Extraordinary grip strength and specialized myology in the hyper-derived hand of *Perodicticus potto*?

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Abstract

Previous behavioral reports of the African lorisid, *Perodicticus potto*, have speculated that these animals have an extraordinary grip strength. This ability is hypothesized to be facilitated by a range of anatomical features within the forelimb, ranging from the presence of a retia mirabilia in its wrist to the hyper-abduction of its pollex. Despite numerous behavioral reports, however, this claim of extraordinary grip strength has not been empirically substantiated. This study quantifies the physiological cross-sectional area of the digital flexor muscles within *P. potto*. These data are compared with a broad primate sample, including several similarly sized strepsirrhines. Contrary to expectation, we found that *P. potto* actually has relatively *below*-average digital flexor PCSA. However, we identified other myological characteristics in the upper limb of *P. potto* that were unexpected, including the largest brachioradialis muscle (an elbow flexor) among our primate sample, and – despite *P. potto* having only a vestigial second digit – an independent digital extensor indicis that is absent in almost a quarter of our primate sample.

Key words: arboreality; forearm; functional morphology; muscle architecture; PCSA.

Introduction

Previous investigations have found that the slow-moving (Jouffroy, 1962; Charles-Dominique, 1977) African lorisid *Perodicticus potto* has several anatomical features that are highly derived and characteristic of the species and its closest relatives (e.g. *Arctocebus*; Nekaris, 2013; Hill, 1953; Nekaris & Bearder, 2007; Walker, 1969). Many of these characteristics relate to its distinctive pincer-like hand, such as the specialized bundle of vasculature located in its wrists called the retia mirabilia (Hill, 1953; Oates, 1984) which reportedly contributes to the animal's endurance grip (Carlisle, 1800, 1804; Wislocki & Straus, 1932; Nekaris, 2013). Additionally, *P. potto* has a hyper-abducted pollex (opposing the other digits at 180° or more) and a severely reduced second digit that is merely a vestigial tubercle (Hill, 1953; Bishop, 1962; Jouffroy, 1962; Walker, 1969; Oates, 1984; Lemelin & Jungers, 2007; Nekaris, 2013). Although much has been written about this specialized morphology, as well as the behavior and diet of this derived species (Murie &

Mivart, 1869; Bishop, 1962; Nekaris et al. 2010), one trait that is highly referenced and yet poorly supported with empirical evidence is its strong grip.

One of the early accounts of *P. potto* grip strength was given by Miller (1943: p. 157) who stated that 'collectors [have reported] instances in which the fingers had to be severed before the animal could be removed from the branch to which it was attached' – a rather extreme anecdotal claim with no explicit supporting evidence. Charles-Dominique (1977), in a description of the species' behavior, reported that *P. potto* hands are very muscular and, as a result, the animal's grip is particularly strong. However, quantitative data were not provided in that report (Charles-Dominique, 1977). Feldhamer et al. (2007) also mentioned the animal's strong grip and attributed it to the hyper-abducted pollex and highly prehensile hands and feet, but it has been previously reported that these anatomical features play a role in hand placement on a substrate during locomotion rather than force production capabilities (Bishop, 1962; Walker, 1969). In their respective studies, Oates (1984) and Lemelin & Jungers (2007) also mentioned the strong grip of *P. potto* and note it as one of the features that is particularly interesting about the species; however, the authors' support for this claim is not myological but rather based on the presence of the retia mirabilia. Although this specialized vascular structure is present in the wrists of *P. potto*, it does not play a role in force production, but

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rather the theoretical ability to maintain grip (Wislocki & Straus, 1932) through the lowering of limb temperature and, as a result, the need for oxygen in the muscle tissue (O'Dea, 1990) – though even this claim has yet to be empirically evaluated. This structure is present in many non-gripping animals that burrow or dive (e.g. the capybara, *Hydochoerus hydrochaeris*, and the manatee, *Trichechus* spp.; O'Dea, 1990), functioning to compensate for oxygen restrictions and not increased contractile abilities or endurance. Understanding the reportedly high grip strength of *P. potto* therefore requires quantitative analyses of grip strength via myological analysis of muscle strength within the digital flexors (e.g. Leischner et al. 2018), or the collection of manual pressure distributions during gripping behaviors (e.g. Williams-Hatala et al. 2018), as opposed to relying upon the presence of an oxygen-regulating vasculature structure alone.

In this study, we quantify the force generation capacity of the digital flexors in *P. potto* by examining their architectural properties [muscle mass, fascicle length, and physiological cross-sectional area (PCSA)] against a broader sample of other primate taxa. As architectural properties of muscle reflect their contractile profile, such data provide an insight into the functional capacity for gripping within these species. As muscle fascicles consist of fibers (which themselves are composed of serially arranged sarcomeres), average fascicle length reflects a muscle's excursion potential and contractile speed (Gans, 1982; Lieber & Ward, 2011). Meanwhile, PCSA (a function of muscle mass and FL, see Methods) reflects a muscle's capacity for force production (Close, 1972). Our comparative sample includes 55 specimens (Table 1), representing 46 primate taxa (of which 10 are strepsirrhines, 18 are platyrrhines and 18 are catarrhines). Eight taxa (including *P. potto*) were dissected for the purposes of this study; the remaining data are derived from a previously published dataset (Leischner et al. 2018).

In addition to analyses of the forearm flexor musculature of *P. potto*, a recent qualitative study of the manual anatomy of this taxon (Boettcher et al. in press) additionally highlights other muscles within the forearm that warrant quantitative investigation. First, despite previous accounts (Murie & Mivart, 1869; Forster, 1934) describing the absence of a true extensor indicis within *P. potto* (as might be expected for a species with a vestigial second digit), this muscle was recently reported as present within this taxon (Boettcher et al. in press). Although the mere presence of this muscle is interesting, quantifying the size and architectural configuration of this muscle relative to other taxa will provide greater insight into the functional capabilities of the second digit within *P. potto*. Additionally, the brachioradialis (an elbow flexor) was found to deviate significantly from typical primate anatomy in its overall size, with an origin spanning almost the entire length of the humerus (Boettcher et al. in press). Despite brief notes on this adaptation (e.g. Nayak, 1933; Miller, 1943; Jouffroy, 1962) in early

reports of this taxon's anatomy, quantitative data on the size of this muscle relative to other primate taxa would help inform whether *P. potto* is truly exceptional in this feature.

Hypotheses

1 Based on previous published suggestions of their extraordinary grip strength, we hypothesize that *P. potto* will possess among the highest relative PCSA values for the digital flexors across our primate sample.
2 As *P. potto* is a relatively slow-moving species (Jouffroy, 1962; Charles-Dominique, 1977), we predict that its forearm musculature will exhibit relatively short fascicle lengths, so as to maximize PCSA without the need for additional, metabolically expensive muscle mass.
3 Due to the reduced size of the vestigial second digit in *P. potto* and its presumably minimal role within locomotion, we hypothesize that the extensor indicis will have an exceptionally low PCSA in this taxon relative to those of other primates.
4 Following recent qualitative observations of the extraordinarily large brachioradialis within *P. potto*, we hypothesize that this muscle will possess among the largest muscle mass and PCSA in our sample, relative to body size.

Methods

Sample composition

Architectural data were collected for the digital flexors of 11 primate specimens, representing eight primate taxa. Our strepsirrhine sample consisted of two specimens of *P. potto*, one specimen of *Nycticebus coucang*, one specimen of *Otolemur crassicaudatus*, one specimen of *Hapalemur griseus* and one specimen of *Eulemur mongoz*. Our platyrrhine sample consisted of three specimens of *Callithrix jacchus*, one specimen of *Callithrix aurita* and one specimen of *Aloutta* sp. Our comparative sample was further supplemented by a recently published dataset by Leischner et al. (2018) in which architectural data are presented for the digital flexors of 38 additional taxa (see Table 1 for comprehensive specimen information).

Data collection

Myological data were collected following a protocol outlined in Herrel et al. (2008). The digital flexors, extensor indicis and brachioradialis (Fig. 1) were excised from their bony attachments and weighed to the nearest 0.0001 g.

Each muscle was then submerged in 35% nitric acid solution at room temperature to break down the connective tissue binding the fascicles together. The length of time each muscle remained in the acid solution ranged from 15 to 24 h, depending on the muscle size and volume of associated connective tissue. When the muscle fascicles were easily separable, we removed the acid and replaced it with a 50% aqueous glycerol solution to prevent further breakdown of the soft tissue. We then separated the fascicles for each muscle and photographed them. From these photographs, the lengths of individual fascicles were measured using the software

Table 1 Species included in this dataset, as well as taxonomic groupings (strepsirrhine, platyrrhine or catarrhine), number of individuals, body mass and architectural variables for the digital flexor functional group, brachioradialis, and extensor indicis

Species	Initials	Taxonomic group	n	Body mass (g)	Digital flexors			Brachioradialis			Extensor indicis		
					Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)	Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)	Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)
Eulemur albifrons	E.a.	Strepsirrhine	1	2215	9.29	2.12	4.24	1.39	3.26	0.40	0.12	0.79	0.14
Eulemur macaco	E.ma.	Strepsirrhine	1	1880	6.69	1.84	3.50	1.32	3.50	0.36	0.18	1.31	0.13
Eulemur mongoz*	E.mo.	Strepsirrhine	1	2000	4.45	0.98	4.43	0.49	2.08	0.23	0.00	0.34	0.01
Galago senegalensis	G.s.	Strepsirrhine	1	213	0.71	0.85	0.80	0.11	1.41	0.07	0.02	0.35	0.05
Hapalemur griseus*	H.g.	Strepsirrhine	1	954	3.36	1.13	3.08	0.64	2.37	0.25	0.08	0.54	0.14
Microcebus murinus	M.m	Strepsirrhine	1	59	0.21	0.68	0.30	0.04	0.56	0.06	—	—	—
Nycticebus coucang*	N.c.	Strepsirrhine	1	842	2.60	1.41	1.78	0.42	2.07	0.19	0.03	0.57	0.06
Otolemur crassicaudatus*	O.c.	Strepsirrhine	1	1190	1.56	2.17	0.84	0.21	1.62	0.12	0.01	0.56	0.02
Perodicticus potto*	P.p.	Strepsirrhine	2	998	2.88	1.23	2.19	2.38	3.25	0.68	0.06	0.78	0.06
Varecia rubra	V.r.	Strepsirrhine	1	3300	9.98	2.13	4.43	—	—	—	—	—	—
Alouatta sp.*	Al.sp.	Platyrrhine	1	12 000	69.15	1.47	44.68	31.02	4.39	6.88	1.38	0.86	1.65
Aotus azarae	A.a.	Platyrrhine	1	1230	3.98	1.35	2.84	0.62	1.87	0.31	—	—	—
Aotus nancymaae	A.n.	Platyrrhine	1	787	3.92	1.17	3.20	0.40	1.89	0.20	—	—	—
Aotus sp.	Ao.sp.	Platyrrhine	1	1230	4.27	1.68	2.54	0.57	4.02	0.13	—	—	—
Cebuella pygmaea	Cb.p.	Platyrrhine	1	116	0.38	0.36	1.01	0.06	0.55	0.10	0.00	0.15	0.00
Callithrix aurita*	Ca.a.	Platyrrhine	1	423	1.77	0.88	1.98	0.48	1.44	0.32	0.04	0.48	0.09
Callithrix geoffroyi	Ca.g.	Platyrrhine	2	359	1.83	1.10	1.61	0.43	2.22	0.23	0.07	0.73	0.09
Callithrix jacchus*	C.j.	Platyrrhine	3	256	0.88	0.70	1.20	0.15	1.21	0.11	0.02	0.59	0.03
Cebus apella	C.ap.	Platyrrhine	1	3085	13.79	1.90	6.99	4.36	4.91	0.84	0.82	1.06	0.73
Leontopithecus chrysomelas	L.c.	Platyrrhine	1	578	3.10	1.46	2.08	0.63	2.05	0.29	0.09	0.90	0.09
Leontopithecus rosalia	L.r.	Platyrrhine	1	609	2.52	1.08	2.41	0.51	2.20	0.22	—	—	—
Saguinas bicolor	S.b.	Platyrrhine	1	429	2.50	1.38	1.74	0.39	2.42	0.15	—	—	—
Saguinas labiatus	S.l.	Platyrrhine	1	539	2.78	1.29	2.05	0.68	2.34	0.28	—	—	—
Saguinas oedipus	S.o.	Platyrrhine	1	404	0.82	1.08	0.72	0.11	3.07	0.03	0.03	1.10	0.02
Saguinus imperator	S.i.	Platyrrhine	1	475	2.34	1.26	1.79	0.56	3.09	0.17	0.05	0.48	0.10
Saguinus midas	S.m.	Platyrrhine	1	515	0.79	1.10	0.69	0.12	1.60	0.07	0.03	0.84	0.03
Saimiri sciureus	S.s.	Platyrrhine	2	724	3.51	1.48	2.25	1.11	3.46	0.31	0.09	1.37	0.08
Sapajus apella	S.a.	Platyrrhine	2	3085	10.00	1.94	5.01	2.90	3.91	0.76	0.08	1.55	0.05
Cercocebus atys	C.at.	Catarrhine	1	8600	73.21	3.11	23.02	20.58	9.15	2.13	1.59	2.25	0.67

(continued)

Table 1 (continued)

Species	Initials	Taxonomic group	n	Body mass (g)	Digital flexors			Brachioradialis			Extensor indicis		
					Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)	Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)	Muscle mass (g)	Avg fiber length (cm)	PCSA (cm²)
Cercocebus torquatus	C.t.	Catarrhine	1	6230	35.90	2.91	11.98	13.17	6.66	1.87	0.75	1.80	0.40
Cercopithecus campbelli	C.ca.	Catarrhine	1	2700	6.54	2.29	2.93	2.72	5.44	0.47	0.72	1.63	0.42
Cercopithecus cephus	C.ce.	Catarrhine	1	4290	27.18	2.79	9.50	12.90	7.04	1.73	0.29	1.85	0.15
Cercopithecus hamlyni	C.h.	Catarrhine	1	3360	7.81	2.11	3.54	2.06	3.42	0.57	0.38	1.90	0.19
Cercopithecus mona	C.m.	Catarrhine	1	4600	8.97	2.30	3.90	1.96	1.14	1.63	0.31	1.28	0.23
Cercopithecus neglectus	C.n.	Catarrhine	1	7350	43.43	2.85	15.21	13.66	7.17	1.80	5.13	2.04	2.38
Cercopithecus petaurista	Ce.p.	Catarrhine	1	2900	16.11	2.33	6.69	5.84	6.79	0.81	0.35	1.45	0.23
Chlorocebus aethiops	Ch.a.	Catarrhine	2	3620	23.23	1.93	12.16	6.79	6.56	0.99	0.47	1.63	0.27
Colocebus guereza	Co.g.	Catarrhine	1	9200	53.39	3.46	15.25	13.70	9.29	1.40	1.09	1.56	0.66
Gorilla	G.g.	Catarrhine	1	120 950	922.10	20.54	126.46	402.39	18.28	20.88	78.35	7.92	9.54
Hylobates lar	H.l.	Catarrhine	2	5620	25.79	3.31	7.60	2.50	4.44	0.54	0.89	1.75	0.48
Macaca sylvanus	M.sy.	Catarrhine	1	16 000	78.79	3.34	23.03	19.83	3.63	5.17	7.61	2.60	2.78
Mandrillus leucophaeus	M.l.	Catarrhine	1	20 000	215.10	2.81	73.75	–	–	–	3.30	2.45	1.27
Mandrillus sphinx	M.sp.	Catarrhine	1	12 900	65.62	3.30	19.40	12.50	3.08	3.84	–	–	–
Miopithecus talapoin	M.t.	Catarrhine	2	1380	7.41	2.46	2.99	2.67	4.85	0.52	0.43	1.49	0.28
Papio sp.	Pa.sp.	Catarrhine	1	17 333	83.12	3.98	20.11	36.25	13.50	2.54	3.44	3.68	0.88
Pongo sp.	Po.sp.	Catarrhine	1	78 200	557.11	6.73	85.12	302.71	10.99	26.08	12.24	6.89	1.68

The presence of an asterisk (*) indicates the species that were dissected for this study and added to the Leischner et al. (2018) dataset. For select individuals, muscle by muscle data were not available (indicated by a blank cell).
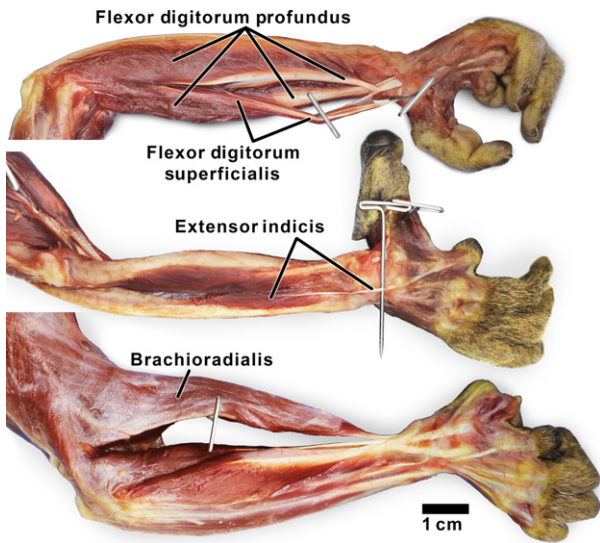
Fig. 1 Dissection photographs of *Perodicticus potto* specimen with muscles of interest labeled.

package IMAGEJ. A representative sample of ~ 40 fascicles was measured to determine fascicle lengths within each muscle. To assess the contractile profile of the digital flexors as a functional group, we additionally calculated a weighted fascicle length using the modified equation from Hartstone-Rose et al. (2012), where FL represents the average fascicle length for the digital flexors as a group and m represents the muscle mass of each respective digital flexor:

$$\text{Average FL} = \frac{(\text{FL}_1 m_1) + (\text{FL}_2 m_2) + \cdots (\text{FL}_{...} m_{...})}{m_1 + m_2 + \cdots m_{...}}.$$

The PCSA, defined in equation below as q) of each muscle was then calculated by dividing each muscle's mass (defined as m) by the product of its average fascicle length (defined as l), and a muscle density constant (defined as p) of 1.0564 g cm^{-3} (following Murphy & Beardsley, 1974). The resulting equation, modified from Schumacher (1961), is as follows:

$$q = \frac{m}{lp}.$$

Finally, to investigate the effect of pennation upon our calculated force variable, we further calculated Reduced PCSA (following Anapol & Jungers, 1986) – a 'reduction' of PCSA that removes the vector of force orthogonal to the fascicle's line of action – to establish the relationship between PCSA and RPCSA across our sample.

Data analysis

Reduced major axis regressions (RMA; conducted in the software package JMP PRO 13; SAS) were used to compare linearized architectural variables (i.e. area and volume variables reduced by the square and cube roots, respectively) relative to body size. Last living body weights for our dissected specimens were used where possible. When unavailable, body mass estimates were derived from published species averages. For one individual of *P. potto*, last living body mass was known; for the second specimen, we used the average body weight reported by Nekaris & Bearder (2007) of 1.03 kg.

Results

PCSA vs. RPCSA

PCSA and RPCSA were strongly correlated throughout our sample ($r^2 = 0.99$), indicating that variation in pennation angle within the forearm musculature is negligible across our primate sample (Fig. 2). Consequently, PCSA alone is used in all species comparisons.
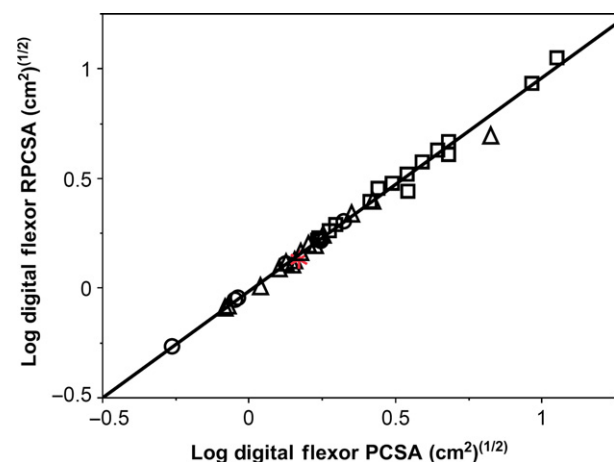
Digital flexor PCSA

Across our sample as a whole, digital flexor PCSA scaled with positive allometry [slope = 1.28, 95% confidence interval (CI) 1.16–1.42, $r^2 = 0.90$]. However, in contrast to Hypothesis 1, relative digital flexor PCSA within *P. potto* was approximately average, plotting slightly below the RMA regression line. Of the 46 species included within our comparative sample, *P. potto* falls within in the 39th percentile in terms of digital flexor residuals PCSA (Fig. 3).

Digital flexor fascicle length

Across our sample, digital flexor fascicle lengths scaled with positive allometry (slope = 1.18, 95% CI 1.02–1.38, $r^2 = 0.81$). In line with Hypothesis 2, *P. potto* possessed relatively short fascicles, with an average fascicle length that ranked close to the bottom quartile (26th percentile) among our comparative primate sample (Fig. 4).

Myology of extensor indicis

Across our sample, 80% of taxa had a true extensor indicis (i.e. a muscle that inserts exclusively on digit II). The pres-


Fig. 2 Correlation between physiological cross-sectional area (PCSA) and Reduced PCSA (RPCSA) of the digital flexors within a primate sample ($r^2 = 0.99$, slope = 0.97, 95% CI 0.94–1.003). All variables were logged and linearized. Asterisk = *P. potto*; squares = catarrhines; triangles = platyrrhines; circles = strepsirrhines. See Table 1 for species abbreviations.
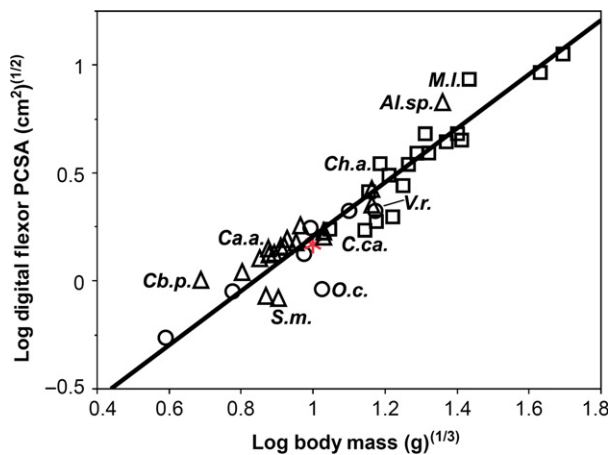
Fig. 3 Reduced major axis (RMA) regression of flexor PCSA and body mass within a primate sample (r^2 = 0.90; slope = 1.25; 95% CI 1.13–1.39). All variables were logged and linearized. See Table 1 for species abbreviations. See Fig. 2 for key.
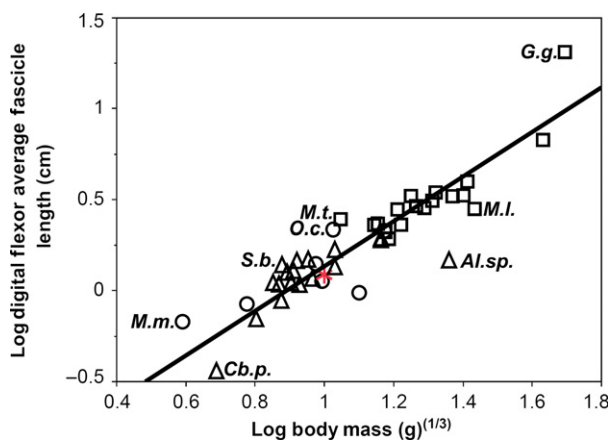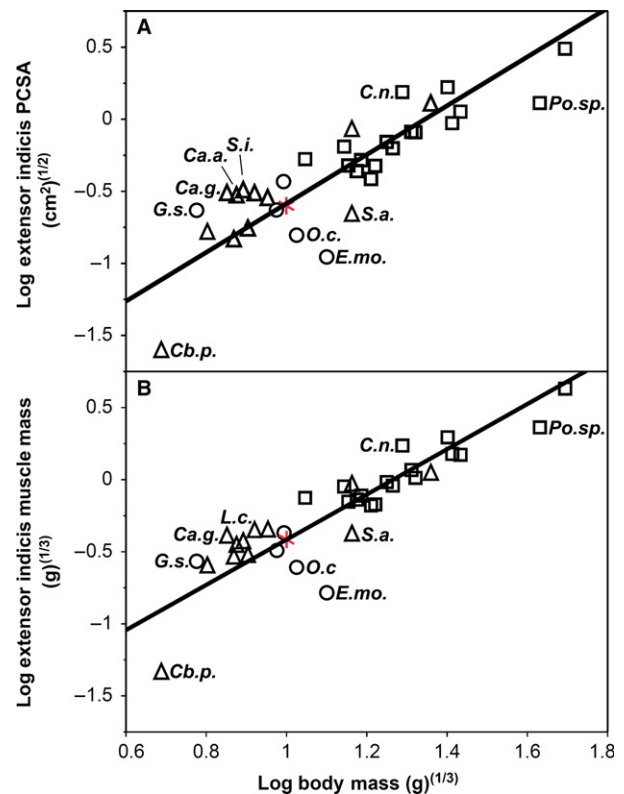

Fig. 4 Reduced major axis (RMA) regression of digital flexor average fiber length and body mass within a primate sample (r^2 = 0.82; slope = 1.23; 95% CI 1.06–1.42). All variables were logged and linearized. See Table 1 for species abbreviations.

Fig. 5 Reduced major axis (RMA) regression of (A) extensor indicis PCSA and body mass within a primate sample (r^2 = 0.72; slope = 1.69; 95% CI 1.35–2.12) and (B) extensor indicis muscle mass and body mass within a primate sample (r^2 = 0.79; slope = 1.57; 95% CI 1.31–1.88). All variables were logged and linearized. See Table 1 for species abbreviations.

ence of this muscle in *P. potto* was nonetheless surprising, given the vestigial nature of this digit (as can be clearly seen in Fig. 1). The architectural properties of extensor indicis also proved to be noteworthy: although this muscle was relatively small within *P. potto* (in terms of both muscle mass and PCSA), of the 80% of the specimens that had this muscle, the extensor indicis of *P. potto* was not among the smallest in either muscle mass or PCSA, falling in the 43rd and 46th percentiles, respectively (Fig. 5).

Myology of brachioradialis

Supporting qualitative observations of the increased size of the brachioradialis within *P. potto*, this taxon possessed the relatively largest brachioradialis among our entire sample,

in addition to the fourth greatest PCSA (behind *Microcebus murinus*, *Cebuella pygmaea* and *Callithrix aurita*; Fig. 6).

Discussion

Digital flexor PCSA

Due to the numerous reports of the supposedly remarkable grip strength of *P. potto* (Miller, 1943; Charles-Dominique, 1977; Oates, 1984; Feldhamer et al. 2007; Lemelin & Jungers, 2007), we hypothesized that *P. potto* would possess among the highest digital flexor PCSA within our primate sample. However, of the primate species (strepsirrhines, as well as the catarrhines and platyrrhines) included in our sample, *P. potto* proved to be relatively average, ranking in the 39th percentile. If the myology of the forearm is not responsible for the animal's strong grip, perhaps other anatomical features have contributed to the illusion of high grip strength. The reorganization of the pollex and reduction of the second digit (giving the hand a pincer-like appearance) have resulted in particular hand placement on substrates during locomotion (Bishop, 1962; Oates, 1984)
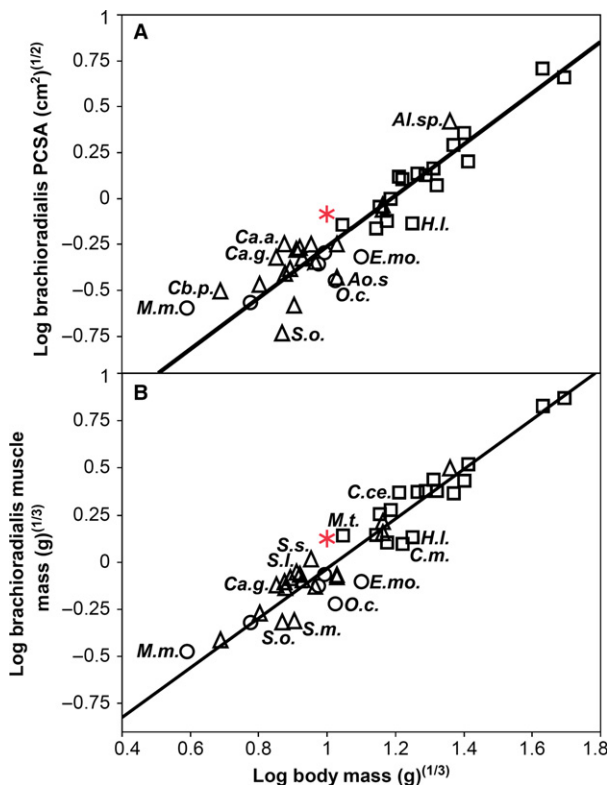
7 **Fig. 6** Reduced major axis (RMA) regression of (A) brachioradialis PCSA and body mass within a primate sample (r^2 = 0.86; slope = 1.39; 95% CI 1.23–1.58) and (B) brachioradialis muscle mass and body mass within a primate sample (r^2 = 0.91; slope = 1.32; 95% CI 1.19–1.46). All variables were logged and linearized. See Table 1 for species abbreviations.

and the distinct grip that results from these anatomical reorganizations could be perceived as a strong, vice-grip. Additionally, the presence of the retia mirabilia in the wrist, which may give *P. potto* the ability to maintain a single grip for an extended period of time, could have resulted in the perception of an exceptionally strong grip. Nonetheless, our findings raise questions about the validity of the previous reports of this taxon's gripping capabilities.

Similarly, several other taxa for which a high digital flexor PCSA might be assumed, displayed relatively low values. Both *Hylobates* and *Pongo* plotted below our regression line, despite habitual use of below-branch suspensory locomotion (Gibbons & Lockwood, 1982; Thorpe & Crompton, 2005; Vereecke et al. 2006), in which the digits grip substrates that support an individual's full body mass. Similarly, *Nycticebus coucang* displayed below-average digital flexor PCSA, despite lorises practicing a slow, deliberate locomotor repertoire which emphasizes a firm and stable grip (Forster, 1934; Jouffroy, 1962; Oates, 1984). Meanwhile, the highest relative digital flexor PCSA was observed in *Mandrillus sphinx*, a terrestrial quadruped. These data support claims by Leischner et al. (2018) that forearm architecture does

not closely reflect locomotor mode. Rather, as they found, this architecture may more related to substrate use – an analysis beyond the scope of this paper.

Digital flexor fascicle length

We had hypothesized that the notoriously slow locomotor speed of *P. potto* (Jouffroy, 1962; Charles-Dominique, 1977) would be reflected by relatively short average fascicle lengths, which, despite reducing contractile velocity, would serve to maximize PCSA without the need for additional, metabolically expensive muscle mass. In line with this prediction, we observed *P. potto* to possess relatively short fascicles across the digital flexor musculature (Fig. 4). Beyond this taxon, however, there appeared to be a limited correlation between fascicle lengths and locomotor speed/agility, as both the highly agile *Hylobates lar* and notoriously slow *Nycticebus coucang* fall towards the middle of our sample. This suggests that, despite the short fascicle lengths found within *P. potto*, forearm muscle fascicle length does not strongly reflect locomotor speed – supporting previous findings by Leischner et al. (2018).

It is possible, however, that locomotor speed differences are reflected more strongly in the fiber type profile of these muscles, as opposed to their architectural properties. A similar investigation into myosin heavy chain distribution within the supraspinatus of pronograde and orthograde primates yielded interesting results, with pronograde taxa demonstrating a preponderance of slow-type fibers with high fatigue resistance, whereas orthograde taxa possessed a profile better adapted for speed and strength (Potau et al. 2011). These data suggest that locomotor mode may be at least partially reflected in the fiber type profile of forelimb muscles, a phenomenon which future studies may wish to further explore within the forearm musculature.

Myology of extensor indicis

Despite the vestigial nature of the second digit in *P. potto*, this taxon possesses a dedicated extensor indicis muscle (Fig. 1), unlike 20% of both our strepsirrhine and broader primate sample, in which this muscle is absent. The presence of this muscle implies the faculty for independent control of this digit within *P. potto*. Moreover, 13 taxa within our comparative sample possessed a relatively smaller extensor indicis than *P. potto* – suggesting that *P. potto* possesses elevated relative strength within this digit compared with several primate species with unreduced second digits. Across our entire comparative sample, there was no clear phylogenetic signal associated with the presence of extensor indicis – 33% of platyrrhines, 20% of strepsirrhines and 6% of catarrhines were lacking a dedicated extensor indicis altogether. These taxa all presented an otherwise normal morphology of the second digit. This finding, as well as the presence of such a muscle in a taxon that lacks a functional

second digit, suggests that the presence of extensor indicis does not necessarily reflect functionality. It should also be considered that this muscle may be variably present across a species (similar to the palmaris longus in humans, which is absent bilaterally in 9% of individuals and unilaterally in 16%; Thompson et al. 2001). The extent of intraspecific variation within the primate forearm, therefore, requires additional consideration.

Myology of brachioradialis

Our analysis of the relative size of brachioradialis revealed *P. potto* to possess the largest such muscle across our entire sample (Fig. 1). This finding supports previous qualitative observations on the expanded size of this muscle within *P. potto* (Nayak, 1933; Miller, 1943; Jouffroy, 1962; Boettcher et al. in press).

There is no discernible phylogenetic signal in the brachioradialis masses; indeed, the entire relative size range for catarrhines is encompassed within the single genus *Cercopithecus*. Similarly, neither *P. potto* nor the taxa with a similarly enlarged brachioradialis – e.g. *Cercopithecus cephus, Miopithecus talapoin, Saimiri sciureus* – employ strongly specialized locomotor repertoires. It is possible that the increased size of brachioradialis in *P. potto* might reflect an increased reliance on small degrees of elbow flexion during slow-moving, above-branch locomotion; in a previous study, Chang et al. (1999) found that each elbow flexor (i.e. biceps brachii, brachialis and brachioradialis) has an optimum muscle length and stress, with brachialis and biceps brachii dominant during more extreme angles of flexion (∼ 100–110°), whereas the brachioradialis is most effective during minor angles of flexion (∼ 50°). Habitual use of such postures may render the brachioradialis the dominant elbow flexor within this taxon. Alternatively, the expanded size of this muscle may compensate for the diminished size of other elbow flexors (e.g. biceps brachii or brachialis). As data were not collected on these muscles, further data are needed to evaluate this hypothesis better.

Conclusion

Digital flexor PCSA in *P. potto*, when compared with other similarly sized strepsirrhines and other members of the primate order, were found to be ultimately unremarkable. Despite previous reports, the digital flexor muscles in *P. potto* were not among the strongest in our sample, but rather were below average in terms of both mass and PCSA. *In vivo* measures of grip strength are needed to explore this conundrum further and to better understand how variation in muscle size and architecture within this species is linked to gripping performance.

Other distinct myological features found in *P. potto* were quantified in this study, including the surprising relative size of brachioradialis and extensor indicis. The brachioradialis

of *P. potto* was, relative to the animal's body size, the largest of all taxa analyzed. Furthermore, the extensor indicis (a muscle whose presence was unexpected due to the severe reduction of the second digit in *P. potto*) was not the smallest such muscle; 13 primate species had a smaller extensor indicis relative to body size and almost a quarter of all taxa lacked the muscle altogether.

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