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Functional Adaptations in the Forelimb of the Snow Leopard (*Panthera uncia*)

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Synopsis The snow leopard (*Panthera uncia*) is anatomically and physiologically adapted for life in the rocky terrain of alpine zones in Central and South Asia. *Panthera uncia* is scansorial, and typically hunts solitarily by using overhead ambush of prey, rather than the typical stalking pattern of other large pantherines. In this study, we conducted dissections, detailed documentation, and illustrated the forelimb anatomy of two adult *P. uncia* specimens (1M/1F). Qualitative and quantitative data revealed an intriguing combination of functional adaptations illustrating a balance between the diverse demands of head-first descent, pouncing, climbing across rocky terrain, restraint of large prey, rapid pursuit, and navigating deep snow. In many forelimb proportions, *P. uncia* is intermediate between the cursorial *Acinonyx jubatus* (cheetah) and the scansorial forest dwelling *Panthera onca* (jaguar). Enlarged scapular and pectoral musculature provide stability to the shoulder girdle during grappling with large prey, as well as support during jumping and climbing. A small, unarticulated bony clavicle may provide greater stability to the forelimb, while still allowing flexibility. In the brachium and antebrachium of *P. uncia*, there is a functional compromise between the powerful grip needed for grasping large prey and the stability necessary for rapid pursuit of prey over uneven, rocky terrain. A unique bifurcation in the tendon of m. biceps brachii may provide additional functional stability at the radiohumeral joint. Intrinsic muscles of the palmar manus are broad and fleshy, acting as an enlarged surface area to evenly distribute body weight while walking on soft snow. However, muscles that act to provide fine manual manipulation are reduced, as in other large prey specialists. Overall, *P. uncia* displays morphological adaptive parallels with scansorial, large prey specializing pantherines, such as *P. onca*, while also showing adaptations for running.

Introduction

The potential drivers of the evolution of felid forelimb morphology are numerous and diverse, ranging from prey specialization and locomotor repertoire to other environmental demands. Because *Panthera uncia* inhabits rugged terrain that is limited in resources, it preys on a wide range of animals from rodents to Siberian ibex (*Capra sibirica*) (Lyngdoh et al. 2014; Wasim et al. 2012), which requires skillful maneuvering and versatility in hunting strategy. It typically hunts solitarily (Macri and Patterson-Kane 2011) by using overhead ambush and relies on powerful grasping to immobilize its large prey (McCarthy et al. 2005; McCarthy and Mallon 2016). Within Felidae, pantherines such as the snow leopard generally specialize on larger-bodied prey species, focusing on strength and speed to subdue them (e.g., Carbone et al. 2007). Grappling with strong prey subjects a predator's limbs to stress, requiring musculoskeletal adaptations to resist (Martin-Serra et al. 2014). In contrast to pantherines, felines typically hunt small-bodied species, focusing instead on manual dexterity to capture and manipulate their prey (Carbone et al. 2007; Viranta et al. 2016). Recent studies have revealed resulting anatomical forelimb differences between felid species that specialize in small versus large prey items (e.g., Iwaniuk et al. 1999, 2000, 2001; Meachen-Samuels and Van Valkenburgh 2009; Julik et al. 2012; Viranta et al. 2016). In particular, large prey specialists require powerful rotatory and joint stabilizing forelimb muscles in order to maintain a secure hold on large prey (Viranta et al. 2016). In contrast, small prey specialists that rely more heavily on manual dexterity tend to possess well-developed digital flexors and extensors (Viranta et al. 2016). Since *P. uncia* hunts a variety of prey taxa, including large ibex, it is likely that its forelimbs exhibit adaptations for powerful grasp. However, the forelimb is also a crucial component of efficient locomotion, and the competing demands of prey capture and locomotor pressures often result in a necessary compromise between forelimb adaptations for these two categories (Van Valkenburgh 1987; Iwaniuk et al. 2000; Viranta et al. 2016).

The locomotor habits of *P. uncia* are generally similar to other pantherines, involving running, climbing, and leaping (McCarthy and Mallon 2016). However, *P. uncia* is more scansorial (specialized for climbing) than most other large cats, and while it is not arboreal, as a skilled climber, it may show myological parallels with other climbing felids. It also has enhanced leaping capabilities (Ognev 1935; Hemmer 1972), and has been documented jumping as far as 15 m across a gorge (Ognev 1962). Yet, *P. uncia* is also a skilled runner, able to engage in rapid pursuit and traverse rocky terrain while chasing its prey (McCarthy and Mallon 2016). Its forelimb proportions are similar to the lion (*Panthera leo*), with a radiohumeral index of 94.6% (lion: 98.3%) (Gonyea 1976). Its hind limb proportions, however, are most similar to the cheetah (*Acinonyx jubatus*) with a femorotibial index of 105% in both species. The cheetah preys using open-country rapid pursuit (Gonyea 1976), suggesting that rapid pursuit of prey may also drive hindlimb proportions in *P. uncia*. Cursorial carnivoran species tend to have more proximal muscle mass in the thoracic limb, while those that require versatility and manual dexterity tend to have more muscle mass in the distal thoracic limb muscles (Souza Junior et al. 2021). Due to the interplay between hunting and locomotor pressures, the forelimbs of large felines tend to display a balance between facilitating powerful grasping abilities and maximizing speed (Meachen-Samuels and Van Vakenburgh 2009; Kitchener et al. 2016; Souza Junior et al. 2021).

An additional ecological pressure may also impact forelimb morphology of *P. uncia*—extremely cold temperatures. Compared with other felids, *P. uncia* is adapted for life in cold, rugged, and rocky environments. Living in snowy mountains, it requires well-developed limb muscles for climbing and stabilization (Lovari et al. 2013). Cold-adapted species tend to be stockier than their warm-adapted counterparts to minimize their exposed surface area and resulting heat loss. For example, Pleistocene glacial cycles likely drove evolution of the appendicular skeleton of North American pine martens (*Martes americana* and *Martes carina*) (Lynch et al. 2021). It is unclear how the limb proportions of *P. uncia* have been affected by the selective climatic pressure of its alpine environment. *Panthera uncia* also has wide forepaws and hindpaws, with relatively short digits in the forepaw. These act to evenly distribute its weight while walking on soft snow (Iwaniuk et al. 1999), which may impact the morphology of muscles of the palmar manus.

Panthera uncia is classified as Vulnerable by the IUCN 3.1, with as few as 5,000 mature individuals currently surviving in the wild, primarily due to habitat fragmentation (McCarthy and Chapron 2003; Nyhus et al. 2016).

Thus, information on forelimb myology of *P. uncia* is scarce. Beyond the general anatomical proportions described above, little is known about muscular adaptations that may assist with their scansorial lifestyle and survival in the harsh alpine terrain. Given the diverse demands of scansorial locomotion, rapid pursuit, overhead ambush and powerful grasping of large prey, and alpine temperatures, it is likely that the musculature of *P. uncia* exhibits a unique set of anatomical adaptations. In order to fill this knowledge gap and test hypotheses relating to functional adaptations in the forelimb of *P. uncia*, we collected qualitative and quantitative data on forelimb muscle morphology and compared it with other carnivorans. Specifically, we tested whether forelimb muscle proportions of *P. uncia* were most similar to other large-bodied pantherines and/or other climbing felids.

Materials and methods

Specimens

Two *P. uncia* specimens, a 22-year-old male (studbook number 2012) and 16-year-old female (studbook number 2438) that each died of natural causes at Santa Barbara Zoological Gardens (SBZ), were donated to Midwestern University's Arizona Research Collection for Integrative Vertebrate Education and Study (ARCIVES) for the purposes of anatomical study. The specimens were preserved via perfusion into the arterial system with a 10% formaldehyde solution. This research was approved by SBZ and the Snow Leopard Species Survival Plan.

Dissection—myology

A detailed dissection of the left and right forelimbs of the two *P. uncia* specimens was conducted. Key sources to navigate the muscles were primary literature and veterinary atlases (e.g., Fisher et al. 2009; Julik et al. 2012; Viranta et al. 2016; Sánchez et al. 2019; Böhmer et al. 2020). Standard anatomical terminology from the Nomina Anatomica Veterinaria 6th edition was employed (World Association of

Veterinary Anatomists 2017). Notes and descriptions of the morphology, orientation, and attachment points of each muscle were recorded. Each muscle was digitally photographed with a Nikon D50100 Digital Camera. Photographs of a loaned osteological specimen from the American Museum of Natural History were produced and printed, and the origin and insertion points for each muscle were drawn in to generate muscle maps. After removal, the mass of each muscle and its tendon was collected with an America Weigh Scales Inc. Model AMW—500i balance. The maximum length of each muscle was measured using Mitutoyo digital calipers.

Quantitative analyses

In order to assess the functional muscle groups in *P. uncia* compared with other Felidae, quantitative muscle data were compared with previously published felid data (Hudson et al. 2011; Julik et al. 2012; Cuff et al. 2016; Viranta et al. 2016; Souza Junior et al. 2020) (Table 1 and Supplementary Table S1). Following Souza Junior et al. (2020), data for individual muscles were combined into functional muscle groups: shoulder extensors (mm. supraspinatus, coracobrachialis), shoulder flexors (mm. infraspinatus, deltoideus, teres major, teres minor), elbow extensors (mm. triceps brachii, tensor fascia antebrachii, anconeus), elbow flexors (mm. biceps brachii, brachialis), carpus extensors (m. extensor carpi radialis), carpus flexors (mm. flexor carpi ulnaris, flexor carpi radialis, extensor carpi ulnaris), digital extensors (mm. extensor digitorum communis, extensor digitorum lateralis, extensor digiti I et II, abductor digiti I longus), digital flexors (mm. palmaris longus, flexor digitorum profundus), supinators (mm. supinator, brachioradialis), and pronators (mm. pronator teres, pronator quadratus). Masses of all included muscles in each group were summed, and then percentage masses were calculated for each group following Souza Junior et al. (2021). For taxa with more than one specimen, values were averaged. The anatomical cross-sectional area (ACSA) was also calculated using the formula: ACSA = (mass/1.06)/length. In order to account for differences in body size, the ACSA values were regressed against log body mass and the resulting residuals used for analyses. Unfortunately, the variables needed for calculating ACSA are not available in the literature for all comparative taxa, and thus a subset of taxa was utilized for these analyses (Table 1). The data were checked for assumptions of normality and it was discovered that non-parametric comparisons were necessary only for the ACSA comparisons.

Taxa were divided into categories based on subfamilies (pantherine versus feline), prey size (small versus large prey specialists), and locomotor categories (based on Wilson and Mittermeir 2009). For the latter, we used two methods to categorize locomotor repertoire: (1) more terrestrial versus more scansorial and (2) climbing specialists versus generalists. The latter category was included because most felids are scansorial to some degree, but only a few, such as *P. uncia*, are truly climbing specialists. In SPSS 27 (IBM Corp. Armonk, NY), a Levene's test of equality of variances was conducted to assess normality of variables. Multivariate analyses of variance (MANOVA) were conducted to assess whether significant differences existed in percentage muscle mass of the functional groups among prey sizes, locomotor groups, or subfamilies. One-way analyses of variance (ANOVA) were also conducted for each muscle group among the aforementioned categories (prey size, climbing ability, subfamily). Sequential Bonferroni corrections were applied to account for multiple comparisons. Principal components analysis (PCA) was performed to visualize taxonomic variation in percentage mass of the functional muscle groups. For the ACSA data, non-parametric Mann–Whitney *U* tests were conducted to evaluate whether significant differences existed in ACSA of functional muscle groups among the groups mentioned above (prey size, locomotor categories, subfamilies).

Results

Quantitative results

Functional muscle groups in *P. uncia* were similar to those in other comparative taxa (Table 2); however, there were a few interesting exceptions. *Panthera uncia* had the highest percentage of elbow extensors in the sample (Table 2). It also had among the highest proportions of shoulder flexors in the sample, second only to *A. jubatus* and *Leopardus pardalis* (Table 2). Conversely, it had the second lowest proportions of carpal extensors, with only *A. jubatus* scoring lower, and among the lowest shoulder extensors with only *P. leo* and *L. lynx* scoring lower (Table 2). The supinator proportions of *P. uncia* were lower than all other pantherines in the sample, similar to the comparative feline taxa (Table 2).

Levene's tests for equality of error variances indicated that the data are normally distributed ($P > 0.05$ for all muscle groups). The MANOVA of all functional muscle groups between large and small prey specialists revealed no overall differences in

Table 1 Felidae species included in quantitative muscle analyses, including details on number of specimens, sex and age (if know), family, locomotor habits, and prey size

Species	*n*	Sex (age in years, if known)	Family	Locomotion	Prey size	Source
*Panthera uncia**	3	2 F (16, unknown age), 1 M (22)	Pantherinae	†Scansorial	Large	Present study; Cuff et al. (2016)
*Panthera leo**	1	1 F (unknown age)	Pantherinae	Terrestrial	Large	Cuff et al. (2016)
*Panthera onca**	1	1 F (unknown age)	Pantherinae	†Scansorial	Large	Cuff et al. (2016)
*Panthera tigris**	1	1 F (unknown age)	Pantherinae	Terrestrial	Large	Cuff et al. (2016)
Acinonyx jubatus	8	4 F (6.5, 8.5, 12, and 15.5) 4 M (6, 11.5, 12.5, and 13.5)	Felinae	Terrestrial	Large	Hudson et al. (2011)
*Caracal caracal**	1	1 M (unknown age)	Felinae	Scansorial	Small	Cuff et al. (2016)
*Felis nigripes**	1	1 F (unknown age)	Felinae	Terrestrial	Small	Cuff et al. (2016)
*Felis silvestris**	1	Not reported	Felinae	Scansorial	Small	Cuff et al. (2016)
Leopardus colocolo	1	Not reported	Felinae	Scansorial	Small	Souza Junior et al. (2021)
Leopardus geoffroyi	1	Not reported	Felinae	Scansorial	Small	Souza Junior et al. (2021)
*Leopardus pardalis**	1	1 M (unknown age)	Felinae	†Scansorial	Small	Cuff et al. (2016)
Lynx lynx	4	2 F, 2 M (unknown ages)	Felinae	Scansorial	Large	Viranta et al. (2016)
Puma yagouroundi	3	Not reported	Felinae	Scansorial	Large	Souza Junior et al. (2021)

*Indicates climbing specialist.
†Taxon included in ACSA analyses.

Table 2 Results of MANOVA and ANOVA comparing average of percentage mass of the functional muscle groups between small and large prey hunters, climbing specialists versus generalists, and Pantherinae versus Felinae subfamilies

Comparison	MANOVA	ANOVA
Prey size	$F = 2.357$, $P = 0.334$	Only ExE significant: $F = 5.795$, $P = 0.035$
Locomotor Category 1- terrestrial versus scansorial	$F = 1.456$, $P = 0.475$	No muscle groups significant
Locomotor Category 2- climbing specialist versus generalist	$F = 0.956$, $P = 0.613$	No muscle groups significant
Subfamily	$F = 5.133$, $P = 0.174$	Only Pron significant: $F = 6.171$, $P = 0.030$

ExE, Elbow extensor muscle group; Pron, Pronator muscle group.

proportions of functional muscle groups ($P = 0.754$). However, the ANOVA revealed significant differences in elbow extensors ($F = 8.23$, $P = 0.024$). The MANOVA of functional muscle groups between climbing specialists and generalized climbers revealed no significant differences between groups ($P = 0.409$), and the ANOVAs of individual muscle groups were also not significant. There was also no significant difference between the two felid subfamilies, Felinae and Pantherinae in either test. In the PCA for functional muscle groups, the *P. uncia* specimens fell closest to the tiger (*Panthera tigris*) and Eurasian lynx (*Lynx lynx*) (Fig. 1). When the individuals *P. uncia* limbs are plotted separately, they fall in a cluster surrounding *P. tigris*. PC 1 (29.4% of the variance) is driven most significantly by elbow flexors (positive direction) and carpal extensors and carpal flexors (negative direction). PC2 (24.9%) loadings indicate that it is driven most strongly by digital extensors and pronators (positive direction) and shoulder extensors and flexors (negative direction) (Supplementary Tables S2 and S3). The Mann–Whitney *U* tests for muscle group ACSA were found to be non-significant between the prey size categories and subfamilies. However, there were significant differences in muscle group ACSA for Locomotor Category 1: The more terrestrial taxa had significantly larger ACSA than the more scansorial taxa for both shoulder extensors ($P = 0.036$) and elbow flexors ($P = 0.036$). In Locomotor Category 2, the climbing generalists had significantly larger elbow extensors ($P = 0.036$) than the climbing specialists (Table 3).

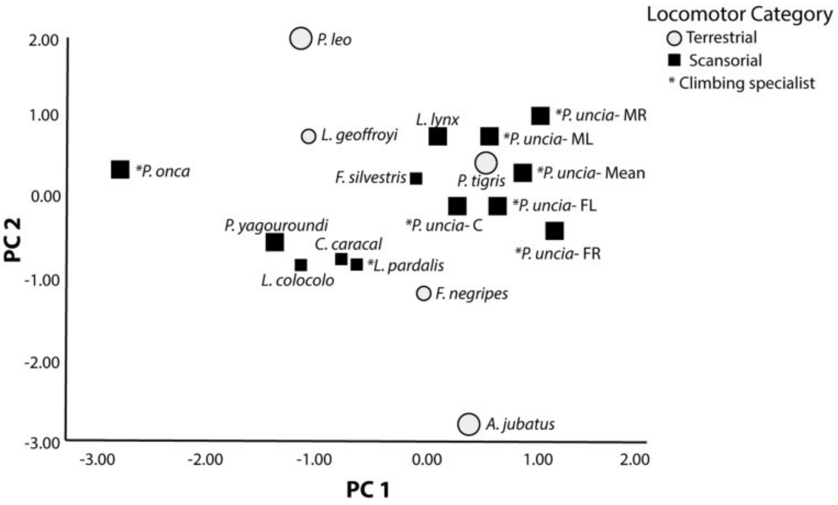

Fig. 1 Plot of the PCA conducted on percentage mass data of functional muscles groups in felid taxa. More terrestrial taxa are indicated by white circles, while more scansorial taxa are indicated by black squares. Asterisk indicates climbing specialists within scansorial locomotor category. Size of the icon indicates prey size: Large icon = large prey; Small icon = small prey. PC1 explains 29.4% of the variance; PC2 explains 24.9% variance. For comparison, the left and right limbs of each of the two *P. uncia* specimens dissected in the current study are plotted separately. Abbreviations for *P. uncia*: C = Female specimen from Cuff et al. (2016); FL = female, left from this study; FR = female, right from this study; ML = male, left from this study; MR = Male, right from this study.

Table 3 Results of non-parametric Mann–Whitney *U* tests of comparison of ACSA between small and large prey hunters, climbing specialists versus generalists, and Pantherinae versus Felinae subfamilies

Comparison	Mann–Whitney *U* results
Prey size	No muscle groups significant
Locomotor Category 1- terrestrial versus scansorial	ExS significant: $P = 0.036$
	FlE significant: $P = 0.036$
Locomotor Category 2- climbing specialist versus generalist	ExE significant: $P = 0.036$
Subfamily	No muscle groups significant

ExE, Elbow extensors; ExS, Shoulder extensors; FlE, Elbow flexors.

Anatomical descriptions

Forelimb muscle morphology of *P. uncia* is generally comparable to that of other previously described felid species. However, there are several notable differences likely relating to their unique ecological niche and locomotor repertoire. Muscles with functionally relevant differences are described below. Full, detailed descriptions of all forelimb muscles in *P. uncia* are provided in Supplementary Table S4.

Back

Back muscles of *P. uncia* are generally well-developed but lean (Figs. 2 and 3). Origins and insertions tend to be similar to those of other published felids (Fig. 4 and Supplementary Table S4), although they are relatively smaller than in *A. jubatus* and other *Panthera* species. There are several vertebral levels of separation between both the origins and insertions of musculus rhomboideus cervicis + capitis and m. rhomboideus thoracis (Fig. 4 and Supplementary Table S4). This condition has not been observed in other carnivoran taxa, in which the musculus rhomboideus bellies lie immediately adjacent (e.g., Fisher et al. 2009; Julik et al. 2012; Viranta et al. 2016).

Scapular region

The scapular musculature of *P. uncia* exhibits a few interesting differences compared with other carnivoran taxa (Figs. 2–5). The rotator cuff muscles are well-developed with m. supraspinatus extending far over the dorsal border of the scapula (Fig. 3). While this muscle may extend slightly over the border in some other carnivorans, such as *L. pardalis* (Julik et al. 2012) and *L. lynx* (Viranta et al. 2016), the degree of extension in *P. uncia* is more pronounced. Musculus infraspinatus and teres minor have larger insertions that are expanded to reach each other (Fig. 5). The origin of m. teres major extends onto the deep surface of the scapula (Fig. 4) unlike *L. pardalis* (Julik et al. 2012) and *Galictis cuja* (Ercoli et al. 2015), and farther than in *L. lynx* (Viranta

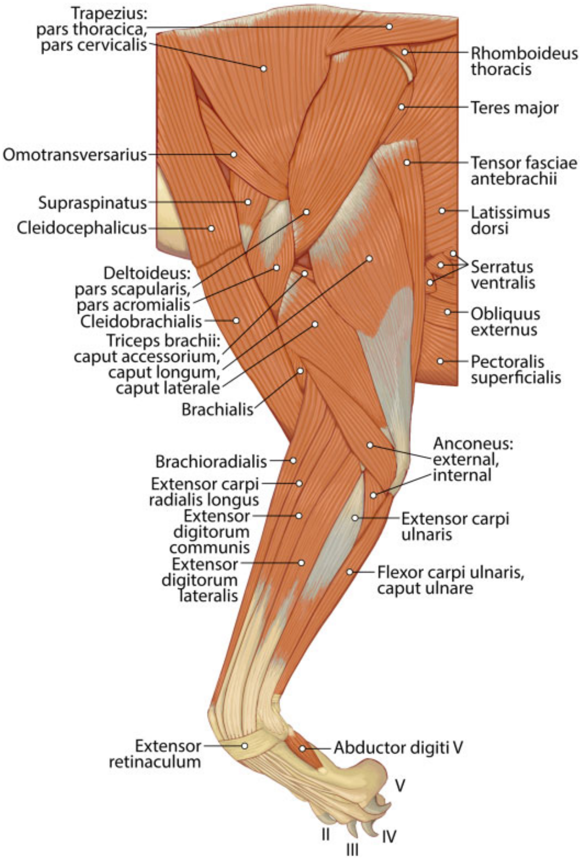

Fig. 2 Lateral view of the left forelimb muscles of P. uncia.

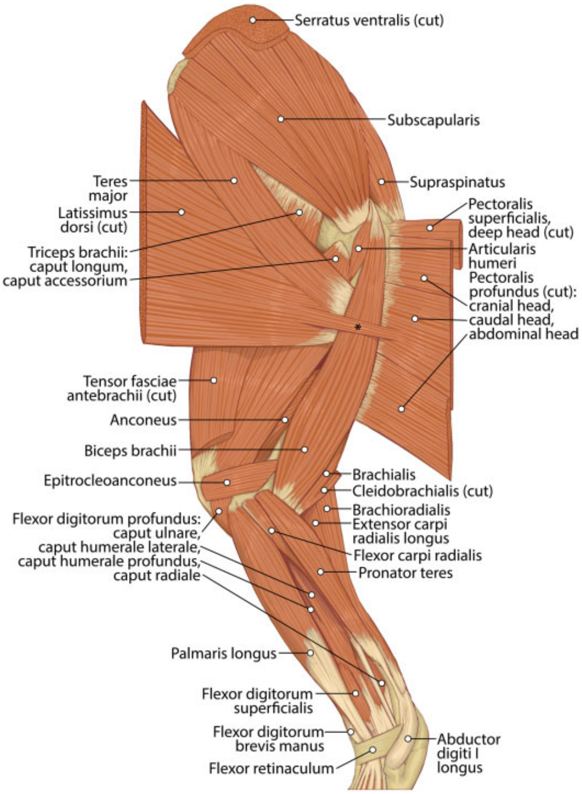

Fig. 3 Medial view of the left forelimb muscles in P. uncia. Asterisk (*) indicates slip of m. latissimus dorsi coursing across m. biceps brachii.

et al. 2016) and *Lycaon pictus* (Smith et al. 2020). Musculus subscapularis is composed of a large number of pennations (8–9) and partially fuses with mm. supraspinatus and teres minor. In other carnivorans, common conditions include four pennations in *L. pictus* (Smith et al. 2020), six in *G. cuja* (Ercoli et al. 2015), six to seven in *L. lynx* (Viranta et al. 2016), and six to nine in *L. pardalis* (Julik et al. 2012). As in other felids, m. teres major fuses with m. latissimus dorsi to form a strong tendon of insertion onto the teres major tuberosity of the humerus (Figs. 3 and 5). The musculus deltoideus pars acromialis is particularly well-developed, relatively larger than in both *A. jubatus* and *Panthera onca* (Cuff et al. 2016).

Pectoral girdle

A small (38 mm), unarticulated bony clavicle was present within mm. cleidocephalicus and cleidobrachialis (Fig. 6). While m. pectoralis superficialis of *P. uncia* is comparable to other carnivorans, m. pectoralis profundus demonstrates unique morphological patterns (Fig. 3 and Supplementary Table S1). In both *P. uncia* specimens dissected, m. pectoralis profundus was found to have a minimum of five distinct bellies, while most other carnivorans generally have two heads, as in *L. lynx* (Viranta et al. 2016) and *G. cuja* (Ercoli et al. 2015), or three heads as in *Ailurus fulgens* (Fisher et al. 2009). However, the positions of the bellies differed between the two *P. uncia* specimens with a cranial to caudal orientation in the male (Fig. 3) and superficial to deep orientation in the female (Supplementary Table S4). The insertion also extends further distally on the humeral shaft than in most other species (Fig. 5; Ercoli et al. 2015; Viranta et al. 2016; Smith et al. 2020). The origin for m. serratus ventralis is more extensive than in small-bodied felids (Julik et al. 2012), but smaller than in *L. lynx* (Viranta et al. 2016).

Brachium

The most unique feature of the brachial region in *P. uncia* is the relationship between mm. biceps brachii, brachialis, and cleidobrachialis. The stout tendon of insertion of m. biceps brachii bifurcates in the cubital fossa to insert onto both the radial tuberosity and proximal shaft of the ulna (Figs. 7–8). The combined tendon of mm. brachialis and cleidobrachialis courses through the split to insert onto the proximal ulna in all but one of the four studied limbs (Fig. 8). This arrangement differs from the pattern of most felids in which mm. biceps brachii

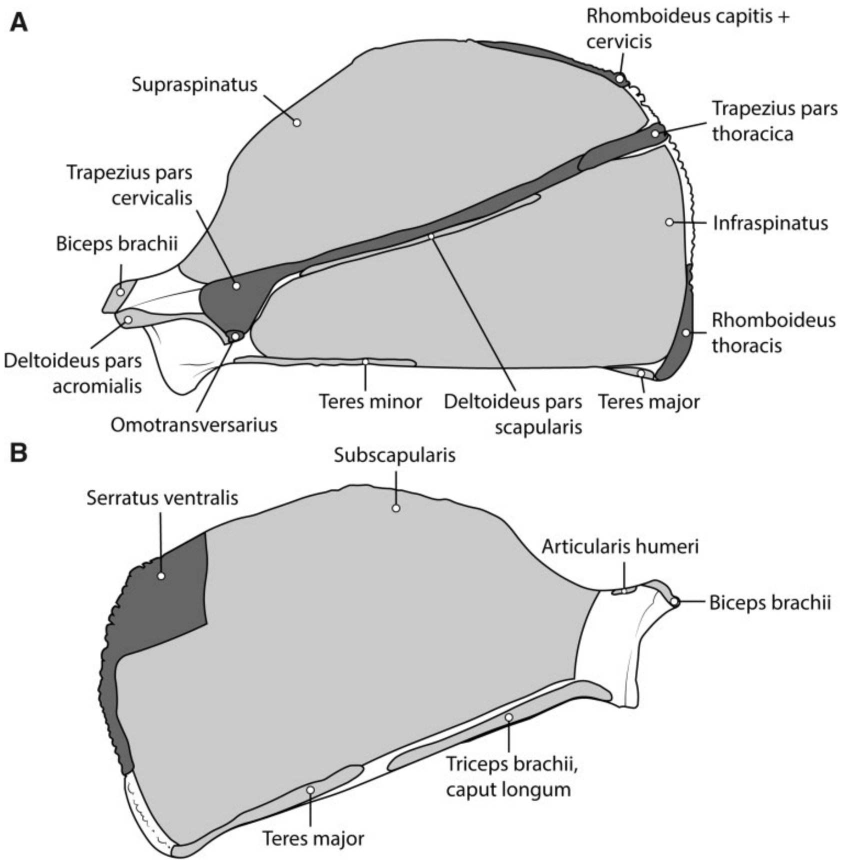

Fig. 4 Scapular muscle maps for *P. uncia* (left side). (**A**) Lateral view and (**B**) medial view. Dark gray indicates insertions, while light gray indicates origins.

inserts exclusively onto the radius (e.g., Julik et al. 2012), and instead resembles the typical pattern of canids (e.g., Evans and de Lahunta 2013; Souza Junior et al. 2018; Smith et al. 2020). However, the bifurcating pattern is also observed in *L. lynx* (Viranta et al. 2016). Musculus brachialis is also relatively larger in *P. uncia* than in either *A. jubatus* or *P. onca* (Cuff et al. 2016). It has both a larger mass and expanded muscle attachment site than comparative taxa (Cuff et al. 2016), and it was found to have three separable bellies in one of the dissected limbs (male right). *Panthera uncia* has five heads of mm. triceps brachii—longum, laterale, mediale, accessorium, and mediale accessorium (Fig. 2), as in *L. pardalis* (Julik et al. 2012), *L. lynx* (Viranta et al. 2016), and *A. fulgens* (Fisher et al. 2009); however, while mm. triceps brachii caput longum is relatively smaller than in *A. jubatus* and *P. onca* (Cuff et al. 2016), mm. triceps brachii caput laterale is relatively larger. *Panthera uncia* lacks the m. triceps brachii caput magnum found in the highly cursorial *L. pictus* (Smith et al. 2020).

Antebrachium

Several antebrachial muscles in *P. uncia* exhibit unique morphological patterns. Musculi pronator teres, pronator quadratus, and supinator are all intermediate in size between the conditions found in *A. jubatus* (small) and *P. onca* (developed) (Figs. 3, 9, and 10). Musculus pronator teres has a large insertion that attaches to the flexor retinaculum, and it continued to a sesamoid on the base of metacarpal I in one limb, as in *L. pardalis* (Julik et al. 2012). In contrast, the typical carnivoran condition appears to be a single insertion onto the distal radius, as in *L. lynx* (Viranta et al. 2016), *A. fulgens* (Fisher et al. 2009), *G. cuja* (Ercoli et al. 2015), and *L. pictus* (Smith et al. 2020). Musculus flexor carpi ulnaris is expanded in *P. uncia* and other large felids (Fig. 2). In addition to the normal insertion on the pisiform, it also inserts onto metacarpal V, and indirectly onto metacarpal IV via a connection with ligamentum accessoriometcarpeum IV. This additional attachment has also been described in *G. cuja* (Ercoli et al. 2015), but is otherwise unknown among carnivorans (Fisher et al. 2009; Julik et al. 2012; Viranta et al. 2016). Additionally, m. abductor digiti V

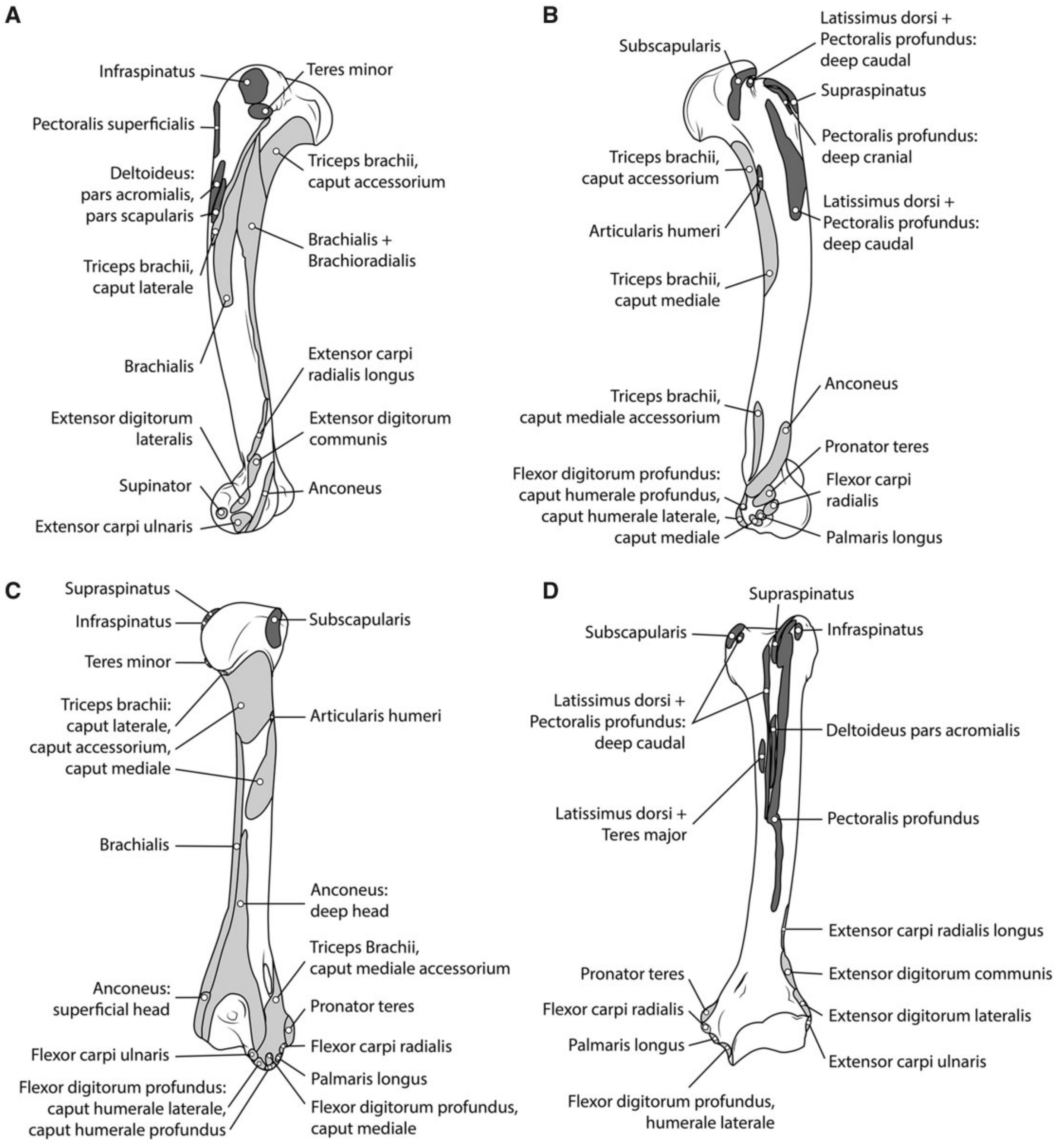

Fig. 5 Humerus muscle maps for *P. uncia* (left side). (**A**) Lateral view, (**B**) medial view, (**C**) caudal view, and (**D**) cranial view. Dark gray indicates insertions, while light gray indicates origins.

originates from m. flexor carpi ulnaris, an arrangement not described in any other species (Fisher et al. 2009; Julik et al. 2012; Ercoli et al. 2015; Viranta et al. 2016). Musculus brachioradialis is relatively small and inserts primarily onto the tendon of m. abductor digit I longus with only a small attachment to the distal radius. The digital flexors, mm. flexor digitorum profundus and flexor digitorum superficialis, were not expanded compared with all other taxa (Cuff et al. 2016). There are two obliquely overlapping heads of m. anconeus (Fig. 2), a condition not described in any other comparative taxon (Fisher et al. 2009; Julik et al. 2012; Ercoli et al. 2015; Viranta et al. 2016; Smith et al. 2020).

Manus

The manus of *P. uncia* is generally broad with wide, fleshy palmar musculature (Figs. 1113). The bellies of mm. adductores digitorum and flexores breves profundi are particularly expanded in comparison to other published taxa (Fisher et al. 2009;

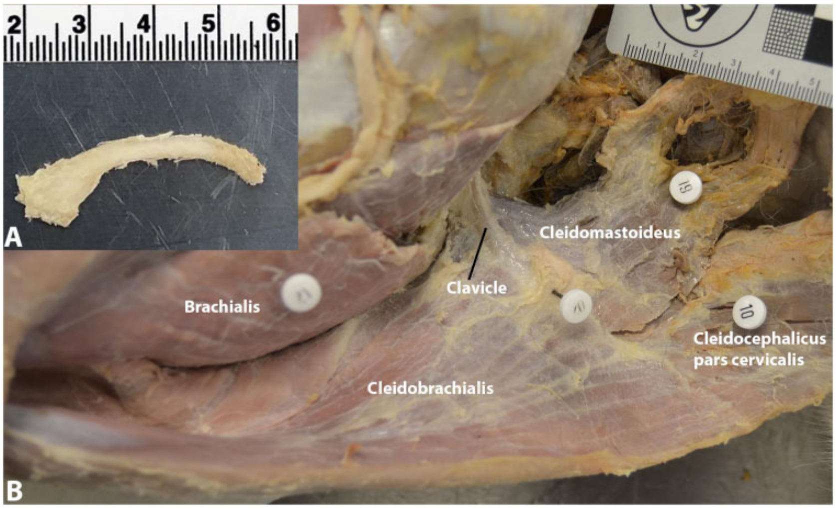

Fig. 6 Photographs of bony clavicle. (**A**) Unarticulated clavicle. (**B**) Clavicle in anatomical position on deep surface of m. brachiocephalicus muscle complex.

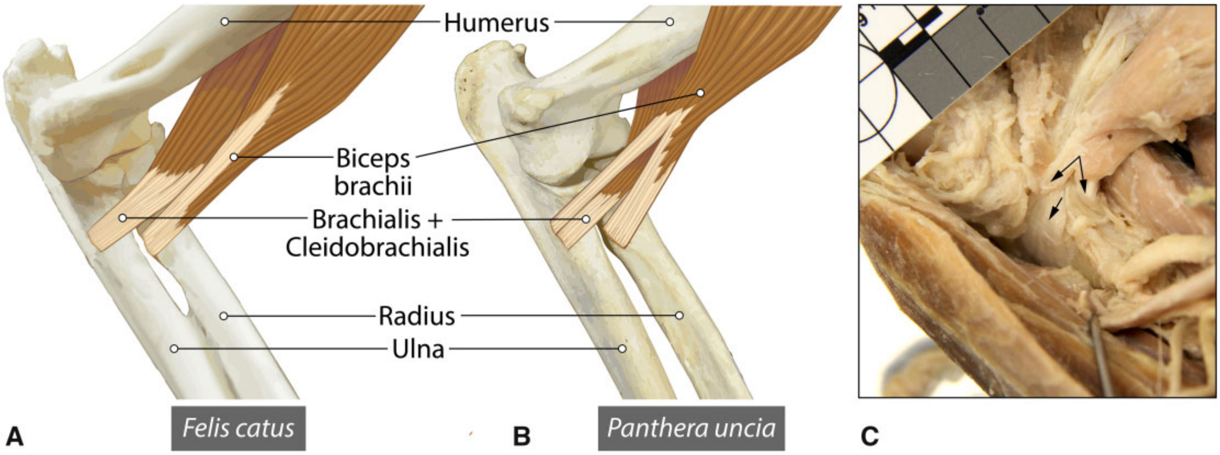

Fig. 7 Insertions of mm. biceps brachii, brachialis, and cleidobrachialis (left side). (**A**) Illustration of typical felid condition illustrated by *F. catus* in which m. biceps brachii inserts exclusively onto the radius. (**B**) Illustration of condition in *P. uncia* in which m. biceps brachii bifurcates to insert onto the radius and ulna, while mm. brachialis and cleidobrachialis tendons course through the split. (**C**) Photograph in *P. uncia* of m. biceps brachii tendon bifurcating.

Julik et al. 2012; Ercoli et al. 2015; Viranta et al. 2016; Smith et al. 2020); however, their tendons are not enlarged (Fig. 11C). In contrast, m. flexor digitorum superficialis was slight, generally with a single belly leading to its three tendons (Fig. 11B), as in *A. fulgens* (Fisher et al. 2009), and *G. cuja* (Ercoli et al. 2015). In contrast, *L. pardalis* exhibits three separate bellies of this muscle, one associated with each tendon (Julik et al. 2012). The musculus lumbricales are thin. As in many comparative taxa, there is no belly serving digit I (Fig. 11A; Fisher et al. 2009; Julik et al. 2012; Ercoli et al. 2015).

Discussion

Qualitative and quantitative evaluations of forelimb myology in *P. uncia* reveal an intriguing combination of potential functional adaptations illustrating a balance between the diverse demands of head-first descent, pouncing, climbing across rocky terrain, restraint of large prey, rapid pursuit, and navigating deep snow. Scapular musculature provides stabilization, rotation, and advancement of the forelimbs, including support of the glenohumeral joint (e.g., Agusti and Antón 2002; Antón et al. 2005). Muscles of the rotator cuff (mm. supraspinatus, infraspinatus, teres minor, and subscapularis) are of particular importance in felids for stabilizing the scapula during such activities as grappling with large prey and climbing (e.g., Julik et al. 2012; Cuff et al. 2016; Viranta et al. 2016). In *P. uncia*, rotator cuff muscles are typically expanded in size beyond that of the feline small prey specialists (Julik et al.

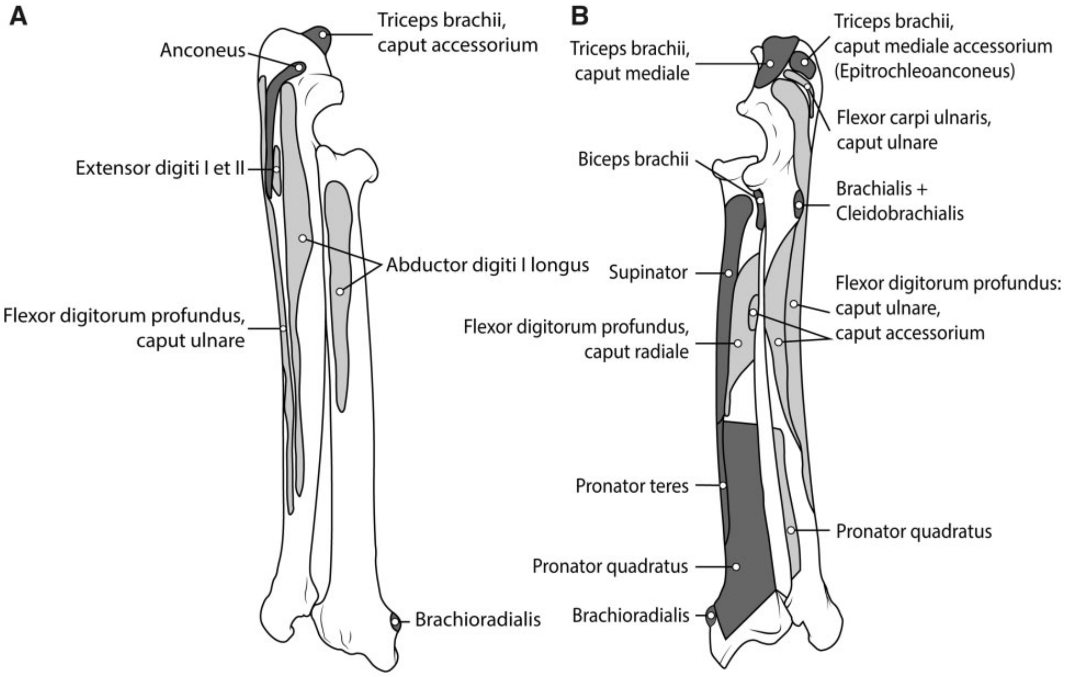

Fig. 8 Radial and ulnar muscle maps for *P. uncia* (left side). (**A**) Caudomedial view and (**B**) craniolateral view. Dark gray indicates insertions, while light gray indicates origins.

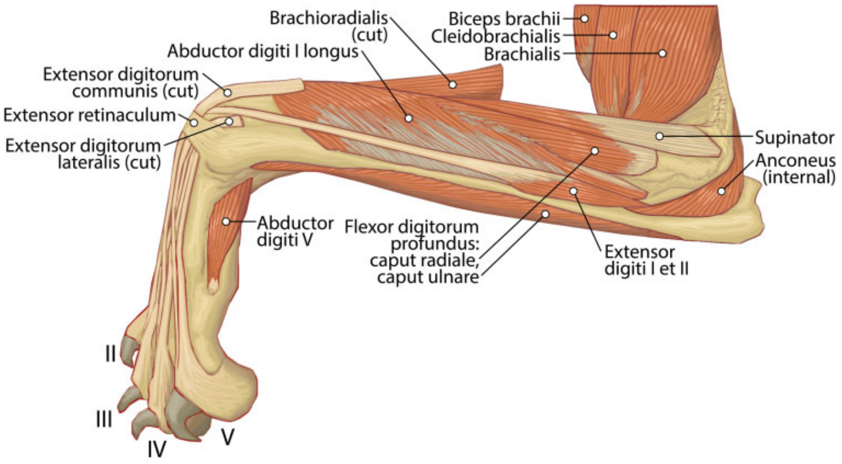

Fig. 9 Lateral view of the deep left antebrachium in *P. uncia*.

2012; Viranta et al. 2016), but they do not exhibit the dramatic expansions that characterize *P. leo* and *P. tigris*, the pantherines that hunt the largest prey. Musculus deltoideus pars acromialis, another scapular muscle found to be enlarged in *P. uncia* in both mass and muscle attachment area (Figs. 2, 4, and 5), is crucial for the forelimb retraction necessary for powerful grip on large prey (Viranta et al. 2016). In contrast, muscles that extend the shoulder joint were found to have enlarged ACSA in the more terrestrial felid taxa (Table 3). It is worth noting that a previous study found that muscles of the scapula and others that support the trunk consistently scale with positive allometry (Cuff et al. 2016). Thus, body size also plays a role in dictating the relative proportions of these muscles.

The pectoral musculature also supports the trunk on the forelimb and functions during pouncing (Viranta et al. 2016). *Panthera uncia* is unique among carnivorans in having m. pectoralis profundus with five distinct bellies, which may provide additional support to the forelimb during the torsion associated with large prey grappling or climbing. *Panthera uncia* is also known to bound from incredible heights when catching prey (McCarthy and Mallon 2016), and this morphology may help *P.*

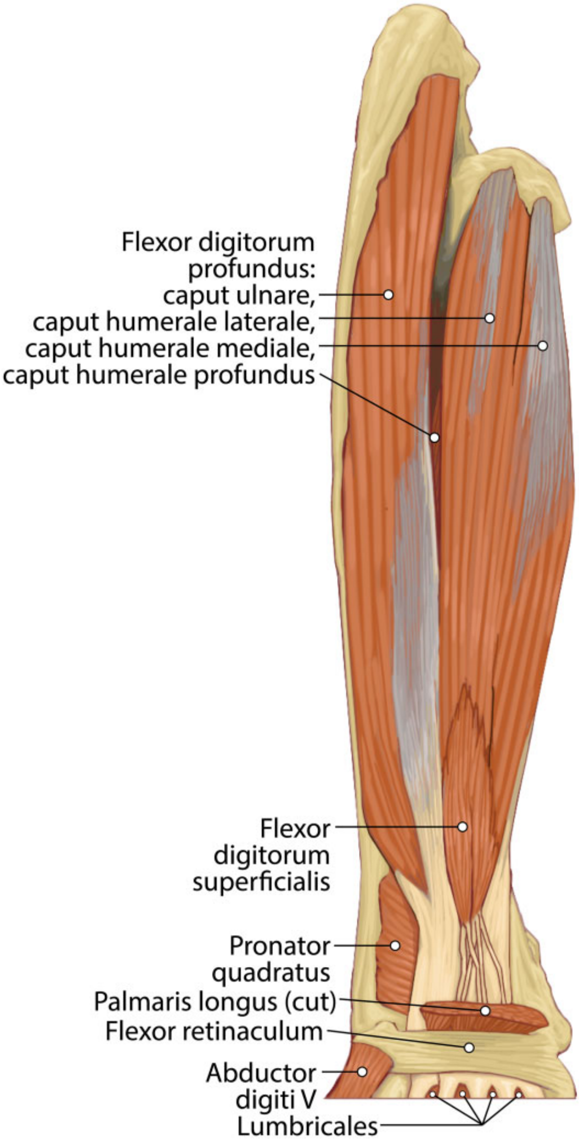

Fig. 10 Caudal view of the left antebrachium in *P. uncia*.

uncia stay balanced while climbing steep, rocky mountains. Musculus serratus ventralis anchors the pectoral girdle to the trunk, and is more extensive in *P. uncia* than in the small-bodied felids (Julik et al. 2012); however, it is smaller than in *L. lynx* (Viranta et al. 2016), which occasionally hunts large ibex.

In the brachium and antebrachium of *P. uncia*, there appears to be a functional trade-off between powerful grip and stability. Rotatory abilities of the antebrachium can be beneficial for gripping prey (Viranta et al. 2016); however, they come at a cost of reduced antebrachial stability. In *P. uncia*, the muscles that pronate and supinate the antebrachium (mm. supinator, pronator teres, pronator quadratus, brachioradialis) are intermediate in size between the stable condition of the cursorial *A. jubatus* and the powerful rotatory abilities of the larger pantherines (*P. onca*, *P. leo*, and *P. tigris*) (Supplementary Table S1). This intermediate condition in *P. uncia* may represent the competing adaptive pressures between large prey capture and rapid pursuit. However, the steep, mountainous terrain inhabited by snow leopards is a heterogeneous and three-dimensionally complex environment. To effectively navigate the uneven distribution and orientation of the substrate would require tremendous flexibility of the forelimb. Enhanced rotatory capabilities, as evidenced by enlarged pronator muscles with additional insertions, would be beneficial both in the context of locomotion over uneven rocky terrain and large prey capture. Musculus brachioradialis, a supinator of the forearm, is comparatively small in *P. uncia*; however, it uniquely inserts onto the tendon of m. abductor digiti I longus. This configuration likely reduces its ability to rotate the antebrachium, but may provide additional leverage to the movements of digit I, which has been described as the most important digit for both climbing and holding onto prey (Salesa et al. 2010).

The bifurcation of the m. biceps brachii tendon, unique among felids in *P. uncia* and *L. lynx*, suggests greater stability and support at the elbow joint. As rotatory movements of the antebrachium occur at the radiohumeral joint, the reduction in radial insertion by m. biceps brachii may further stabilize the elbow. This bifurcating arrangement is found in most canid species and provides stability to the elbow and antebrachium (e.g., Souza Junior et al. 2018; Taverne et al. 2018; Smith et al. 2020). Instead of m. biceps brachii inserting primarily onto the rotatory radius, the bifurcation allows it to instead insert primarily onto the more stable ulna. In highly cursorial canid species, such as the African wild dog (*L. pictus*), where forelimb stability is paramount for endurance running, the condition is more dramatic with mm. biceps brachii and brachialis fusing proximally before bifurcating together to insert onto both the radius and ulna (Smith et al. 2020). Musculus flexor carpi ulnaris is significantly larger in large prey than small prey specialists (Table 2). In *P. uncia*, its two heads converge at the pisiform, have an extra insertion onto metacarpal V, and connect to the ligamentum accessoriometacarpeum IV, which insert onto digit IV. This morphology is unique to *P. uncia* and would provide enhanced abduction and flexion at the carpal joint.

As in other large prey specialists, relative reductions are observed in certain muscles associated with fine digital manipulation (e.g., mm. extensor digitorum, flexor digitorum profundus, and flexor digitorum superficialis) compared with small prey

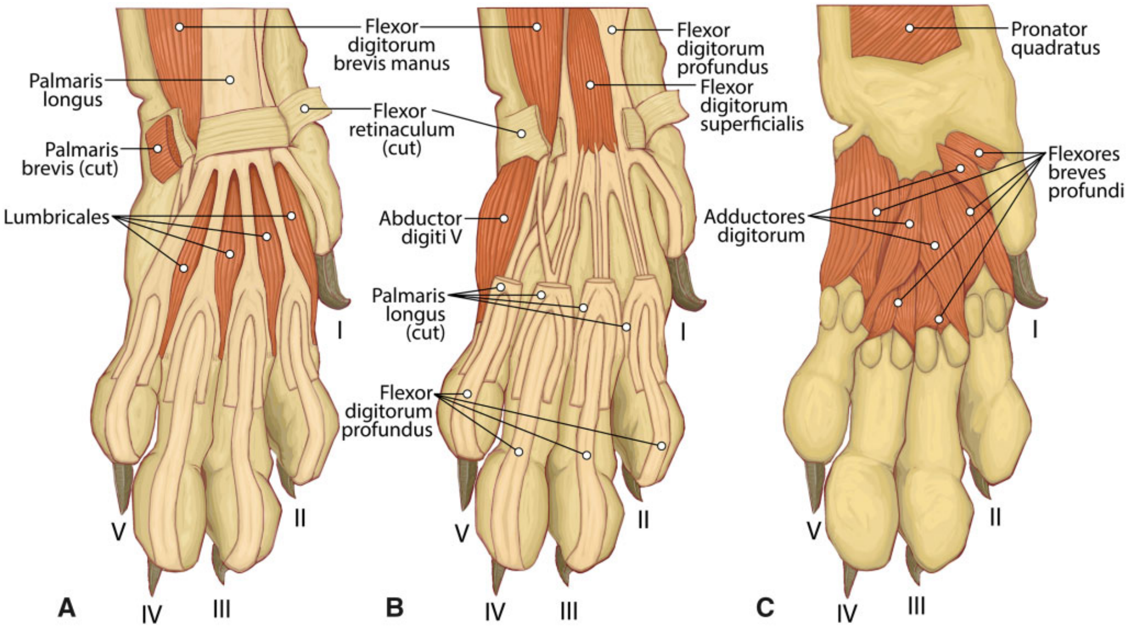

Fig. 11 Palmar view of manus muscles in *P. uncia* (left side). (**A**) Superficial layer, (**B**) intermediate layer, and (**C**) deep layer. .

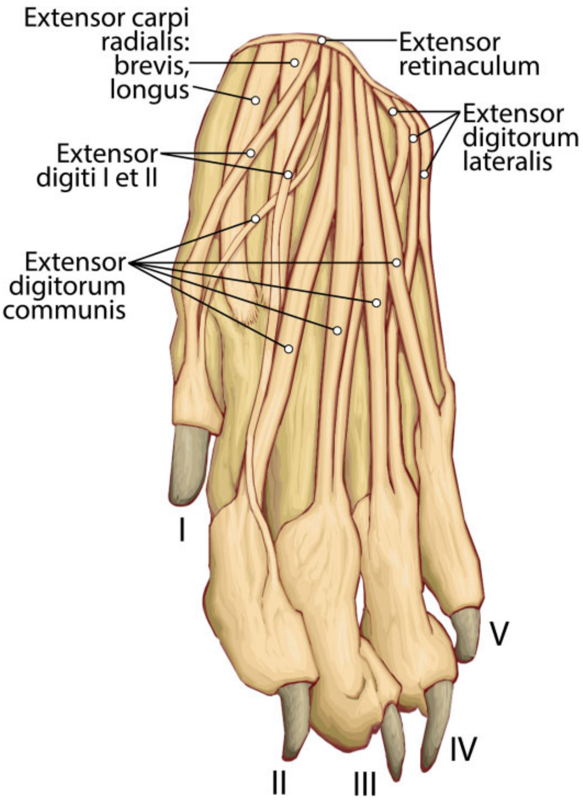

Fig. 12 Dorsal view of manus tendons in *P. uncia* (left side).

specialists. Musculus flexores breves profundi digit I was absent in the male *P. uncia* specimen; however, this muscle was present in the female specimen. Felines *L. pardalis* and *Felis catus* are also missing the lateral belly of m. flexores breves profundi digit I; however, it is present in *P. leo* (Julik et al. 2012). This suggests the snow leopard does not have comparatively extensive individual movement of digit I. As this digit is instrumental in climbing and manual restraint of prey (Viranta et al. 2016), *P. uncia* is inferred to have reduced fine manual manipulation capabilities compared with felines and may have to rely more heavily on other methods of prey restraint, such as grasping with its teeth and grappling that is powered by scapular and pectoral musculature (Viranta et al. 2016). However, digit I in *P. uncia* is also comparatively short and stout, a trait which has been linked to increased forces in other pantherines, such as the extinct *Promegantereon ogygia* (Salesa et al. 2010).

Among carnivorans, the clavicle generally lacks bony articulation with the rest of the shoulder girdle, and hangs suspended within the brachiocephalicus muscle complex, connected to the scapula via fibrous connections (Field and Taylor 1950; Cerny and Cizinauskas 1995). *Panthera uncia* was found to possess a small (38 mm), unarticulated bony clavicle, similar in size (37.4 mm) and shape to that of *P. onca* (Souza Junior et al. 2021). In comparison, *P. leo* and *P. tigris* have longer clavicles of 78.6 and 58.8 mm, respectively, while the clavicle of more cursorial felid taxa, such as *A. jubatus* , is further reduced (30.5 mm) (Hartstone-Rose et al. 2012). Aclaviculate mammals or those with reduced clavicles generally have greater scapular mobility in the sagittal plane (Jenkins 1974; Nyakatura and Fischer 2010). The vestigial clavicle of

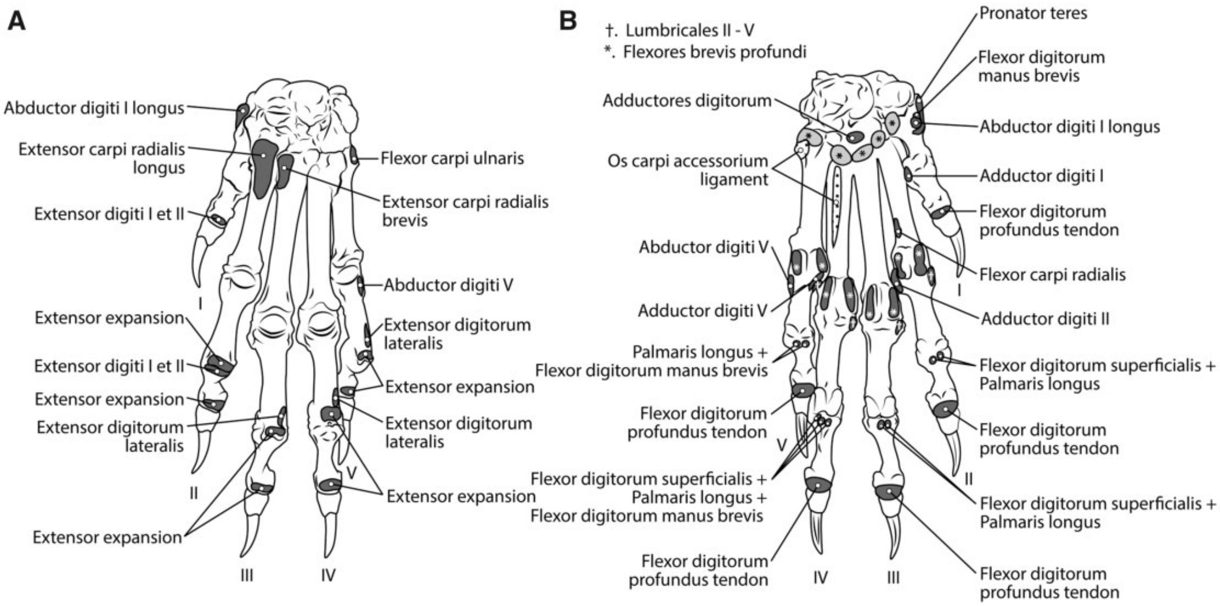

Fig. 13 Manus muscles maps for *P. uncia* (left side). (**A**) Dorsal view and (**B**) palmar view. Dark gray indicates insertions, while light gray indicates origins.

Note: Figure Replacement Requested.

felids facilitates flexibility at the glenohumeral joint and permits greater extension of the forelimbs, resulting in increased stride length (Lamberski 2015; Senter and Moch 2015). A reduced clavicle also provides greater absorption of impact from landing following a jump (Hartstone-Rose et al. 2012). Thus, the small clavicle of *P. uncia* may facilitate greater advancement of the forelimb, while walking through deep snow for example, and may allow pectoral musculature to serve as increased shock absorbers in this saltatorial (leaping) species (Hartstone-Rose et al. 2012). In contrast, retention of a clavicle, albeit reduced, has been argued to allow felids greater manual dexterity while hunting than cursorial canids that may be entirely aclaviculate (Trotter 1885). Thus, it appears that the retention of a small clavicle in *P. uncia* may reflect another functional trade-off between the forelimb versatility needed for navigating a complex environment and the strength needed for hunting ibex and other large prey.

Finally, we wish to acknowledge the potential limitations of using captive specimens for this study; however, wild snow leopard specimens are essentially unattainable. As zoo specimens do not experience the same pressures as a wild individual, it is possible that patterns observed do not reflect the true range of form–function relationships of wild snow leopards. However, general morphological patterns should be similar and can provide insight into adaptations in the wild. In addition, future studies could increase the sample size to evaluate variation within *P. uncia*.

Data availability statement

The data underlying this article are available in the article and in its online supplementary material.

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Supplementary data

Supplementary data are available at *ICB* online.

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