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Reconstruction of pectoral musculature in non-avialan paravians and basal birds: implications in the acquisition of flapping flight

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Abstract

Several studies analyzed the origin of flapping birds, but only a few of them explored the scapular girdle myology in early birds and non-avian paravians. We analyze the pectoral girdle morphology in different groups of non-ornithothoracine paravians with the aim to hypothesize the anchorage sites of selected pectoral muscles and determine their main functions in forelimb movements. Notably, the pectoral girdle remained morphologically stable among non-ornithothoracine paravians since certain aspects of the coracoid and scapula are similar in non-flying taxa, such as the cursorial *Buitreraptor*, as well as those with the ability to fly, such as the four-winged *Microraptor*, the long-tailed *Archaeopteryx* and the pygostylians *Confuciusornis* and *Sapeornis*. The distinctions among these taxa are slightly discernible in bone morphology, but they are obvious in the forelimbs feather coverage. In this sense, main pectoral muscles (i.e., *mm. supracoracoideus*, *pectoralis* and *deltoideus scapularis/major*) had similar origin and insertion places, and their inferred functions were similar across a wide array of body shapes of early paravians. The most significant muscular changes occurred in the common ancestor of Pygostylia, and consisted in the displacement of the origin of the *mm. biceps brachii* and *coracobrachialis p. cranialis*, accompanying the greater development of the acrocoracoid process and the loss of the subglenoid fossa. These modifications allowed more muscles to participate in humeral protraction and in the maintenance of wing extension. Subsequently, in the Ornithothoraces node, coracoid transformations contributed to the medial reorientation of the supracoracoidal canal thus allowing the *m. supracoracoideus* to fulfill a wing elevation function. Our study suggests that in non-ornithothoracine paravians, the main movements of the forelimb (either fliers or not) were predominantly craniodorsal to caudoventral. The humeral movements were performed in a similar manner, in which the main elevators were the *mm. deltoideus* and *latissimus dorsi* group, while the *mm. supracoracoideus* and *pectoralis* would have acted as protractor and depressor, respectively. Therefore, the ability to maintain a continuous flapping flight present in extant volant birds may have been acquired at the Ornithothoraces node, while Archaeopterygidae, Confuciusornithidae and Omnivoropterygidae may have had functional flight, short in duration and space displacement.

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Keywords Myology, Forelimb, Pectoral girdle, Functional morphology, Origin of flapping flight, Paravian, Enantiornithes, Euornithes, Aves

Background

Since the seminal work of Ostrom [1], which supports the origin of birds from a group of theropods similar to *Deinonychus*, several authors have analyzed key anatomical and biomechanical traits in extant birds and basal paravians with the aim to understand the acquisition of the flapping flight [2–16, 17]. Despite these outstanding advances, there are still few studies analyzing the muscular distribution in the pectoral girdle and hypothesized forearm movements among basal paravians (e.g., [10, 11, 18, 17] . Among recent works, we can highlight that of Pittman et al. (2022), who analyzed the pectoral musculature with new technologies and interpreted that the ancestral flight of basal birds was controlled primarily by two muscle groups, the shoulder and chest muscles that powered the upstroke and the downstroke, respectively. At the same time, integrative works such as that by Wu et al. [15] promoted a better knowledge about how the changes in the shoulder girdle occurred in the pennaraptoran lineage leading to living birds. Among the string of recent contributions, Wang et al. [12] analyzed the shoulder girdle of key taxa such as *Sapeornis* and Enantiornithes, achieving a detailed understanding of the osteological elements.

As different authors have indicated (e.g., [2, 11, 19–21]), basal paravian theropods and basal birds have a particular pectoral girdle morphology which is reminiscent of that of extant flightless paleognaths, allowing it to be used as a good osteological, myological and morphofunctional analogs.

Previous works about the pectoral muscles involved in forelimb movements in extinct non-avian theropods, based on extant volant birds as models, has expanded what was known about the muscular attachment and their respective functions linked to the acquisition of flight (see [10, 11, 18, 22, 23]). However, some aspects of the morphological changes in the pectoral girdle and their relationship to muscle function in paravian taxa have not been addressed.

The aim of the present paper is to discuss flight capabilities in selected taxa of non-avian paravians as well as some basal birds, on the basis of reconstruction of their pectoral girdle myology.

Methods

Phylogenetic framework

We use the phylogenetic framework proposed first by Agnolín & Novas [24] and followed with modifications by Agnolín et al. [2], Motta et al. [25], and Novas et al. [11]. These analyses exclude Scansoriopterygidae and Oviraptorosauria from Paraves. Besides, Troodontidae, Eudromaeosauridae, Microraptoria, Unenlagiidae and Anchiornithidae are interpreted as successively closer relatives to Avialae (Fig. 1). Considering this phylogenetic framework, Deinonychosauria (sensu [26]) results paraphyletic. We choose this scheme because a detailed overview of other phylogenetic analyses (e.g., “Theropod Working Group"—TWiG [27, 28],) resulted in poorly resolved phylogenetic relationships among derived paravians [2, 11]. Definition of the clade Avialae follows Gauthier [26], Gauthier & de Queiroz [29] and Novas et al. [11] in being composed of Archaeopterygidae, Jinguofortisidae, Jeholornithiformes, Confuciusornithidae, Omnivoropterygidae, Enantiornithes, and Euornithes (Fig. 1).

The objectives and results of this work are not altered by the phylogeny chosen.

Data collection

Muscular reconstruction was made on four different basal Paravians, namely the Dromaeosauridae *Bambiraptor feinbergi* AMNH 001; the Unenlagiidae *Buitreraptor gonzalezorum* MPCN-PV-598, MPCA 245; the Archaeopterygidae *Archaeopteryx lithographica* MB.Av.101, WDC-CSG-100; and the Confuciusornithidae *Confuciusornis sanctus* BMNHC PH766; GMV-2132/2133.

For the osteological descriptions we used casts and photographs of various non-avian paravians (*Bambiraptor feinbergi* AMNH 001; *Buitreraptor gonzalezorum* MPCA 245; *Archaeopteryx lithographica* MB.Av.101, WDC-CSG-100, NHMUK 37001; *Confuciusornis sanctus* BMNHC PH766, PH931, PH987; GMV 2130; DNHM D2859; LPM 0228, 0229; HGM 41HIII0400, 41HIII0401). These were complemented with specific bibliography that allowed comparisons and muscular extrapolations (see [18, 20, 23, 30–35]).

We follow muscular nomenclature and data sources published by Ostrom [32, 33], Nicholls & Russell [23], Baumel et al. [36], Jasinoski et al. [18], Maxwell & Larsson [31], Burch [37], Suzuki et al. [35], Picasso & Mosto [34], Novas et al. [11], and Lo Coco et al. [20, 30], with the aim of determining the sites of origin and insertion of selected muscles. Extrapolation to fossil taxa of musculature in the pectoral girdle of living archosaurs (i.e., crocodylians, palaeognaths and neognaths) using the Extant Phylogenetic Bracket (EPB [38]).

In total, five muscles (*mm.*) were selected due to the fact that they present an origin and insertion in bony elements (e.g., *mm. deltoideus scapularis/major*, *pectoralis*, *supracoracoideus*, *coracobrachialis brevis p.*

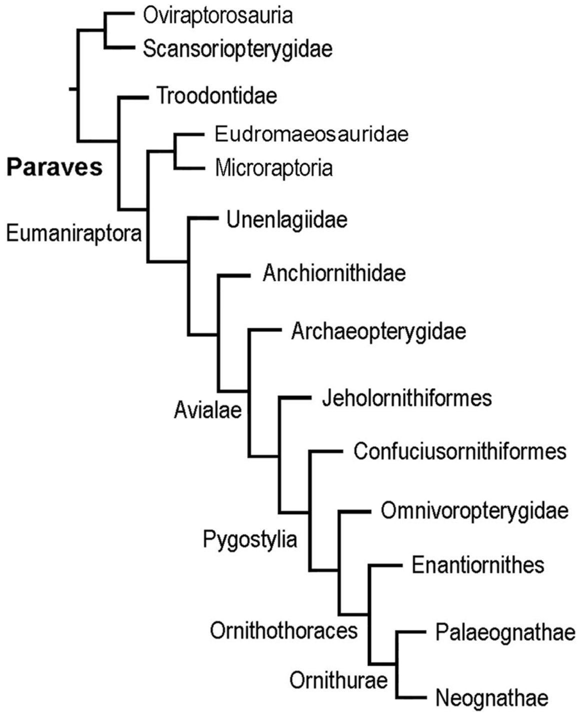

Fig. 1 Phylogenetic framework of Paraves with selected clades following Agnolín & Novas [24], Agnolín et al. [2], Motta et al. [25], and Novas et al. [11]

ventralis/p. cranialis, *biceps brachii*). These muscles are mainly located in the module of the pectoral girdle, and they present the largest mass volume in Crocodylia [39, 40], paleognath and neognath birds [18, 20, 30, 31, 34–36]. For this reason, these muscles are predominantly involved in the main movements of the humerus and, therefore, of the entire forelimb [10, 22]. Moreover, in Crocodylia the *muscle* (*m.*) *pectoralis* is the heaviest muscle, followed by *mm. levator scapulae*, *triceps brevis*, with the *m. supracoracoideus* remaining between the 5th and 7th heaviest muscle of the forearm (see [39]).

We adopt the interpretations regarding the function of the selected muscles mainly expressed by Raikow [41], Jasinoski et al. [18], Lo Coco et al. [20] and Lo Coco [42].

Nomenclature

The anatomical nomenclature follows Baumel et al. [36] for birds. Following Ostrom [1], the “coracoid tuberosity” or “biceps tubercle” present in theropods is considered homologous with the modern avian “acrocoracoid process”.

We follow Nicholls & Russell [23], Jasinoski et al. [18] and Burch [37] who proposed that the *mm. coracobrachialis brevis p. ventralis* and *deltoideus scapularis* of Crocodylia, are homologous to the *mm. coracobrachialis p. cranialis* and *deltoideus major* of extant birds, respectively. The former denominations will be used to name the respective muscles of the non-avian paravians and the latter to name these muscles in basal birds.

Photographs of the bones and muscles were taken using a Nikon D5200 digital camera and the figures were processed using Adobe Photoshop v.2019.

Results

Of the pectoral musculature, we have selected the five muscles (i.e., *mm. deltoideus scapularis/major*, *pectoralis*, *supracoracoideus*, *coracobrachialis brevis p. ventralis/p. cranialis*, *biceps brachii*) due to the fact that they are the largest and perform the main movements of the forelimb. The origins and insertions of these pectoral muscles are studied in different groups of extant archosaurs (crocodiles and birds) in order to hypothesize their functions in four selected taxa of basal paravians (i.e., *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis*).

M. deltoideus scapularis/major

In living crocodiles, the *m. deltoideus scapularis* originates in the distal end of the lateral surface of the scapular blade [18, 43]. This muscle inserts on the dorsal surface of the proximal end of the humerus close to the humeral head. In these archosaurians, the function of this muscle is to abduct the humerus [18], Table 1).

In living birds, the *m. deltoideus scapularis* is homologous with the *m. deltoideus major* [18, 36]. In neognath birds and Tinamiformes, the origin of this muscle is on the lateral surface of the scapula, in the medial border of the acromion [18, 35, 36]. The insertion is into the caudal edge of the deltopectoral crest, and its function is to retract and elevate the humerus [18], Table 1). Particularly in *Rhea* and other non-volant paleognaths, the origin is also established on the lateral aspect of the proximal end of the scapula and inserts widely, extending beyond the middle of the dorsal border of the humerus [18, 20].

Due to the similarity of the scapula blade among non-avian paravians (e.g., *Bambiraptor*, *Buitreraptor*), basal birds (e.g., *Archaeopteryx*, *Confuciusornis*), and extant birds [2, 11, 12, 15], we infer that the *m. deltoideus scapularis/major* would be also similar in all these living and extinct paravians. The origin could reach the medial border of the proximal end of the scapula, and could extend over the lateral surface of the scapula, towards the glenoid cavity, occupying a larger area than that found in extant flying birds, as is observed in non-volant paleognaths (see [20]).

Regarding the insertion of the *m. deltoideus scapularis/major*, it could be anchored on the first section of the deltopectoral crest, on its caudal side, as occurs in living crocodiles [18, 43] and extant birds [18, 20, 30].

Table 1 Function of five pectoral girdle muscles of different archosaur groups (e.g., crocodile, paravians, basal birds, non-volant paleognath and neognath). Abbreviations: BB, *m. biceps brachii*; CBB/CBCr, *m. coracobrachialis brevis p. ventralis/p. cranialis*; DM/DS, *m. deltoideus scapularis/major*; P, *m. pectoralis*; SC, *m. supracoracoideus*

Species	Pectoral muscles				
	DS/DM	**P**	**SC**	**CBB/CBCr**	**BB**
Caiman latirostris	Abduct	Adductor	Protractor	Protractor Depressor	Protractor
Bambiraptor feinbergi	Elevator	Adductor Protractor	Protractor	Protractor Depressor	Protractor Depressor
Buitreraptor gonzalezorum	Elevator	Adductor Protractor	Protractor	Protractor Depressor	Protractor Depressor
Archaeopteryx lithographica	Elevator	Adductor Protractor	Protractor	Protractor Depressor	Protractor Depressor
Confuciusornis sanctus	Elevator	Adductor Protractor	Protractor	Protractor Depressor	Protractor Depressor?
Rhea americana	Elevator Retractor	Depressor Protractor	Protractor Elevator	Depressor	Abductor Protractor
Gallus gallus	Retractor Elevator	Adductor Depressor	Elevator Abductor	Protractor	Protractor

As suggested by Olson & Feduccia [44] and Ruben [45], the *m. deltoideus major* rather than *m. supracoracoideus* may have been the main elevator of the humerus in *Archaeopteryx*. We concur with these authors' proposal, considering that it origin is located slightly dorsal and medially to the glenoid cavity (Fig. 2) generating an elevator function of the humerus. The same function may be also applied to the *m. deltoideus scapularis/major* of *Bambiraptor*, *Buitreraptor*, and *Confuciusornis*, as well (Table 1). In this way, the *m. deltoideus scapularis/major* together with other elevator muscles present in extant diapsids (i.e., the *m. latissimus dorsi* group; [20, 43, 46]), would have performed a fundamental role as the exclusive elevators of the humerus in paravians and basal birds. With the morphological changes occurring in the scapular girdle of the derived birds (i.e., acrocoracoid well developed anterodorsally, glenoid cavity subhorizontal oriented, scapulocoracoid articulation located caudally from glenoid cavity in Enantiornithes, and Euornithes), the function of main elevator of humerus came to be carried out mainly by the *m. supracoracoideus* which is primarily responsible for the rapid upstroke of the wing in extant volant birds [41, 47]. We would expect the morphological transition between these taxa to have been gradual, but the fossil evidence known to date suggests that there would have been abrupt osteological changes in the pectoral girdle and forelimbs between Confuciusornithidae and Enantiornithes (see also [10, 11]).

M. pectoralis

In all present-day archosaurs (crocodiles and birds), the *m. pectoralis* is composed of one to three bellies which originate at different parts of the pectoral girdle: ventral to the glenoid cavity, at the coracoid and/or on the sternum; in some cases, the fibers of the *m. pectoralis* reach the furcula (i.e., Tinamiformes and Neognathae), or are attached over the sternal ribs (as in non-avian reptiles and neognaths; [18, 30, 36, 43]). In all cases, the *m. pectoralis* inserts onto the cranial aspect of the proximal end of humerus, at the dorsal edge of the deltopectoral crest [18, 20, 23, 30, 36, 43].

Its function in crocodiles is to adduct the humerus [43], Table 1). In Tinamiformes and neognaths, the main function of the *m. pectoralis* is to depress the humerus, although it also assists in its adduction [18, 41], Table 1). In non-volant paleognaths the function of *m. pectoralis* is different from other extant birds, its main role being protracting and depressing the humerus [18], because its origin is ventral and cranioventral with respect to its insertion and the glenoid cavity [20], Table 1).

Based on the coracoid attachments observed in modern flying birds and particularly in *Rhea*, it is inferred that, in the selected fossil taxa, the *m. pectoralis* also originated on the cranial side of the coracoid [10], on its lateral half, ventral to the glenoid cavity and the acrocoracoid process (Fig. 2). It is possible that its origin also expanded over the gastralia or sternal plates (bony or cartilaginous), even when the sternal keel was not well-developed. In turn, it can be inferred that it could even cover part of the sternal ribs and reach the lateral border of the furcula and the *sternocoracoclavicularis* membrane [10, 42, 44].

In *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis* it is inferred that the insertion of the *m. pectoralis* was located on the craniodorsal margin of the deltopectoral crest of the humerus (Fig. 3; [18, 23]), as occurs in reptiles and modern birds [18, 20, 23, 30, 36, 41, 43].

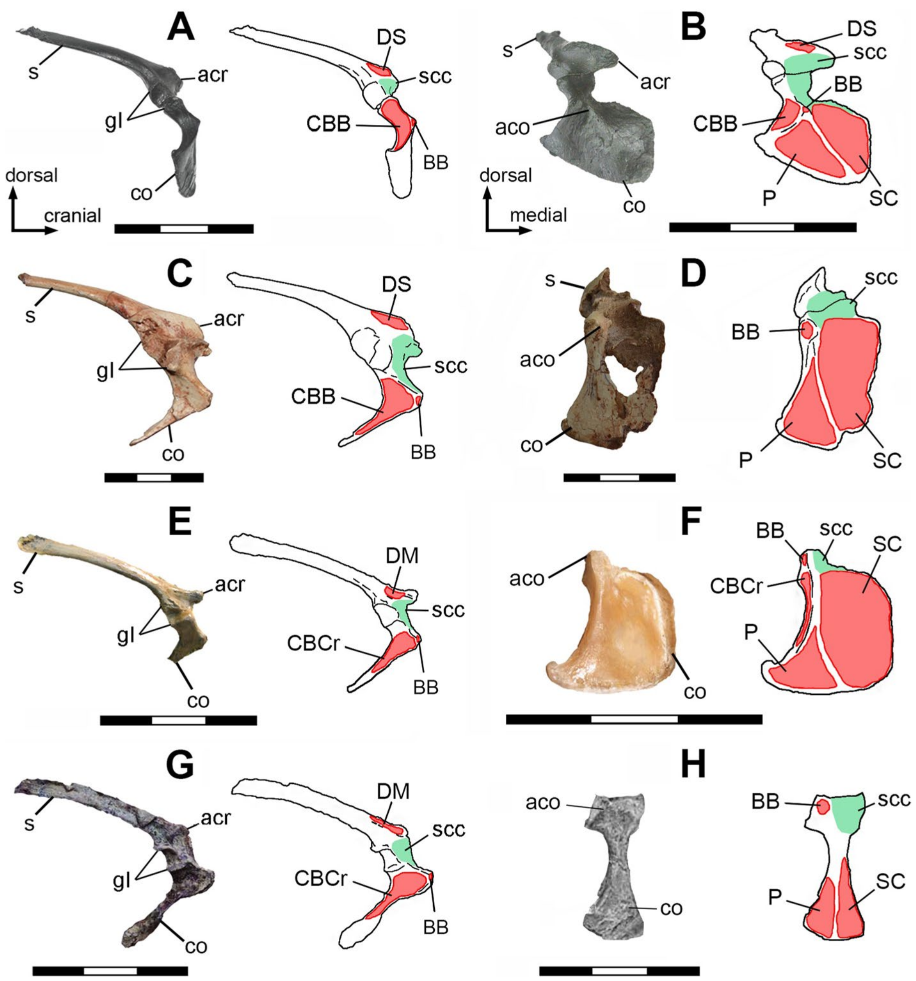

Fig. 2 Muscular maps showing the sites of origin (red) of right scapula and coracoid of *Bambiraptor feinbergi* AMNH 001 (**A**, **B**); *Buitreraptor gonzalezorum* MPCN-PV-598 (**C**, **D**); *Archaeopteryx lithographica* WDC-CSG-100 (**E** rotated and modified from [48], **F**); *Confuciusornis sanctus* BMNHC PH766 (**G**, rotated and modified from [49]), and *Confuciusornis sanctus* GMV-2132 (**H**; modified from [50]), in lateral (**A**, **C**, **E**, **G**) and cranial (**B**, **D**, **F**, **H**) views. Abbreviations: aco, acrocoracoid process; acr, acromion, co, coracoid; gl, glenoid cavity; s, scapula, scc, supracoracoidal canal; BB, *m. biceps brachii*; CBB, *m. coracobrachialis brevis p. ventralis*, CBCr, *m. coracobrachialis p. cranialis*; DM, *m. deltoideus major*; DS, *m. deltoideus scapularis*; P, *m. pectoralis*; SC, *m. supracoracoideus*. Light green, supracoracoidal canal surface. Scale bars 3 cm

Although the coracoid of *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis* lacks bony scars indicating a separation between the origin of the *m. pectoralis* and the *m. supracoracoideus*, it can be thought that they bordered each other, but did not overlap. The growth in volume of the *m. pectoralis*, like the overlapping of the *m. supracoracoideus*, can be inferred to have occurred in more derived taxa of Avialae, where there was a great development of the sternal keel [10, 51], and consequently the *m. pectoralis* volume has been greater reaching the furcula.

Considering that the main protractor function of the *m. pectoralis* in extant crocodilians and birds, it is suggested that in *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis* the function was similar and protracted the humerus in a cranioventral direction and adducted the arm (Table 1), in agreement with what was proposed by Ostrom [1] and Novas et al. [11]. This can be explained based on the ventral, ventrocaudal and ventrocranial location of the origin of this muscle (i.e., on the coracoid, sternum and/or furcula, respectively) with respect to the glenoid cavity. In all cases, this muscle would have been inserted directly in the humerus, without generating any type of pulley with the acrocoracoid process.

M. supracoracoideus

In non-avian reptiles the *m. supracoracoideus* is made up to two or three bellies, which can originate mainly on the scapula and coracoid, positioning itself cranially to the glenoid cavity (e.g., *Chamaeleo*, *Alligator*, *Caiman*; [23, 43, 52]). Although in paleognaths and neognaths the origin is ventral to the glenoid cavity, its anchorage area may be the coracoid and/or the sternum. In tinamids and neognaths the origin is wide, reaching the lateral and

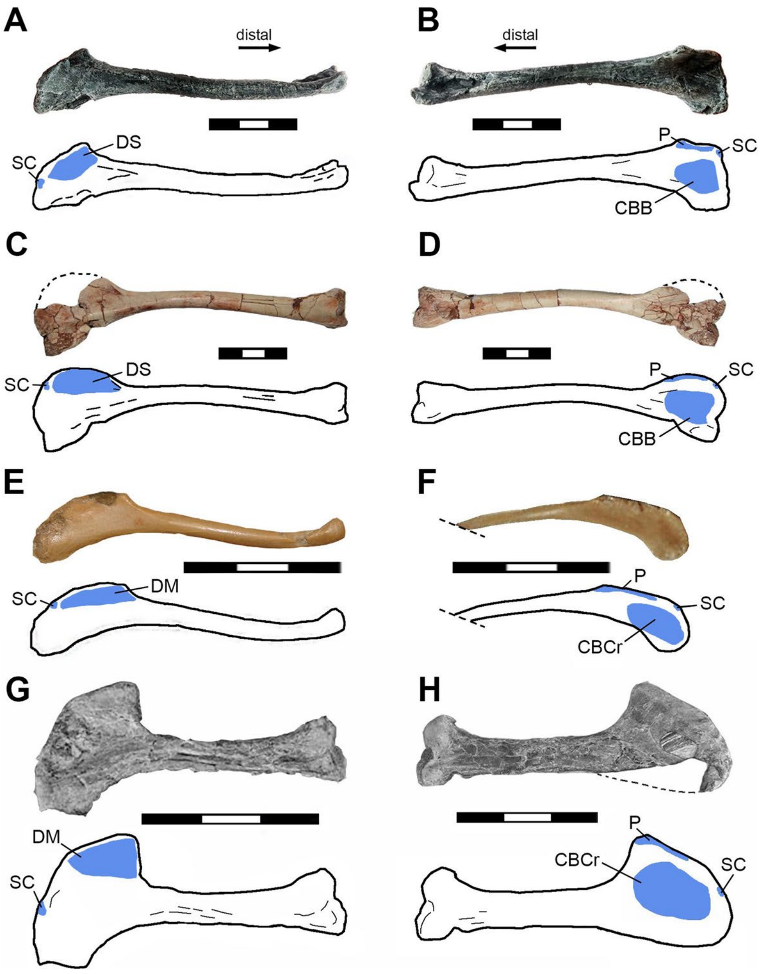

Fig. 3 Muscular maps showing the sites of insertion (blue) of right humerus of *Bambiraptor feinbergi* AMNH 001 (**A**, **B**); *Buitreraptor gonzalezorum* MPCA 245 (**C**, **D**); *Archaeopteryx lithographica* MB.Av.101 (**E**); *Archaeopteryx lithographica* WDC-CSG-100 (**F**; the distal end is not uncovered); *Confuciusornis sanctus* GMV-2133 (G*; rotated and modified from [50]),and *Confuciusornis sanctus* GMV-2132 (H*; rotated and modified from [50]),in caudal (**A**, **C**, **E**, **G**) and cranial (**B**, **D**, **F**, **H**) views. Abbreviations: CBB, *m. coracobrachialis brevis p. ventralis*, CBCr, *m. coracobrachialis p. cranialis*; DM, *m. deltoideus major*; DS, *m. deltoideus scapularis*; P, *m. pectoralis*; SC, *m. supracoracoideus*. Scale bars 3 cm

basal area of the sternal keel, the lateral margin of the furcula next to the *sternocoracoclavicularis* membrane, and the medial part of the coracoid and the *processus procoracoideus* [11, 18, 30, 31, 35, 36]. In non-flying paleognaths (e.g., *Rhea*, *Struthio*, *Dromaius*) the origin of the *m. supracoracoideus* is located on the cranial side of the coracoid, with a small surface area covering the sternum or without anchoring on it [18, 20, 31].

The insertion of this muscle in extant crocodilians and living birds is located on the dorsal-dorsocranial side of the proximal end of the humerus, usually at the proximal end of the deltopectoral crest [18, 23, 30, 36, 43]. The *m. supracoracoideus* group in non-avian reptiles (e.g., Crocodylia; [43]), and flightless paleognaths (e.g., *Rhea, Struthio*, [11, 18, 20]) plays a role of humeral protractor. In neognaths and Tinamiformes this muscle is channeled into the "triosseal canal" (structure bounded by the acrocoracoid, acromion, and furcula), and its main function is to elevate and abduct the wing [22, 30, 35, 41, 53], Table 1).

Considering that the specimens of *Buitreraptor gonzalezorum* MPCN-PV-598, MPCA 245, *Archaeopteryx lithographica* MB.Av.101, WDC-CSG-100, and *Confuciusornis sanctus* BMNHC PH766, GMV-2132/2133, did not preserve an ossified sternum, and that *Bambiraptor feinbergi* AMNH 001 present two sternal plates but did not preserve an ossified keel, it is inferred that in these taxa the *m. supracoracoideus* had a smaller development than in extant volant birds [1, 10, 19, 45]. In the above mentioned extinct paravians the *m. supracoracoideus* could have originated on the cranial and medial surfaces of the coracoid, although it has probably extended caudally to reach the sternal plates or even the gastral ribs [10, 54].

Buitreraptor, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis* do not present a "triosseal canal" because the furcula could contact the acromion but did not reach the acrocoracoid process [1, 12, 55, 56]. In these taxa, and non-volant paleognaths (i.e., *Rhea*, *Struthio*), a supracoracoidal canal is formed by the concave area between the acromion and acrocoracoid process [11, 20]. The presence of this canal in *Buitreraptor*, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis*, suggests that the *m. supracoracoideus* was channeled through this space (Figs. 2; 4; see Additional file 1). In these taxa the supracoracoidal canal was probably tapered by the acrocoraco-acromial ligament that connects both processes as occurs in the extant *Rhea* [11, 20]. The insertion of the *m. supracoracoideus* would be located on the dorsal margin of the deltopectoral crest, being proximal to the insertion of the *m. pectoralis* (Figs. 3, 4).

Based on the muscle anchoring sites inferred for *Buitreraptor*, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis*, the origin of the *m. supracoracoideus* would be located ventromedially to the glenoid cavity (Figs. 2; 4; see Additional file 1), thus generating an obliquely oriented force (in cranial view), from a laterodorsal to medioventral direction, following the orientation of the supracoracoidal canal [11]. In the particular case of *Archaeopteryx*, some authors like Ostrom [1], Walker [57] and Olson & Feduccia [44], indicate that the shape of the coracoid would not allow the *m. supracoracoideus* to form a pulley, a conclusion that we agree. In our interpretation, the main probable function of the *m. supracoracoideus* in *Buitreraptor*, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis* was the protraction of the humerus, in contrast to other authors that support an elevator function of this muscle (see Pittman et al., 2022). This protractor function would be more similar to what occurs in *Rhea* and other non-flying paleognaths than the elevator function performed by extant volant birds [20], see Table 1).

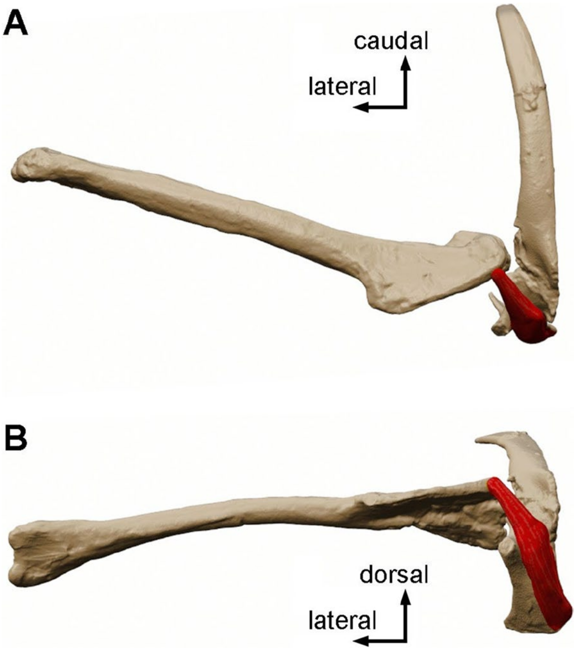

Fig. 4 Three-dimensional model of the *m. supracoracoideus* (red) on the right pectoral girdle and humerus of *Buitreraptor gonzalezorum* (MPCN-PV-598) in dorsal (**A**) and cranial (**B**) views. Scale bar 3 cm

We agree with Mayr [10] in that the *m. supracoracoideus* of basal birds did not have a large origin as occurs in crown group birds. However, it is important to emphasize here some issues about the *m. supracoracoideus* origin that were previously overlooked. We propose that even assuming that this muscle had a major origin in paravians and basal birds (i.e., onto the furcula, sternocoracoclavicular membrane, gastralia, and/or sternum/sternal plates), it would still be routed through the supracoracoidal canal (see [11]). Therefore, the enlargement of the area of origin cranially, ventrally and/or caudally with respect to the glenoid cavity, would not modify the protraction function of the *m. supracoracoideus*. The same condition can be found in Enantiornithes as well, as the *m. supracoracoideus* passes through the supracoracoidal canal, in the medial side of the coracoid. Therefore, the elevating function of this muscle would not change if it were attached on the coracoid or distally on the sternum.

As Biewener & Roberts [58] have shown, an anchorage of *m. supracoracoideus* placed further away from the glenoid cavity would have generated a change in the power output employed by the muscle, being greater with a larger anchorage area and muscle mass.

Thus, with the information obtained in the present paper, we suggest that the key factors that have modified the function of the *m. supracoracoideus* include the type of scapulocoracoid joint, the inclination and orientation of the supracoracoidal canal, and the orientation of the glenoid cavity. A change in the origin of the muscle, from a cranial (i.e., on the coracoid) to a more caudal position (i.e., on the sternum), would not influence the route through the supracoracoidal canal.

M. coracobrachialis brevis p. ventralis/p. cranialis

In extant non-avian reptiles (i.e., Crocodylia) the *m. coracobrachialis brevis p. ventralis* originates on the lateral surface of the coracoid and close to its caudal edge, being ventral to the glenoid cavity [18, 43]. The insertion is located at the proximal end of the humerus, on its ventral side and close to the cranial edge [18, 43].

In non-volant paleognaths the *m. coracobrachialis p. cranialis* originates from the entire area of the subglenoid fossa and inserts on the cranial aspect of the proximal end of the humerus, between the deltopectoral crest and the bicipital crest [11, 18, 20, 23, 31]. In Tinamiformes and neognath birds the *m. coracobrachialis p. cranialis* originates at the end of the acrocoracoid process, being ventral to the origin of the *m. biceps brachii*, and its insertion occurs on the cranial aspect of the proximal end of the humerus, ventrally to the insertion of the *m. pectoralis* [41, 59].

The function of this muscle in non-avian reptiles is to protract and depress the humerus [18], thus generating adduction of the forelimb (Table 1). In non-volant paleognaths, like *Rhea*, its function is to depress the humerus [11, 18], Table 1), due to the ventral position of the origin with respect to the glenoid cavity. In contrast, in extant flying birds, this muscle has a protractor function [41], Table 1) because its origin is located in a craniodorsal position and is medial to the glenoid cavity.

The subglenoid fossa of *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis* may represent the origin of the *m. coracobrachialis brevis p. ventralis*/*p. cranialis* (Fig. 2), and its insertion must have occupied the cranial area of the proximal end of the humerus, being ventral to the edge of the deltopectoral crest Fig. 3; [38]. Due to the ventral location of the origin of this muscle with respect to the glenoid cavity, it is considered that the function in all the selected taxa was twofold (Table 1): first, the protraction of the humerus would be performed when the forelimb was folded or close to the body [1, 18], and second, the depression of the humerus would occur when the forelimb was extended, in agreement with the proposal of Nicholls & Russell [23].

M. biceps brachii

In extant non-avian reptiles (i.e., Crocodylia) the *m. biceps brachii* originates from the cranial edge of the lateral surface of the coracoid, taking a cranioventral position to the glenoid cavity [18, 43]. The insertion in these extant archosaurs is found only at the proximal end of the radius [18, 43].

In neognath and paleognath birds, the main origin of the *m. biceps brachii* is located at the end of the acrocoracoid process [18, 36, 60, 61], whereas in some birds it originates on the lateral border of the coracoid (e.g., *Rhea*, [20, 62]), or on the ventral border of the cranial side of the proximal end of the humerus (e.g., *Tyto furcata*, [30, 36]). The insertion is mostly at the proximal end of the radius and ulna, except for some taxa that present a single insertion at the proximal end of the ulna (e.g., *Struthio*, [18]). The main function of this muscle in extant archosaurs is to flex the forearm and, in turn, contributes to the protraction of the arm [18, 20, 41, 43], Table 1.

It is inferred that in *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*, and *Confuciusornis* the origin of the *m. biceps brachii* was at the end of the acrocoracoid process (Fig. 2), in agreement with the original proposals of Jasinoski et al. [18], Nicholls & Russell [23] and Ostrom [1].

In *Buitreraptor*, there are no muscular scars referring to the *m. biceps brachii* on either the ulna or radius, therefore the insertion site of this muscle cannot be established with certainty [56]. Moreover, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis* have a tubercle at the proximal end of the radius that would indicate the insertion of the *m. biceps brachii* [50, 55, 63]. Considering this characteristic and based on extrapolation from extant archosaurs, it is highly probable that in paravians and basal birds this muscle is anchored at the proximal end of the radius, although insertion into the ulna would be doubtful (see [37, 50, 63]).

The function of the *m. biceps brachii* in *Bambiraptor*, *Buitreraptor*, *Archaeopteryx* and *Confuciusornis* probably was to flex the forearm, protract, and depress the humerus (Table 1). This is due to the cranioventral position of the end of the acrocoracoid process with respect to the glenoid cavity, consistent with the function proposed by Ostrom [1], Nicholls & Russell [23] and Jasinoski et al. [18].

Our results suggest that the anchorage of pectoral muscles were remarkably similar in the non-avian paravians *Buitreraptor* and *Bambiraptor*, and the basal avialan *Archaeopteryx* and *Confuciusornis*, being different from most Ornithothoraces (see also [10, 11, 20]).

Discussion

Myology of the pectoral girdle of paravians and basal birds

The sites of origin and insertion of the shoulder muscles considered above allow comparison of forelimb movements among different groups of paravians. Furthermore, several osteological features enable tracing the lines of force of each muscle and hypothesize the changes of their function within the selected taxa.

As follow, we enumerate the main functional changes that occurred in the selected muscles:

M. deltoideus scapularis/major

As occurs in extant archosaurs, in non-avian paravians and basal birds this muscle may have acted as an elevator of the humerus.

Its main origin in basal paravians and basal birds would occur at the anterior end of the scapula. Further, there is the possibility that there may have been a second origin caudally in the scapular blade, as was reconstructed by Jasinoski et al. [18] and Burch [37] for the non-avian theropods *Saurornitholestes* and *Tawa*, respectively, and as occurs in modern flying birds (see [36]). However, no traces of the anchorage of this muscle at the posterior end of the scapular blade were found in early paravians and basal birds. Regardless of the single or double origin, the elevating function of the *m. deltoideus scapularis/major* would not change, although a retracting function would be added in case a second attachment existed.

As mentioned above, there is consensus among authors (e.g., [1, 10, 11]) that in non-avian paravians and basal birds, the *m. supracoracoideus* would not elevate the humerus, and therefore the main elevator function may have been performed by the *m. deltoideus scapularis/major* [1, 42]. It is interesting to note that the *m. deltoideus major* of extant volant birds contributes to the elevation function but do not have the mass to achieve the wing upstroke on its own [64]. Nevertheless, it is worth mentioning that in *Alligator* and *Crocodylus* [43] the *m. latissimus dorsi* with the *m. teres major* (the latter one undeveloped in birds) both assist to *m. deltoideus scapularis* in humeral elevation, as also occurs in extant birds [20, 46]. We can not dismiss that the same function of the *m. latissimus dorsi* group was performed in basal paravians and basal birds [42].

Biewener & Roberts [58] indicate that muscles with greater mass generate higher power output. Based on this, we can hypothesize that a large mass of the *m. deltoideus scapularis/major* would generate a rapid and powerful elevator function capable of achieving active flapping flight. However, in order to achieve a large muscle mass, there would need to be a large area of origin for this muscle on the scapula. Nevertheless, the scapular blade is anatomically stable in non-avian paravians and basal birds because it remains relatively long and narrow. Therefore, this muscle could not reach a wide origin on the scapula. An alternative explanation has been proposed by Pittman et al. (2022), who considered that the *m. deltoideus major* would increase its volume in the wide insertion area in the humerus. This possibility would occur in some members of Pygostylia (e.g., *Sapeornis*, *Confuciusornis*) in which the deltopectoral crest is wide and well-developed, providing a large surface area for muscle insertion, although this condition is not observed in other early paravians (e.g., *Buitreraptor*, *Bambiraptor*, *Anchiornis*, *Jeholornis*, *Archaeopteryx*). In other words, while a broad insertion of the *m. deltoideus scapularis/major* on the humerus may have played an important role in humeral elevation of *Confuciusornis* and *Sapeornis* (Pittman et al., 2022), this condition was not observed in most other taxa (e.g., *Buitreraptor*, *Bambiraptor*, *Anchiornis*, *Jeholornis*, *Archaeopteryx*), suggesting reduced strength power of this muscle without altering its function.

M. pectoralis

This muscle is one of the most voluminous and important muscles in the shoulder girdle of archosaurs, especially in birds [36, 41, 43]. In these animals, it acts as the main adductor and protractor of the humerus due to the ventral position of its origin in relation to the glenoid cavity [18].

In the non-avian paravians *Buitreraptor* and *Bambiraptor*, and the basal avialan *Archaeopteryx* and *Confuciusornis*, the *m. pectoralis* would have acted as a depressor of the humerus, as occurs in extant birds [11, 33]. In birds, it occupies a large area of origin (i.e., on the sternum, the furcula and, in some cases, the ribs), but it remains to be inferred how far its origin expanded in fossil taxa.

Different force vectors could be hypothesized for the *m. pectoralis* depending on the site of its attachments, mainly on its origin. First, with the feeble development or lack of an ossified sternum in several basal paravians (e.g., *Archaeopteryx*, *Anchiornis*, *Sapeornis*), we infer a single point of origin on the coracoid for the *m. pectoralis*; its position would be cranioventral to the glenoid cavity, as occurs in non-volant paleognaths [18, 20] and, therefore, a protractor and depressor component may be added to the resulting muscle forces. Second, if the *m. pectoralis* reaches a caudoventral position with respect to the glenoid cavity (e.g., for example on the sternal plates of *Bambiraptor*), it would have generated a higher depressor and retractor function. Third, if the *m. pectoralis* was also anchored cranially at the border of the furcula (as occurs in extant volant birds), it would have contributed to the resultant forces with a protractor vector (see [65]). Additionally, it is important to highlight that assuming that the enlargement of the origin surface on the sternal plates, sternal keel and, eventually, on the ribs as occurs in volant birds, including living Neornithes [10, 36, 41], undoubtedly influenced an increase in the muscle mass and force applied, but did not modify its main depressor function.

M. supracoracoideus

The major changes in the forearm movements of archosaurs are associated with the origin and function of the *m. supracoracoideus* (see [10, 11, 33, 66], and references therein). The protractor function of this muscle observed in crocodilians changed to an elevator function in flying birds, based on a pulley mechanism generated by the supracoracoidal canal (see [10, 11, 21, 36, 41]). In both non-avian paravians (e.g., *Bambiraptor*, *Buitreraptor*) and basal birds (e.g., *Archaeopteryx*, *Confuciusornis*) retained the ancestral diapsid protractor function of the *m. supracoracoideus*. The osteological modifications in the shoulder girdle that allowed the change in the function of this muscle in flying birds include: strut-like coracoid with acrocoracoid dorsocranially developed [1, 15], subhorizontal glenoid orientation [2], pectoral girdle positioning over the thorax [11, 67], the morphology of the omal end of the coracoid and, the position of the supracoracoidal canal in the coracoid bone [11]. Some of these features were previously explored in detail by Ostrom [1], Novas et al. [11], and Wu et al. [15]. In the present study we add another relevant feature which is the position of the scapulo-coracoid articulation relative to the glenoid cavity (see below).

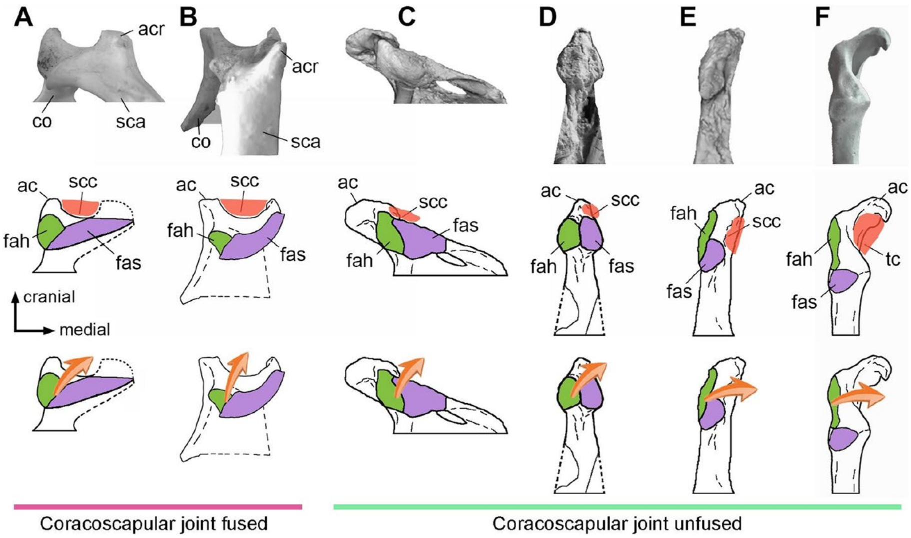

Fig. 5 Comparative anatomy of the left coracoid in selected paravians, basal birds and neornithes in dorsal view. *Rhea americana** (**A**; scapulocoracoid); *Buitreraptor gonzalezorum** (**B**; MPCA 245; scapulocoracoid), *Sapeornis chaoyangensis* (**C**; PMoL-AB00015; modified from [12]), *Jeholornis prima* (**D**; IVPP-V 13353; right coracoid mirrored for comparison), *Piscivorenantiornis inusitatus* (**E**; IVPP V 22582; modified from [12]), and *Gallus gallus* (**F**). Abbreviations: ac, acrocoracoid process; acr, acromion process; co, coracoid; fah, facies articularis humeralis; fas, facies articularis scapularis; sca, scapula; scc, supracoracoidal canal; tc, triosseal canal. Green, facies articularis humeralis; violet, facies articularis scapularis; red, section of the *m. supracoracoideus* occupying the supracoracoidal canal; orange arrow, main action vector of the *m. supracoracoideus*. *: the area of articulation with the scapula is estimated because it cannot be directly observed due to the fusion between scapula and coracoid. Not to scale

In non-avian paravians and some early birds (e.g., *Deinonychus*, *Velociraptor*, *Bambiraptor*, *Buitreraptor*, *Archaeopteryx*; [32, 55, 56, 68] a flat to concave bone surface is located craniomedially and adjacent to the glenoid, corresponding to the join between scapula and coracoid ("coracoidal plate" sensu [11]). This proximal portion of the coracoidal body is aligned with the main axis of the scapula conforming an L-shaped contour in lateral view (see Fig. 2A, C, G, E). In paravians with L-shaped coracoid with "coracoidal plate", the supracoracoidal canal is cranial or craniomedial oriented and therefore the *m. supracoracoideus* played a protractor function (see Fig. 5).

This proximal portion of the coracoid was reduced, but not entirely absent, in early birds such as *Jeholornis*, *Confuciusornis* and *Sapeornis* (see [12, 50]). Apparently, this shortening did not generate a modification of the orientation of the supracoracoidal canal, because the *m. supracoracoideus* would still be channeled anteriorly into its canal and passed through the anterior surface of the "coracoidal plate" (see also [10, 11]).

The change from an L-shaped to a strut-like coracoid could have ensured a greater expansion of the *m. supracoracoideus* over the coracoid, increasing the distance between its origin and the glenoid cavity. This change could have generated greater muscle strength (see [58]), but would not impact its protractor function.

In contrast with the condition described above for mentioned early paravians and basal birds, in Enantiornithes and most Euornithes except in flightless paleognaths [20], the path of the *m. supracoracoideus* through the supracoracoidal canal became medial to the glenoid cavity, thus changing the ancestral protractor function to an elevator one [1, 10, 11]. This morphofunctional novelty is related to the development of the sternal keel, mirroring the caudal extension of the site of origin of the *m. supracoracoideus*, as advocated by Mayr [10].

It is interesting to note that certain modifications in the way the coracoid articulates with the scapula may have also affected the change of the *m. supracoracoideus* path and function. In *Buitreraptor*, *Bambiraptor*, *Archaeopteryx*, *Confuciusornis*, *Jeholornis* and *Sapeornis*, the coracoscapular articulation is lateromedially extended and it is positioned medial to the glenoid cavity (Fig. 5B-D; see also [12, 63]). A similar condition occurs in non-volant paleognaths (e.g., *Rhea*, *Struthio*, [20]), with the contact surface latero-medially extended (Fig. 5A). On the contrary, in Enantiornithes, neognaths and flying paleognaths, the articulation between the coracoid and scapula is located caudal/ventral to the glenoid cavity (Fig. 5E, F; see also [12]). Thus, the coracoidal portion of the glenoid cavity results positioned immediately lateral to the supracoracoidal (or triosseal) canal (Fig. 5E, F). Associated with this positional change, a reduction of the joint area between the scapula and coracoid is observed in both Enantiornithes (e.g., *Enantiornis*, *Piscivorenantiornis*, [69, 70]) and most Euornithes (e.g., *Gallus*, *Vultur*), when compared with the transversely wide articulation or joint area observed in *Rhea* and most non-avian paravians such as *Buitreraptor* and *Bambiraptor*. This condition is associated with the reduction of the omal end of the coracoid, the composition of its strut-like shape (i.e., jeholornithiforms, confuciusornithids, and Ornithothoraces; [10, 15]) and the mobility in the coracoscapular joint (i.e., omnivoropterygiforms, jeholornithiforms and Ornithothoraces except flightless paleognaths [71, 72]).

We suggest that the drastic changes in the orientation and the joint area between the scapula and coracoid observed in Enantiornithes and most Euornithes is related to the reduction of the wide surface of the omal end of the coracoid, with the acquisition of a strut-like conformation, and with the re-orientation of the glenoid cavity from subvertical to horizontal. All these osteological modifications of the scapulocoracoid bone affect the path, the muscular force line direction and the function of the *m. supracoracoideus* giving it a protractor function in non-avian paravians and early birds, in contrast with the elevating role evolved in the Ornithothoraces node.

M. coracobrachialis brevis p. ventralis/p. cranialis

As occurs in the extant *Rhea* [11, 20] and as it was suggested by Jasinoski et al. [18] and Nicholls & Russell [23] for *Struthiomimus* and *Saurornitholestes*, respectively, we infer that in non-avian paravians and early birds (e.g., *Buitreraptor*, *Bambiraptor*, *Archaeopteryx* and *Confuciusornis*) the origin of the *m. coracobrachialis brevis p. ventralis/p. cranialis* occupied the subglenoid fossa and that it may have acted as protractor and depressor of the humerus. In other basal birds, like *Sapeornis*, the absence of the subglenoid fossa suggests that the *m. coracobrachialis brevis p. ventralis/p. cranialis* may have originated on the lateral surface of the poorly developed and anteriorly located acrocoracoid process, suggesting that its function was to protract the humerus. In Enantiornithes and extant volant birds the subglenoid fossa is also absent, but the acrocoracoid process is well-developed and craniodorsally projected with respect to the glenoid cavity. In these birds the *m. coracobrachialis p. cranialis* originates on the acrocoracoid process and has protractor function (see [36, 41]). An overlooked novelty of these changes is in the reconfiguration of the *m. coracobrachialis brevis p. ventralis/p. cranialis* in paravians that included a decrease in its area of origin, thus implying a reduction in its volume/mass and probably of its power, changing its role from a depressor/protractor to a protractor of the humerus from the Pygostylia node.

M. biceps brachii

In theropods, the origin of the *m. biceps brachii* is directly related with the “biceps tubercle” or acrocoracoid process [1]. In extant crocodiles and birds, this muscle acts as a flexor of the forearm, protractor or depressor of the humerus [18, 36, 41] varying its function according to the position of its origin. In some basal paravians (e.g., *Buitreraptor*, *Bambiraptor*, *Archaeopteryx*) the acrocoracoid process is ventrally located with respect to the glenoid cavity (see Fig. 2A-F), and thus the main function performed by the *m. biceps brachii* was to protract and depress the humerus. In *Confuciusornis* and *Sapeornis*, the acrocoracoid process is located cranially and slightly dorsally with respect to the glenoid cavity, and this suggests that this muscle was a main arm abductor and protractor, similar to the function in the living paleognath *Rhea* [11, 20], see Fig. 2G-H). The well developed acrocoracoid becomes more evident in Euornithes, in which its position is craniodorsal to the glenoid cavity, producing a protractor function of the muscle like in extant volant birds (see [36, 41]). This condition was present in Enantiornithes and thus it would be probable that this feature was acquired from Ornithothoraces node.

Changes of the position of the origin of the *m. biceps brachii*, from an anteroventral to an anterodorsal location relative to the glenoid cavity, are seen from the Pygostylia node, linked to the greater development of the acrocoracoid. From the common ancestor of Pygostylia this muscle changes its main function from depressor to protractor of the humerus.

Implication of the myology in the early flight of basal paravians

Many studies about flight origins assume that basal birds moved their wings like in modern flying birds (see [73–84]). Furthermore, many authors explored the flight capacity of basal birds and selected non-avian paravians (e.g., *Microraptor*,*Anchiornis*) by analyzing wing surface (see [85–87], 88]), ontogeny (see [89]), changes in body center of mass (see [90]), capacity to generate aerodynamic forces for weight support (see [80, 85, 86, 88, 91], 92]), and the importance of the aerodynamic stability during flight (see [87]). Nevertheless, these works are based on estimations and extrapolation from highly specialized living flyers (e.g., *Sturnus*, *Columba*). We have to be aware that extant flying birds exhibit a pectoral girdle shape and its placement over the thorax which are considerably different from those of non-avian paravians and early birds (e.g., *Deinonychus*, *Archaeopteryx*, *Confuciusornis*, [1, 2, 11, 21, 42, 67]. In this line of thought, it has been observed that the flightless ratites have a pectoral girdle that resembles that of non-avian paravians and that may be used as the best analogues to understand the evolution of early paravian forelimb movements [2, 11, 21, 42]. Based on these studies, it was proposed that the wing posture of early paravians and basal birds was similar to that of extant flightless paleognaths, being the arc of movement of its wing anterodorsal to posteroventral [11, 21]. In this interpretative context, the acquisition of “Wing Assisted Incline Running” behavior (i.e., WAIR), in which individuals flap their wings synchronously to help their hindlimb traction to climb inclined surfaces, has been considered as achieved in the common ancestor of Ornithothoraces [21]. This proposal is evolutionarily later than originally proposed by Bundle & Dial [93], Dial [6], Dial et al. [7], Heers & Dial [94], and Heers et al. [8, 9, 95], which placed the emergence of this behaviour among basal Paraves.

It is important to highlight that the pectoral girdle morphology reached a relative stasis in non-ornithothoracine paravians since certain aspects of the coracoid and scapula remained similar (i.e., coracoid wider than long, presence of the "coracoidal plate" conforming an L-shaped contour in lateral view, acrocoracoid developed in a cone shape and located anterolaterally to the glenoid cavity, facies articularis scapularis located medially to the glenoid cavity; long and narrow scapular blade). Among non-ornithothoracine paravians were non-flying taxa, such as the cursorial *Buitreraptor*, as well as those with the ability to fly, such as the four-winged *Microraptor*, the long-tailed *Archaeopteryx* and the pygostylians *Confuciusornis* and *Sapeornis*, differentiated primarily by the feather coverage of their wing [96, 4, 11, 12, 15, 21, 66, 85, 87, 88, 97, 98,99]. In this sense, the origin of the main pectoral muscles (i.e., 20*mm. supracoracoideus*, *pectoralis* and *deltoideus scapularis/major*) and their function would be similar across a wide array of body shapes and locomotory behaviours of early paravians. We note that the most significant changes in the set of muscles of the scapular girdle occurred in the common ancestor of Pygostylia involving the cranial displacement of the site of origin of the *mm. biceps brachii* and *coracobrachialis p. cranialis*, accompanying the loss of the subglenoid fossa and the greater development of the acrocoracoid process. These modifications changed the function of these muscles from depressors/protractors to protractors of the humerus, allowing more muscles to be involved in pronating the humerus, and thus, in maintaining the extended wing.

How do these characteristics, described in early birds, relate to the ability to perform gliding or flapping flight?

The type of wing movement linked to gliding performed by extant volant birds, requires fine tuned movements and a more significant force carried out by the pronator and depressor muscles of the humerus (i.e., *mm. pectoralis*, *coracobrachialis p. cranialis*, and *subscapularis*; see [53]) to maintain the wing unfolded and parallel to the ground,but does not require substantial intervention of elevator muscles (e.g., *m. supracoracoideus*; see [1, 10, 20, 22, 30, 33, 41, 65, 100]). Furthermore, an active flight requires a powerful downstroke and a fast and wide upstroke recovery of the wing. To execute the downstroke the *m. pectoralis* is activated. For the upstroke, the *m. supracoracoideus* is mainly activated with the contribution of the *mm. coracobrachialis p. cranialis, deltoideus* and *latissimus dorsi* group [22, 41].

Thus, in non-avian paravians and basal birds the *mm. pectoralis* and *coracobrachialis brevis p. ventralis/p. cranialis*, but also the *m. supracoracoideus*, may have participated in depressor functions and, therefore, they would have been involved in maintaining the wing extended, an action that would favor gliding behaviour (see Chatterjee & Templin, 2012; [9, 54, 87, 101]).

These interpretations allow us to assume that basal birds with a considerable wing area (e.g., *Archaeopteryx*, *Confuciusornis*), would have been able to achieve passive flight (see [1, 98]) as long as they extended the wings with its ventral surface oriented subparallel to the ground (see [9, 54, 87, 101]). This ability would have been difficult if the wings were obliquely oriented, with the wing surface oriented ventrocaudally, as suggested by Novas et al. [11, 21].

Otherwise, the upstroke in non-ornithothoraces paravians was performed only by dorsal muscles, the *mm. deltoideus* and *latissimus dorsi* group, suggesting a weaker wing recovery without reaching a wide range of motion (see [1, 100]). This condition does not exclude the possibility of taking brief active flights, but with a restricted dorsal excursion of the wing, that is, in a different way from that of extant volant birds [1]. This assumption is congruent with the poor flight aptitude proposed for these basal birds by different authors (see [86, 98, 102, 103], Pittman et al., 2022). In this context, the maintenance of a more sustained flapping flight was acquired from the common ancestor of ornithothoraces, with the vectorial modifications of the muscle set imposed by the cranio-dorsal development of the acrocoracoid process and the medial orientation of the supracoracoidal canal, with the consequent elevator role of the *m. supracoracoideus*.

Conclusions

Our myological analyses suggest that there were no radical changes in the function of the selected pectoral muscles in the portion of the phylogenetic tree including non-ornithothoracine paravians. These muscular functions are more similar to those performed by extant ratites than those performed by extant volant birds [11, 20]. This is related to the osteology of the coracoid and scapula, which retained plesiomorphic features and remained relatively stable through the different clades of non-ornithothoraces paravians. This indicates that the model of shoulder girdle present in non-ornithothoraces paravians remained relatively stable in their morphology for millions of years in phylogenetically distant and morphologically disparate taxa (i.e., different body shapes, sizes and weights, forelimb proportion, presence or absence of large bony tails, presence or absence of long feathers, etc., see [54]), which were geographically and temporally separated, and in all probability, occupied different ecological roles.

Taking into account that in non-avian paravians and basal birds the *m. supracoracoideus* acted as a wing protractor rather than as a humeral elevator [1, 11, 21], this latter function was instead performed by the *deltoideus* and *latissimus dorsi* muscle groups. Nevertheless, these muscles were neither sufficiently voluminous nor powerful enough to reach a rapid elevation of the humerus. Consequently these taxa would not be able to achieve the continuous flapping flight as performed by extant volant birds. This new myological and osteological study lead us to suggest that *Archaeopteryx* and *Confuciusornis* could have achieved at least an active flight with less dorsal excursion of the wing than in living birds, in concordance with other studies with different approaches such as: wing area, wingspan, estimated body mass, wing feather type, covering feathers (see [1, 104, 105]).

The important changes in the pectoral girdle, particularly in the articulation between the scapula and the coracoid, are observed in derived paravians, particularly at the Ornithothoraces node, suggesting that the function of the pectoral musculature would favor continuous flapping flight more similar to that present in extant volant birds.

Abbreviations

AMNH	American Museum of Natural History, New York, United States
BMNHC	Beijing Museum of Natural History, Beijing, China
DNHM	Dalian Natural History Museum, Dalian, China
GMV	National Geological Museum of China, Beijing, China
HGM	Henan Geological Museum, Zhengzhou, China
IVPP-V	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
LPM	Museum of Beipiao, Sihetun, Chaoyang, Liaoning, China
MB.Av.	Natural History Museum of Berlin, Berlin, Germany
MPCA	Museo Provincial Carlos Ameghino, Cipolletti, Neuquén, Argentina
MPCN-PV	Museo Provincial de Ciencias Naturales, Vertebrate Paleontology Collection, General Roca, Río Negro, Argentina
NHMUK	Natural History Museum, Londres, United Kingdom
WDC-CSG	Wyoming Dinosaur Center, Thermopolis, Wyoming, United States

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12862-025-02454-z.

Additional file 1. Three-dimensional model of the ***m. supracoracoideus*** on the left pectoral girdle of ***Buitreraptor gonzalezorum*** .

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Authors' contributions

GEL: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing. MJM: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing. FLA: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; supervision. FEN: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; supervision. All authors read and approved the final manuscript.

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Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare no competing interests.

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