scapular blade and the glenoid in *Unenlagia* was laterodorsally exposed, a condition resembling derived flying birds. Such reconstruction was critizised by some authors (Carpenter 2002; Senter 2006) who suggested that the glenoid in *Unenlagia* probably faced posteroventrally, as plesiomorphically occurs in Theropoda. However, in *Unenlegia* the glenoid surface curves in such as a way that its floor tends to be dorsolaterally oriented, implying that the continuation of the glenoid surface into the coracoid must also be dorsally faced, a condition also seen in *Buitreraptor* (Novas 2009). In this way, the scapulae of unenlagiids lie close to the vertebral column, dorsal to the ribcage, with the flat costal surface of the scapular blade facing ventrally, a condition seen in microraptorans (i.e. *Microraptor*), basal avialans (e.g. *Archaeopteryx*, *Rahonavis*), and ornithothoracine birds (Senter 2006), in which the shoulder socket sits high on the back, and the margins of the glenoid are smooth, thus this surface becomes shalower and consequently more continuous with the rest of the lateral surface of scapula (Burnham 2008). In sum, the lateral orientation of the scapular glenoid in unenlagiids (and probably also in other basal averaptorans), together with the absence of acute ridges delimitating the glenoid cavity, suggest that the humerus in these taxa was able to be elevated close to the vertical plane, as proposed by Novas and Puerta (1997) (Figs. 5.1, 5.2).

It is important to mention that scansoriopterygids retained a caudoventrally oriented glenoid, a subrectangular coracoid with reduced biceps tubercle, and a distally fan-shaped scapular blade, all representing plesiomorphic character states in respect to paravians.

Available information indicates that theropods acquired the ability to fly at the base Averaptora. At this node, main osteological characters correlated to flapping flight can be recognized, as well as integumentary modifications (e.g., alula, asymmetric feathers in ulna and manus, propatagium; Xu et al. 2003; Zhang 2004; Senter et al. 2004).

5.3 Body Size Increase and Loss of Flying Capabilities Among Paravians

Several authors (e.g., Paul 2002; Turner et al. 2007a, b; Senter 2007) interpreted that the common paravian ancestor was a small-sized, flying animal, and that flying capabilities were independently lost in different deinonychosaurian lineages, in association with an increase in body mass. Turner et al. (2007a; see also Turner et al. 2011), for example, hypothesized that Dromaeosauridae underwent three parallel trends in body size increase: one corresponding to *Deinonychus*, another one to *Unenlagia*, and a third one to the clade formed by *Utahraptor* and *Achillobator*. In this evolutionary context, Turner et al. (2007b) considered that aerodynamical capabilities became lost in large-bodied dromaeosaurids, which reduced their set of forelimb feathers (as suggested by the poor development, or absence, of papilae for feather attachment along the caudal margin of ulna). However, in the context of the phylogeny here defended, a single event of body size increase is recovered among dromaeosaurids, and it corresponds to the node made up by *Deinonychus* + (*Atrociraptor* + (*Utahraptor* + *Achillobator*)). Outside Dromaeosauridae, an increase in body size is also manifested in Unenlagiidae, with the basal and turkey-sized *Buitreraptor*, as sister taxon of the ostrich-sized *Unenlagia* and the large *Austroraptor*, reaching approximately 5 m long. Probably, secondary remiges were already present in basal paravians or eumaniraptorans (or more inclusively in tetanurines, as suggested by the presence of feather ulnar papilae in the early carcharodontosaurid *Concavenator*; Ortega et al. 2010), but development of large, asymmetrical secondary remiges for aerodynamic purposes, apparently occurred at the base of Averaptora, with the acquisition of flying cappabilities.

5.4 Independent Origin of Flying Capabilities Among Paravians

Senter (2007) noted the existence of several derived traits shared by microraptorians and unenlagiids (*Rahonavis*, in particular), but according to the results of his phylogenetic analysis, he explained these birdlike characteristics as acquired within each dromaeosaurid clade independently from Aves and also independently from each other. In agreement with this view, Zheng et al. (2009) recently described the short-armed basal dromaeosaurid *Tianyuraptor* as a possible early microraptorine, indicative that more derived, long-armed members of this clade might have developed aerial capabilities independently from birds (Xu et al. 2003; Chatterjee and Templin 2007). The present study, however, removes Microraptoria from Dromaeosauridae, *Tianyuraptor* from Microraptoria, and *Rahonavis* from Unenlegiidae. As a result, our analysis supports that the acquisition of aerial locomotion is more parsimoniously recovered as occurred just only once among paravians, that is at the common ancestor of Averaptora.

5.5 Averaptoran Radiation and Center of Origin of Birds

Available chronological and phylogenetic information strongly suggests that for Middle Jurassic times, at least, main maniraptoran theropods, including Avialae, were already diversified. *Anchiornis*, here posited as the sister-group of Avialae, is at least 150 Ma old, thus implying at least a Lower Jurassic origin for most maniraptoran theropods, including Avialae (Chatterjee 1999). It must be said that some molecular clock analyses considered a probable Triassic origin for birds (Kumar and Hedges 1998).

Xu and Zhang (2005) proposed a Laurasian, or more precisely Asiatic, origin for birds, indicating that most plesiomorphic representatives of Troodontidae and Dromaeosauridae were recorded from Eastern Asia. However, in the present phylogeny, Unenlagiidae is depicted as the immediate sister-group of *Anchiornis* + Avialae, and all presently known unenlagiids came from South America (Makovicky et al. 2005; Novas 2009). In addition, the oldest known Avialae, *Archaeopteryx*, has been recorded in Europe, and the basal bird *Rahonavis* comes from another Gondwanan landmass, Madagascar. In view of the extremely incomplete fossil record of basal paravians, is not possible to confidently establish a center of origin for the Avialae, mainly considering that their diversification occurred during the Mid-Jurassic, when continents were joined in a single landmass.

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