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RESEARCH ARTICLE

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A primate with a Panda's thumb: The anatomy of the pseudothumb of *Daubentonia madagascariensis*

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Abstract

Objectives: Accessory digits have evolved independently within several mammalian lineages. Most notable among these is the pseudothumb of the giant panda, which has long been considered one of the most extraordinary examples of contingent evolution. To date, no primate has been documented to possess such an adaptation. Here, we investigate the presence of this structure within the aye-aye (*Daubentonia madagascariensis*), a species renowned for several other specialized morphological adaptations in the hand, including a morphologically unique third digit.

Materials and Methods: We combine physical dissection techniques with digital imaging processes across a sample of seven individuals (six adults and one immature individual) to describe and visualize the anatomy of the wrist and hand within the aye-aye.

Results: A distinct pseudothumb, which consists of both a bony component (an expanded radial sesamoid) and a dense cartilaginous extension (the "prepollex") was observed in all specimens. We demonstrate that this pseudodigit receives muscular attachments from three muscles, which collectively have the potential to enable abduction, adduction, and opposition. Finally, we demonstrate that the pseudothumb possesses its own distinct pad within the palm, complete with independent dermatoglyphs.

Discussion: Pseudothumbs have been suggested to improve palmar dexterity in taxa with overly -generalized first digits (e.g., pandas) and to widen the hand for digging (e.g., some fossorial moles), but the aye-aye's pseudothumb represents what we believe is a heretofore unrecognized third functional role: its accessory digit compensates for overspecialization of its fingers for non-gripping functions (in this case, the aye-aye's unique "tap foraging" practices).

KEYWORDS
anatomy, digital dissection, evolution, functional morphology, prepollex

1 | INTRODUCTION

Daubentonia madagascariensis (the aye-aye) is the only extant member within the family Daubentoniidae (Martin, 1990). Native to Madagascar, this highly derived lemur presents a unique mosaic of anatomical features in both the cranium and postcranium that distinguish it from its closest living relatives (Oxnard, 1981), resulting in two centuries of debate regarding its phylogenetic position (Elliot, 1913; Owen, 1866; Shaw, 1800; Simpson, 1945). These features include hypselodont (evergrowing) incisors that are morphologically similar to sciuriform rodents

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(Morris, Cobb, & Cox, 2018) and enlarged, bat-like ears that contain a complex geometry of internal ridges specialized for three-dimensional echolocation (Ramsier & Dominy, 2012)—an ability unique among primates. Most notable, however, are the unusual adaptations associated with the aye-aye's hand, including a highly specialized third digit which is increased in length and slenderness and possesses a ball-and-socket metacarpophalangeal joint (Soligo, 2005). These adaptations, which closely resemble the morphological characteristics of the striped possum *Dactylopsila trivirgata* (Cartmill, 1974; Rawlins & Handasyde, 2002), reflect the specialized dietary strategy of percussive "tap" foraging practiced by this species. This food acquisition method involves tapping of the third digit against wood to generate acoustic reverberations that enable the animal to locate the wood-boring larvae, which are then fished out with exceptional dexterity (Erickson, 1991; Erickson, 1994; Sterling, 1994). Collectively, these anatomical specializations render the aye-aye a true anatomical anomaly among the Primate order.

The presence of a bony ossicle in the radial portion of the wrist—commonly referred to as the radial sesamoid—has been described across many mammalian orders, particularly among pentadactyl groups (Forster, 1932; Le Minor, 1994; Lessertisseur & Saban, 1967). Though this bone is nearly ubiquitous among primates (though rarely found in humans), it remains small and relatively immobile in members of the order (Le Minor, 1994). Among other taxa, however, this structure is more prominently developed: an expanded radial sesamoid increases hand surface area in talpid moles, enlarging their digging apparatus (Mitgutsch et al., 2011), and functions as a pincer-like mechanism in the wrist of the cotton rat (*Sigmodon* spp.) to improve food item manipulation and to allow them to better grasp small branches (Abella et al., 2016). Accessory digits have also been identified in the fore limb and hind limb of elephants, with both limbs featuring five anterior-facing rays supplemented by enlarged, posteriorly -oriented sesamoid bones that provide stabilization during changes in foot posture (Hutchinson et al., 2011). Most notably, in the giant panda (*Ailuropoda melanoleuca*), expansion of the radial sesamoid into a "pseudothumb" structure allows a degree of digital manipulation (Davis, 1964; Endo et al., 1996; Endo et al. 1999; Endo et al. 1999; Pocock, 1939). This example has long fascinated anatomists and has been highlighted as one of the clearest and most extraordinary examples of contingent evolution (Gould, 1978; Gould, 1980).

As in other terrestrial arctoids, the first manual digit of *A. melanoleuca* does not function as a thumb but rather sits in line with the other digits, essentially serving as a fifth undifferentiated finger (Davis, 1964; Gould, 1978). However, the ability to grasp and manipulate objects within the palm is integral to the feeding mechanics of the panda, in which bamboo stems and other plant material are grasped between the radial sesamoid and the opposing palm (Davis, 1964; Wood-Jones, 1939a; Wood-Jones, 1939b). Thus, in place of an opposable thumb, the radial sesamoid of *A. melanoleuca* (and to a lesser extent, *Ailurus fulgens*; Roberts & Gittleman, 1984) functions as a pseudometacarpal, performing an abductive–adductive movement alongside the hand's remaining digits to enable palmar manipulation of objects held within the hand (Davis, 1964; Wood-Jones, 1939a; Wood-Jones, 1939b). To enable this dexterity, this "pseudothumb"—a functional unit composed of the radial sesamoid and a cartilaginous extension referred to as the prepollex—is directly associated with several intrinsic and extrinsic muscles of the hand: *M. abductor pollicis brevis*, *M. opponens pollicis*, and a portion of the tendon of the *M. abductor pollicis longus* (Endo et al., 1996). Additionally, a membranous muscle (termed *M. aponeurosis palmaris*) extends from the palmar aponeurosis to the radial sesamoid in a longitudinal direction (Endo et al., 1996). Collectively, these muscles enable the radial sesamoid and cartilaginous prepollex to function as a pseudodigit, providing the panda with a specialized pincer-like grip seemingly adapted for the manipulation of bamboo stems.

In this study, we describe the anatomy of a similar "pseudothumb" structure within the hand of the aye-aye. Previously undocumented, this structure serves as yet another anatomical specialization unique to the aye-aye among primates. In addition to anatomical descriptions, we provide photographic evidence of these associated structures in situ, alongside digital reconstructions of the bony, cartilaginous, and muscular components of the aye-aye's pseudothumb. Finally, we propose a broader framework to describe the evolutionary circumstances through which a pseudothumb may be seen to emerge across various mammalian lineages and interpret the functional role of this structure within the aye-aye in the context of this framework.

2 | MATERIALS AND METHODS

2.1 | Sample

Our sample consisted of six adult and one immature aye-aye specimens (Table 1): three captive-raised specimens acquired from the Duke Lemur Center (two adults, one immature specimen at 1.5 years of age), three wild-born adult individuals housed in the collections of the Muséum National d'Histoire Naturelle, Paris, and one wild-born adult female from Tsimbazaza Botanical and Zoological Park, Anatananarivo, Madagascar (Perry, MacNeill, Heckler, Rakotoarisoa, & Hartstone-Rose, 2014). No animals were sacrificed for the purposes of this study. Dissections were performed on six specimens (bilaterally, where possible) to analyze the anatomy of the hand and wrist. The seventh specimen (MNHN 1924-184, Paris) was used to create a digital reconstruction of these anatomical structures following MRI scanning and manual segmentation. MRI was deemed the most suitable visualization technique for these purposes, as several structures were highly tendinous or cartilaginous.

2.2 | Dissection protocol

Our samples (Table 1) included both frozen and formalin fixed specimens. Frozen specimens were thawed at room temperature and dissected without fixation; formalin fixed specimens were first fixed using a 10% formalin solution and subsequently transferred into 70% ethanol prior to dissection. In order to maximize our ability to describe and quantify the structures associated with the pseudothumb, and to ensure the bilateral presence of key structures, the hand and forearm compartment of each side of our specimens were dissected where possible. For graphic comprehensibility, all dissection figures are derived from a single adult male specimen (DLC 6905), and all images of the left hand were digitally reversed to maintain visual consistency relative to the digitally scanned specimen (MNHN 1924-184). During

TABLE 1 *Daubentonia madagascariensis* specimens dissected or observed in the course of this study and notes on the configuration of the pseudothumb

Specimen ID	Age	Source	Preservation	Dissection: Unilateral vs. Bilateral	Notes
MNHN 1924-184	Adult	MNHN, Paris	Formalin fixed	Digital, unilateral	Used in digital reconstruction
DLC6905	Adult	Duke Lemur Center	Frozen one side, Formalin fixed one side	Bilateral	Used in dissection photos in this manuscript
DLC2602	Adult	Duke Lemur Center	Formalin fixed	Unilateral	Comparative specimens; all structures relating to the pseudothumb (radial sesamoid, prepollex, and muscular reorganization) were observed
MNHN 1924-183	Adult	MNHN, Paris	Formalin fixed	Bilateral	
MNHN 1910-21	Adult	MNHN, Paris	Formalin fixed	Bilateral	
WILD	Adult	Tsimbazaza Park, Antananarivo	Fresh (wild specimen)	Bilateral	
DLC6262	Immature (1.5 years)	Duke Lemur Center	Frozen	Unilateral	

dissection, the skin and overlying fascial tissue were first removed to provide a visual overview of the structures of the upper limb and hand. Individual muscles were then photographed, excised, and weighed to the nearest 0.00001 g.

2.3 | Digital reconstruction protocol

MRI acquisitions on the specimen from the MNHN collections (MNHN 1924-184) were performed with a Bruker Biospec System (Bruker, Germany), at the Institut du Cerveau et de la Moelle épinière, Paris, France, at a resolution of 0.25 × 0.25 ×0.25 mm. The resultant MRI scans were then manually segmented using Avizo 8.0 (Visualization Sciences Group, 2013) and Amira 6.5 (Thermo Fisher Scientific, 2018). In each slice, all bony structures associated with the wrist and hand were first isolated. Individual muscles and tendons (alongside the palmar aponeurosis and flexor retinaculum) were then labeled and added to the model. All structures associated with the pseudothumb and thenar eminence were segmented; additionally, several reference muscles (including the *M. extensor pollicis longus*, *M. flexor carpi radialis*, *M. abductor digiti minimi*, and *M. flexor digiti minimi brevis*) were also included within the reconstruction (Figure 1). Once segmentation was complete, a lightly smoothed (unconstrained smoothing, intensity = 3) three-dimensional volume representing the composite model was generated within Amira (ThermoFisher Scientific). This model was used to generate snapshots presented in Figures 1–3, and the video presented in Supplementary file S2.

3 | RESULTS

The body of the aye-aye's pseudothumb consists of two components: the bony radial sesamoid (Figures 1–3, red), and a dense cartilaginous extension hereafter referred to as the prepollex (sensu Endo et al., 1996; Figures 1–3, pink). The proximal surface of the radial sesamoid articulates with the scaphoid, while its distal surface gives rise to the prepollex, which extends distally and curves slightly toward the body of the first metacarpal. These structures share a trio of muscular attachments, which mirror those reported for the pseudothumb of *A. melanoleuca* (Table 2; Figures 1–3; Supplementary Video S1). The bifurcating tendon of *M. abductor pollicis longus* (most clearly seen in Figure 3C, purple), which extends down the posterior surface of the forearm, sends one insertion to the dorsal surface of the radial sesamoid, which comprises ~30% of the total cross-section of the tendinous tissue. The remaining ~70% of this tendon inserts into the base of the first metacarpal bone.

Second, the muscle equivalent to *M. opponens pollicis* (Figures 1–3, yellow) appears to have been co-opted within the aye-aye to function as an adductor of the prepollex and, to a lesser extent, an abductor of the first metacarpal; attaching proximally to the tip and mediodistal aspect of the cartilaginous prepollex and distally to the shaft of the first metacarpal just proximal to its distal head. Thus, if the pseudothumb is stabilized, the co-opted *M. opponens pollicis* is likely used more substantially to adduct the prepollex and is therefore more appropriately termed (and hereafter called) *M. adductor prepollicis* on the grounds of its presumed function. Due to its configuration, this muscle may also provide some weak abduction of the thumb—though this would be much less forceful than the abductive forces provided by the *M. abductor pollicis longus*.

Finally, a small muscular body coupled with a thin musculo-aponeurotic sheet (Figures 1–3, dark green and light green, respectively) extends from within the prepollucial pad and the medial surfaces of both the radial sesamoid and the cartilaginous prepollex to the aponeurosis of the palm and lateral border of the tendon of *M. palmaris longus*. This muscle appears to match the description of *M. aponeurosis palmaris* (sensu Endo et al., 1996) within the giant

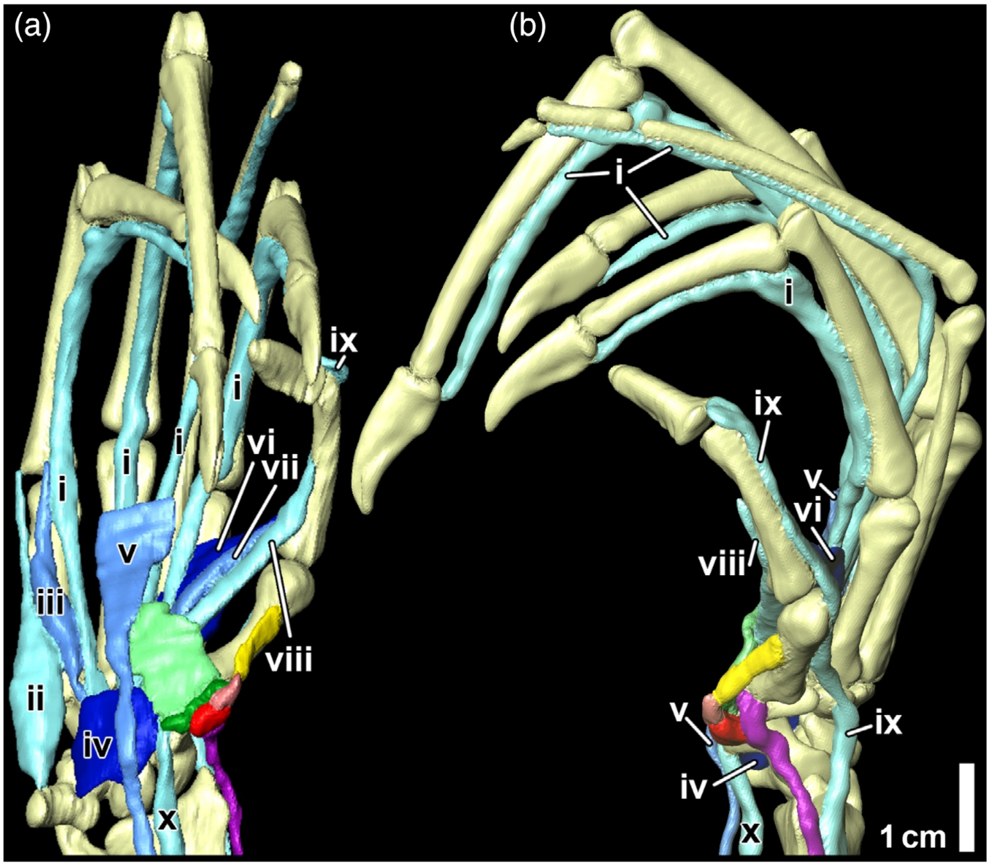

FIGURE 1 Volume rendering of an MRI of the right hand of *D. madagascariensis* (MNHN 1924-184) musculoskeletal structures [(a) palmar view; (b) lateral view). See Table 2 for explanation pseudothumb muscle abbreviations and homologies. Red = radial sesamoid; pink = cartilaginous prepollex; yellow = *M. abductor prepollicis*; dark green = *M. palmaris radialis*; light green = aponeurosis of *M. palmaris radialis*; purple = *M. adductor pollicis longus*. Structures not associated with the pseudothumb are in shades of blue and numbered (i = tendons of *M. flexor digitorum profundus* and *superficialis*; ii = *M. abductor digiti minimi*; iii = *M. flexor digiti minimi brevis*; iv = *flexor retinaculum*; v = palmar aponeurosis and tendon of *M. palmaris longus*; vi = *M. adductor pollicis*; vii = *M. flexor pollicis brevis*; viii = *M. abductor pollicis brevis*; ix = tendon of *M. extensor pollicis longus*; x = tendon of *M. flexor carpi radialis*)

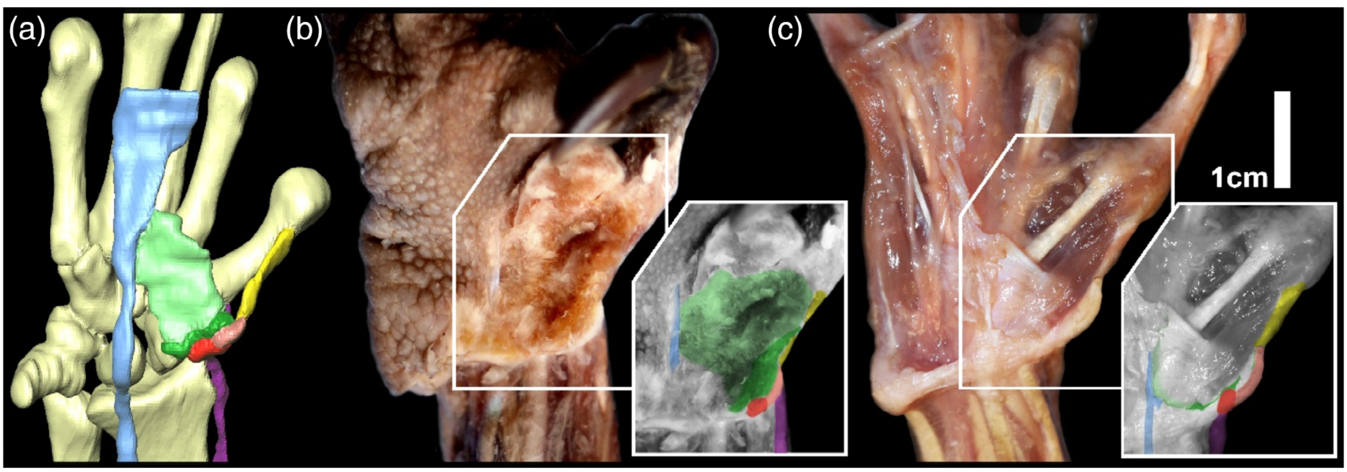

FIGURE 2 Palmar (anterior) view of pseudothumb structures in (a) volume rendering of an MRI of the right hand of *D. madagascariensis*, (b) superficial and (c) deep dissections (lateral is to the right). Blue = tendon of palmaris longus. All other structures are color-coded the same as in Figure 1 (note: only origination area of *M. palmaris radialis* is shown in deep dissection c)

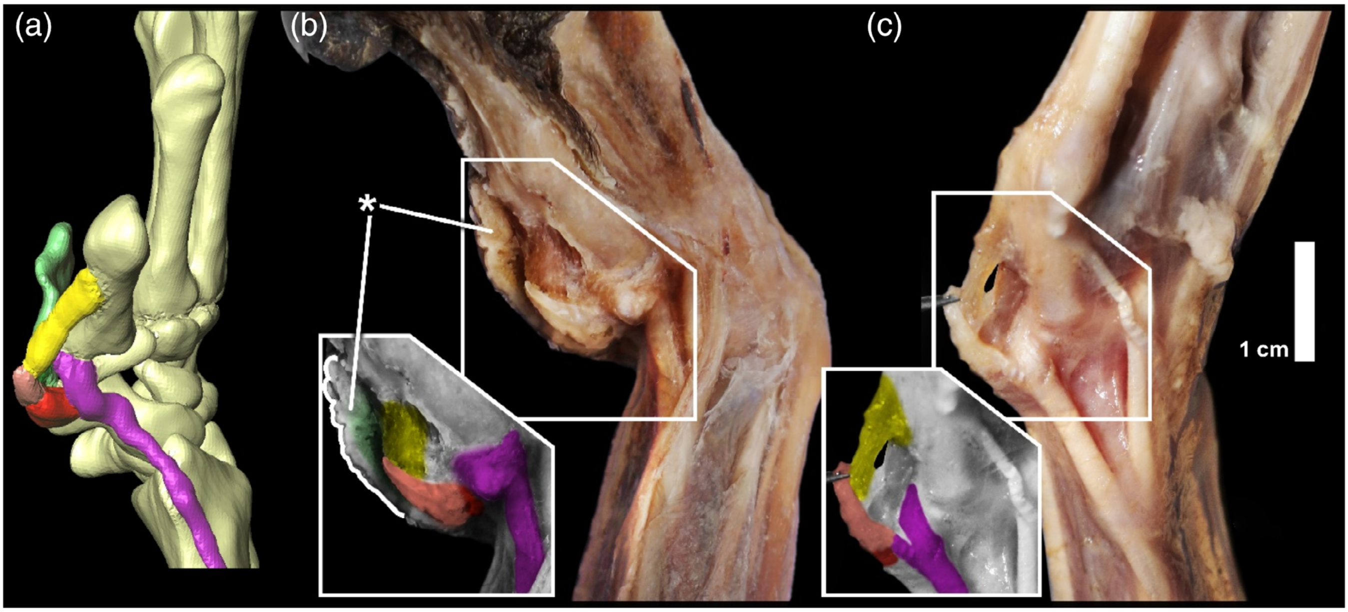

FIGURE 3 Lateral view of pseudothumb structures in (a) volume rendering of an MRI of the right hand of *D. madagascariensis*, (b) superficial and (c) deep dissections (palmar is to the left). Asterisk = a sagittal section view of the pseudothumb pad. All else the same as in Figure 2

TABLE 2 Muscles associated with the pseudothumb of *D. madagascariensis*

Muscle homologous to:	Function in *D. madagascariensis*	Additional comments
M. abductor pollicis longus	Primary tendon (70%) has the capacity to abduct the pollex; secondary tendon (30%) has the capacity to abduct the prepollex	Suggested name based on function in aye-aye: *M. abductor pollicis longus/ prepollicis*
M. aponeurosis palmaris (*sensu* Endo et al., 1996)	Major function is interpreted to enable opposition of the prepollex; may also facilitate minor adduction of the prepollex	Suggested name based on function in aye-aye: *M. palmaris radialis*
M. opponens pollicis	Interpreted to enable adduction of the prepollex; may also facilitate minor abduction of the pollex	Suggested name based on function in aye-aye: *M. adductor prepollicis*

panda but, as it is a muscle and not merely an aponeurosis, it is more appropriately referred to as (and hereafter called) *M. palmaris radialis*, distinguishing this muscle both from the palmar aponeurosis and the palmar muscle of the medial side of the hand (*M. palmaris brevis*). In terms of mass, *M. abductor pollicis longus* and *M. palmaris radialis* (0.692 and 0.133 g, respectively) are significantly larger than *M. adductor prepollicis* (0.102 g). However, as described above, only approximately 30% of the tendon of *M. abductor pollicis longus* associates with the pseudothumb, while the mass of *M. palmaris radialis* also contains some degree of integrated connective tissue.

All aye-aye specimens observed during the course of this study displayed the full suite of anatomical structures described above (i.e., bony, cartilaginous, and muscular features of the pseudothumb)—demonstrating that this anatomy is conservative across the species. To provide a comparative sample, this anatomy was directly compared to dissections of the hand and wrist in two additional strepsirrhine taxa (*Lemur catta* and *Varecia rubra*). A visual comparison of these specimens against the aye-aye is presented in Figure 4. In each case, both specimens presented no expansion of the radial sesamoid, or the presence of any projecting cartilage from this bone. Moreover, both *M. opponens pollicis* and *M. abductor pollicis longus* remain associated with only the first ray, while the former muscle is situated medial to the first digit in both *L. catta* and *V. rubra*, as opposed to lateral to this digit in *D. madagascariensis*. In addition to these two lemurid comparative specimens, we have dissected several other primate taxa (e.g., see Leischner et al., 2018, Boettcher, Leonard, Dickinson, Herrel, & Hartstone-Rose, 2019), and have never seen another primate taxon with a cartilaginous prepollex or this muscle configuration. Consequently, no evidence for the presence of this digital adaptation can be observed within comparative taxa.

4 | DISCUSSION

4.1 | Functional implications of the aye-aye pseudothumb

Collectively, the muscles associated with the aye-aye pseudothumb are anatomically positioned to enable abduction, adduction, and opposition of this digit relative to the palm. This mobility and functional diversity may reflect the extremely derived and specialized nature of the aye-aye's hand. Indeed, within *D. madagascariensis*, the hand accounts for about 41% of the total length of the forelimb, a higher proportion than any other primate (Soligo, 2005). This extension is chiefly a result of the extreme elongation of the phalanges: especially those of the fourth digit, which account for 71% of the total length of the hand (Jouffroy, Godinot, & Nakano, 1993). The most extreme specialization within the aye-aye hand, however, lies in the third digit, which is both extremely slender (Figure 1) and mobile, possessing a ball-and-socket joint at the metacarpophalangeal junction and a mechanism for folding the third digit over the fourth during locomotion (Soligo, 2005). This digit also appears to possess a uniquely dynamic vascular supply, resulting in significant changes in surface temperature during flexion of this joint (Moritz & Dominy, 2012). Functionally, this digit is principally used as a foraging tool for the extraction of xylophagous larvae, but is additionally used for drinking liquids (such as egg yolks), extracting pulp from soft fruits, and as an all-purpose probe (especially by younger animals) to explore their environment (Lamberton, 1911; Petter & Peyrieras, 1970). However, we speculate that, from a functional perspective, the specialization of the third and fourth digit in the aye-aye may come at a significant cost to fine manipulative control, and the ability of the aye-aye to grip smaller arboreal substrates, due to the diminished leverage of these fingers during flexion. The presence of a pseudothumb, however, may enhance the ability of the aye-aye to enclose smaller items within a palmar grip, and improve their stability on such substrates.

Beyond the pseudothumb itself, aye-ayes also present additional adaptations within the hand toward enhancing their palmar grip. Six prominent pads were identified across the palm of the hand, all of which feature raised dermatoglyphic ridges (Figure 5). The first pad is associated with the prepollex, and lies toward the radial side of the palm immediately distal and palmar to the cartilaginous structure of the prepollex. The second pad is associated with the first metacarpal and sits superficial to *M. adductor pollicis*, halfway between the heads of the first and second metacarpals. The other four pads lie above the distal heads of the second, fourth, and fifth metacarpals, and the ulnar sesamoid (pisiform), respectively. While this structure seems to mirror the pseudothumb—a dermatoglyphic pad overlying a sesamoid on the lateral side of the wrist—unlike the pseudothumb, it does not have dedicated muscular control, and therefore the relatively immobile structure does not confer any grasping abilities. All pads contain quantities of muscle fibers (not shown here): pads associated with the second, third, and fourth metacarpals contain small quantities of muscle fibers arranged in thin, cylindrical bundles, while pads associated with the prepollex, first metacarpal, and fifth metacarpal contain larger

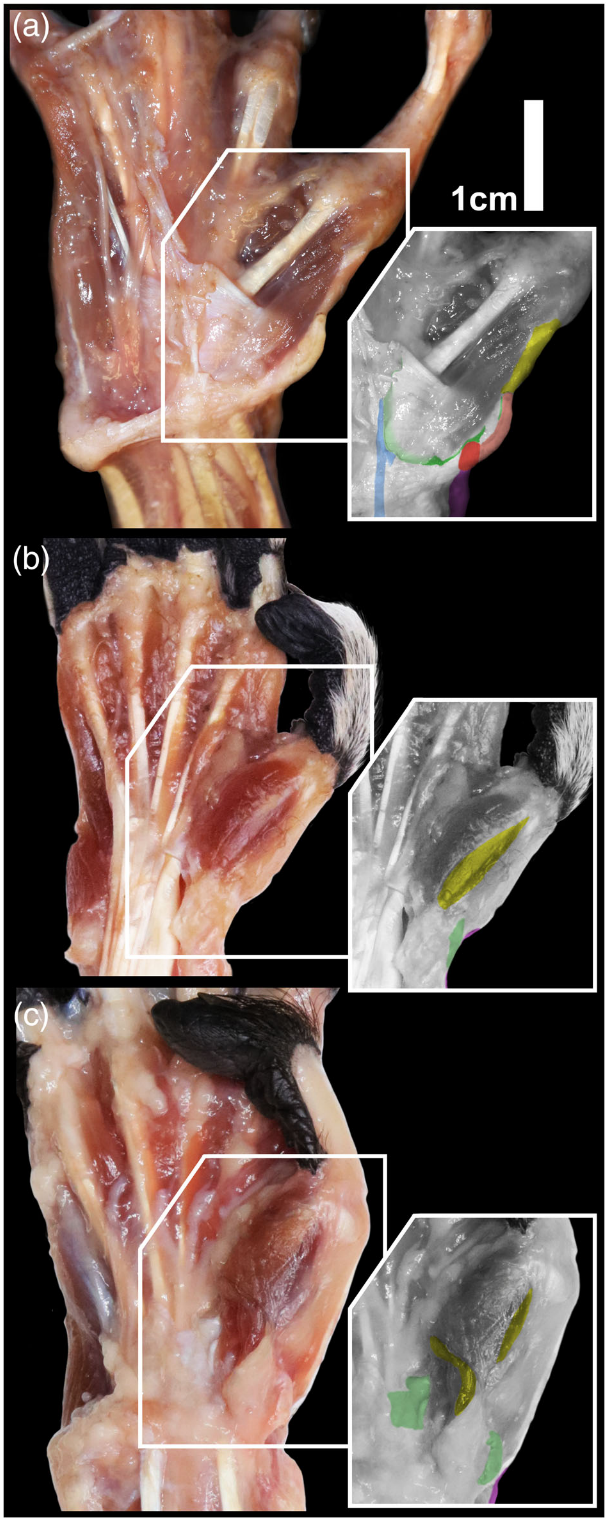

FIGURE 4 Palmar view of the hand and wrist in (a) *D. madagascariensis* (DLC 6905), (b) *Lemur catta* (UVA 8051), and (c) *Varecia rubra* (UVA 8026). As in Figures 1–3, the bony and cartilaginous portions of the pseudothumb are highlighted in red and pink, respectively; these structures are present only in *D. madagascariensis*. The *M. opponens pollicis* (yellow) is also laterally reconfigured in *D. madagascariensis* to associate with the cartilaginous prepollex, while this muscle sits medial to the first digit as part of the thenar eminence of both *L. catta* and *V. rubra* (note: in [c], this muscle has been cut but both proximal and distal attachments are highlighted). As in Figures 1–3, remnants of the palmar aponeurosis (and the muscular sheet attaching the pseudothumb to this aponeurosis in *D. madagascariensis*) are highlighted in green and the tendon of *M. abductor pollicis longus* is highlighted in purple

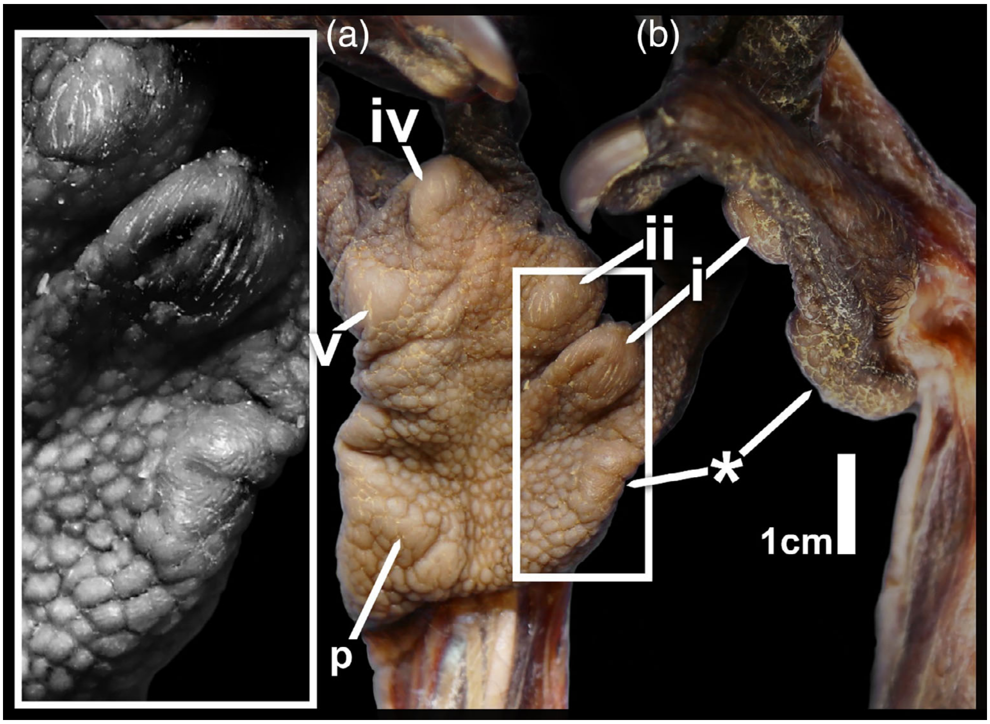

FIGURE 5 Pads of the palm of the hand of *D. madagascariensis* (DLC 6905); (a) palmar view (thumb is to the right); (b) lateral view (palm is to the left). *Pseudothumb pad; i–v = pad overlying the distal heads of the first, second, fourth, and fifth metacarpals, respectively; p = pad overlying the pisiform. Note that, unlike the other metacarpal pads, the first metacarpal pad (i) sits medial and distal to the head of its metacarpal—perhaps to be more evenly spaced between the pseudothumb (*) and second metacarpal (ii) pads. Inset is digitally contrast enhanced to show dermatoglyphs of the pseudothumb, MCI and MCII pads

fibrous structures with a more heterogeneous organization. The ability to maximize palmar dexterity and grip capacity therefore appears to be responsible for several of the unique adaptations associated with the aye-aye hand.

4.2 | The evolution of accessory digits

Accessory digits within the hand have evolved independently across several vertebrate lineages, seemingly for a myriad of different purposes (Abella et al., 2015; Abella et al., 2016; Endo et al., 1996; Endo et al. 1999; Endo, Sasaki, Kogiku, Yamamoto, & Arishima, 2001; Endo, Yamagiwa, et al., 1999; Fabrezi, 2001; Fontanarrosa & Abdala, 2016; Mitgutsch et al., 2011; Otero & Hoyos, 2013; Salesa, Antón, Peigné, & Morales, 2006; Whidden, 2000). Despite this phylogenetic diversity, we propose that these instances of convergence can be classified into one of three evolutionary scenarios—three modes by which a pseudothumb may be adapted or exapted (sensu Gould & Vrba, 1982).

First, a pseudothumb may appear in species in which the thumb has become undifferentiated—essentially just another non-opposable finger. In the case of bears and other carnivores, who lost the need for a differentiated thumb, the migration of the first ray into the non-opposable digital row results in a significant loss of overall manual dexterity. Within ursids—such as the giant panda—for which dexterity is important, the pseudothumb fulfills this function by allowing the dexterous opposition of materials (in this instance, bamboo shoots) against the palm (Davis, 1964; Wood-Jones, 1939a; Wood-Jones, 1939b). In other words, the panda lineage reacquired the functional capacity for manipulating bamboo through the development of a pseudothumb.

Within elephant feet, meanwhile, morphologically undifferentiated, anterior-facing rays are supplemented by enlarged, posteriorly oriented sesamoid bones co-opted into false digits to provide additional support and stabilization during changes in foot posture (Hutchinson et al., 2011). While the elephant's first podal ray could have re-diverged to support the posterior aspect of the pad, functional stability was achieved instead by the presence of additional osteological structures (Hutchinson et al., 2011). Thus, overgeneralization of the often divergent first rays of the hands or feet (i.e., turning them into undifferentiated digits indistinct from the other rays) may therefore directly contribute toward the development of a sixth pseudodigit when additional functionality is reacquired but not accompanied by re-divergence of the first ray.

Second, pseudodigits may emerge in taxa for which maximizing the surface area of the hand is strongly linked to enhancing palmar function. Within talpid moles, the expansion of the radial sesamoid into a functional pseudothumb—which receives tendinous insertions from both *M. abductor pollicis longus* and *M. palmaris longus* and which is capable of independent movement like a true digit (Whidden, 2000)—enhances the surface area of their manual digging apparatus, increasing the efficiency of this obligate behavior. This sesamoid bone may also function, in addition to a podal structure derived from a pronounced tibial sesamoid, to brace the hands and feet during digging (Mitgutsch et al., 2011). Several genera of ichthyosaurs, including *Stenopterygius*, similarly display supernumerary digits as a means of expanding the surface area of their propulsive flippers (Caldwell, 1997). These taxa also demonstrate severe hyperphalangy, with as many as 11 phalanges associated with a single ray (Caldwell, 2002). Despite their vast phylogenetic separation, both moles and ichthyosaurs therefore appear to have evolved accessory digits for a similar purpose.

A third and final scenario in which a pseudodigit may be acquired reflects an inverse case, in some ways, of our first example: for taxa in which the hand has become hyperspecialized and in which the evolution of a pseudothumb may facilitate greater manual dexterity. This scenario would appear to explain the presence of a pseudothumb within the aye-aye. As such, we suggest that the adaptations of the aye-aye hand reported here—which include an expansion of the radial sesamoid, an elongated cartilaginous prepollex, co-option of several thenar muscles, and a series of complex palmar pads which themselves include small intrinsic muscle fibers—have evolved to directly compensate for the loss of grip dexterity associated with the hyperspecialization of the aye-aye's digits. Other mammalian taxa that possess a similarly derived manual morphology—such as the striped possum *Dactylopsila trivirgata*, whose digital configuration closely mirrors that of the aye-aye (Cartmill, 1974; Rawlins & Handasyde, 2002)—may possess similar structures associated with the enhancement of palmar dexterity. Similarly, other examples of highly derived manual morphologies—such as those found within bats—might be associated with similar structures; indeed, during terrestrial locomotion, it would appear that the common vampire bat (*Desmodus rotundus*) relies heavily on bony expansions within the wrist for traction when attempting to approach unsuspecting prey without detection. Additional exploration of the hand and wrist within such specialized groups may reveal new insights into the anatomical diversity of this region across the mammalian order.

5 | CONCLUSIONS

The extreme derivation of the aye-aye hand is singular among primates, as a result of its unusual feeding strategy. This extreme degree of anatomical specialization may explain the presence the aye-aye's pseudothumb, as a means of maintaining palmar dexterity and grip capacity. The presence of this structure in *D. madagascariensis* is yet further evidence of the specialized, mosaic-like *Bauplan* of this species, which demonstrates several anatomical traits convergent on those seen in distantly related taxa. Understanding the integration between these structures, particularly during development, may provide further insights into an already fascinating species. Similarly, a detailed exploration of the hand and wrist within other hypo- and hyper-specialized taxa may provide additional insights into the development and evolutionary history of the pseudothumb.

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AUTHOR CONTRIBUTIONS

Conceptualization: A.H.-R.; Data curation: E.D., M.L.B, A.H.-R.; Formal analysis: E.D., M.L.B., A.H.-R.; Funding acquisition: A.H.-R.; Investigation: A.H.-R., E.D., M.L.B., A.H.; Methodology: A.H.-R., E.D., M.L.B., A.H.; Project administration: A.H.R.; Resources: A.H.-R., A.H.; Software: A.H.-R., A.H.; Supervision: A.H.-R., A.H.; Validation: A.H.-R.; Visualization: E.D., A.H.-R.; Writing-original draft: E.D., A.H.-R.; Writing-review and editing: A.H.-R., E.D., M.L.B., A.H.

DATA AVAILABILITY STATEMENT

All digital renderings are available on morphosource. Please contact the authors for other dissection photographs and notes.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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