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Getting a grip on tetrapod grasping: form, function, and evolution

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ABSTRACT

Human beings have been credited with unparalleled capabilities for digital prehension grasping. However, grasping behaviour is widespread among tetrapods. The propensity to grasp, and the anatomical characteristics that underlie it, appear in all of the major groups of tetrapods with the possible exception of terrestrial turtles. Although some features are synapomorphic to the tetrapod clade, such as well-defined digits and digital musculature, other features, such as opposable digits and tendon configurations, appear to have evolved independently in many lineages. Here we examine the incidence, functional morphology, and evolution of grasping across four major tetrapod clades. Our review suggests that the ability to grasp with the manus and pes is considerably more widespread, and ecologically and evolutionarily important, than previously thought. The morphological bases and ecological factors that govern grasping abilities may differ among tetrapods, yet the selective forces shaping them are likely similar. We suggest that further investigation into grasping form and function within and among these clades may expose a greater role for grasping ability in the evolutionary success of many tetrapod lineages.

Key words: grasping, grip force, biomechanics, tetrapods, lizards, amphibians, mammals, birds, digits, dexterity, manus, pes, feeding, locomotion, morphology.

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I. INTRODUCTION

The ability to grasp an object with an appendage is an action that is often taken for granted on a day-to-day basis, but is fundamentally important from an evolutionary standpoint. In its simplest form, this functionality has paved the way for the advanced levels of fine motor control and precision gripping to which many groups of vertebrates owe their evolutionary success. Nevertheless, outside of the human biomechanics, kinesiology, and medical literature, grasping behaviour has received relatively little attention compared with other aspects of animal behaviour, despite its prevalence in the behavioural repertoires (i.e. locomotion, feeding, and reproduction) of many vertebrates, and its implications for fitness. Perhaps the greatest advancements in our understanding of the ecological and evolutionary implications of grasping capability in the past 40 years or so have emanated from physical anthropology (e.g. Susman, 1998; Marzke & Marzke, 2000). These studies have demonstrated how structural variations of the hominid hand throughout evolutionary history have resulted in unparalleled enhancements of prehensile capabilities, ranging from power to precision grips that have facilitated the construction and use of tools and the evolution of human society as we know it today (Napier, 1956; Marzke, Wullstein & Viegas, 1992; Marzke, 1997; Susman, 1998; Kivell *et al.*, 2011). Prehensile behaviour is defined as the application of functionally effective forces by an appendage to an object for a task. Such a behaviour can be accomplished by the limbs, the tail, the trunk, the tongue, the teeth, or other animal parts (Mackenzie & Iberall, 1994). When focusing on hands and feet, prehension involves the orientating and positioning of the fingers or toes with the appropriate displacement of the limb to the correct location in space (Mackenzie & Iberall, 1994). Prehensile behaviour involving hands and feet has been defined according to the degree of precision of the digit movements needed for grasping and holding an object. The words grip and grasp are used interchangeably in the literature although the grip suggests a static posture, whereas grasping is a dynamic unfolding of a posture (Malek, 1981). Napier (1956) differentiated power *versus* precision requirements and in so doing gave anatomical definitions that involve the matching of the finger position with respect to the palm of the hand or foot. In the power grasp the emphasis is on stability and security, and the primary grasp attribute is defined as the ability to resist slipping. In the precision grasp the emphasis is on the dexterity and sensibility, i.e. how accurately fingers can sense small changes in force and position. Differences between power and precision grasping were expanded upon by specialists in robotics (Cutkosky & Wright, 1986; Cutkosky, 1989; Cutkosky & Howe, 1990) giving a classification of nine subordinate types of power grasp and seven subordinate types of precision grasp. Although the aforementioned definitions are based on human hands and grasping behaviour, they can be applied to other groups of tetrapods.

Outside of mammals, other groups of tetrapods, such as frogs and lizards, have also evolved significant forelimb prehensile capabilities (e.g. Manzano, Abdala & Herrel, 2008; Abdala *et al.*, 2009). Iwaniuk & Whishaw (2000) suggested that ‘rudimentary skilled forelimb movements’ (which include grasping and manipulating with the digits) likely originated at the base of the tetrapod clade. They suggested, therefore, that these types of movements are homologous in frogs and mammals, and that various losses in these abilities across taxa occurred independently. More recently, Abdala & Diogo (2010) examined the tetrapod forelimb musculature that ultimately underlies these movements and demonstrated a large number of homologies across clades. Most relevant to this review are the six ‘muscular complexes’ of the hand and forearm (ulnar extensors/flexors, radial extensors/flexors, and extensor/flexor digitorum communis/longus). Thus, grasping behaviour would appear to be phylogenetically conserved in tetrapods, perhaps even more so than the pentadactylous digit pattern that underlies it (Kardong, 2011). Although these hypotheses remain to be tested explicitly, the data to do so are currently lacking. Digital dexterity has evolved in the manus in most groups of tetrapods, from tree frogs to classical piano players, but some groups (e.g. tree frogs, arboreal mammals, and birds) have evolved comparable levels of prehensile capabilities in the pes.

The origins of manual grasping ability are often thought to be derived from the selective pressures associated with digging and/or arboreal locomotion (e.g. Grillner & Wallen, 1985; Bracha, Zhuravin & Bures, 1990). However, Iwaniuk & Whishaw (2000) suggested that prey-handling behaviour, even in basal amphibian lineages, might have been an important driving force for the evolution of manual grasping. The origins of pedal grasping are less clear, in part because they have received considerably less attention, but both arboreal support/locomotion (e.g. Gebo, 1985; Feduccia, 1999; Youlatos, 2008) and feeding (e.g. Fowler *et al.*, 2011) have been implicated in the evolution of pedal grasping across taxa. Here we explore the anatomical and functional specializations that underlie manual and pedal grasping ability among major tetrapod taxa. This paper was inspired by a symposium entitled, 'Grasping in tetrapods: origins, variation, and evolution,' during the Ninth International Congress of Vertebrate Morphology in Punta del Este, Uruguay (2010). The objective was to bring together morphologists working independently on aspects of grasping form and function across disparate vertebrate taxa, and to gain insights into the phenotypic variation and selective forces shaping the evolution of grasping ability across major groups of tetrapods. We feature many of the topics covered by participants of the symposium and provide an overview of this emerging field. In so doing, our goal was to highlight the contributions to our understanding of grasping functional morphology and behaviour emanating from recent work on a diversity of tetrapod groups, primarily from an evolutionary perspective. We present grasping form, function, ecology, and evolution in the context of each of the major tetrapod clades: Lissamphibia, Lepidosauria, Aves, and Mammalia. In recognition of the paradigmatic importance of performance for linking morphology with fitness (Arnold, 1983) and ecology (Wainwright, 1996), we pay particular attention to recent approaches incorporating *in vivo* measurements of grasping performance (i.e. force and precision). Because 'grasping' has been qualified and quantified in a variety of ways across disciplines, we define grasping performance as the capacity to manipulate objects or adhere to substrata through voluntary movements of the manual and/or pedal digits by exerting force. Our over-arching objective is to elucidate both the functional and ecological consequences of variation in musculoskeletal morphology and behavioural patterns of grasping among major tetrapod groups.

II. GRASPING IN LISSAMPHIBIANS

Most studies on frog functional morphology focus on their locomotion and unique saltatory mode of life (e.g. Gans & Parsons, 1966; Lutz & Rome, 1994; Shubin & Jenkins, 1995). Forelimbs are historically considered to be conserved among frogs and are thought to support the body during standing or walking, being *de facto* decoupled from a role in generating power for propulsion. However, the forelimbs are thought also to play an important role in absorbing the impact forces during landing (Nauwelaerts & Aerts, 2006; but see Essner *et al*., 2010). In many arboreal frogs the forelimbs show a surprising dexterity of movement (e.g. *Phyllomedusa bicolor*; Gray, O'Reilly & Nishikawa, 1997; Manzano *et al*., 2008). The anatomy of the forelimb in many arboreal species appears specialized. The forelimbs are relatively long, and intercalary skeletal elements (additional structures between the penultimate and ultimate phalanx in the digits of many anuran amphibians) and adhesive sub-digital pads are often present on the hands and feet (Manzano, Fabrezi & Vences, 2007). In some genera, such as *Phyllomedusa*, *Chiromantis*, and *Pseudis*, opposable digits are present. These characteristics have been related to arboreality or, more specifically, to locomotion on thin branches in complex three-dimensional habitats.

Most frogs that can grasp with their hands also develop similar capabilities with their feet. However, studies on the feet of frogs are scarce and have focused mainly on toe pad anatomy and their sticking abilities (Hanna & Barnes, 1991), as well as the integrated modular system formed by intercalary elements and digital extensor muscles in relation to arboreal locomotion (Manzano *et al*., 2007). Arboreal walking is achieved by using both hands and feet to grasp the branch. The feet can also develop movements other than grasping during locomotion. The most complex limb movements occur during the 'wiping behaviour' observed in frogs with opposable digits such as *Polypedates maculatus* and species of *Phyllomedusa* (Lillywhite *et al*., 1997; Barbeau & Lillywhite, 2005). During wiping, frogs spread lipid substances all over their body using their hands and feet (Blaylock, Ruibal & Platt-Aloia, 1976). Other arboreal frogs use their hands and feet to build leaf nests in which they deposit their eggs (Kenny, 1966; Biju, 2009). These frogs also belong to arboreal groups with opposable digits (Rhacophoridae, Hyperolidae, and Phyllomedusinae hylids). However, frogs with skilled wrist movements that use their hands to reach for prey and move it into or out of the mouth (Gray *et al*., 1997), incidentally do not appear to use their feet to move prey into or out of the mouth. Also the aquatic *Pseudis*, a hylid frog genus with opposable digits on the manus, has fully webbed feet, and limited toe movements.

(1) Anatomical correlates of anuran grasping

Intercalary elements have been considered a modular part of the limbs that evolved independently, but have been integrated in the developmental program of the forelimb (Manzano *et al*., 2007). Distal phalanges, intercalary elements, muscles, and adhesive sub-digital pads act as integrated units for enhancing the ability to climb (Noble, 1931; Emerson & Diehl, 1980; McAllister & Channing, 1983; Paukstis & Brown, 1987, 1991; Burton, 1996, 1998*a*, *b*). Nevertheless, the presence of intercalary elements or well-developed sub-digital pads is not always associated with arboreality (Manzano *et al*., 2007). The presence of opposable digits is thought to reflect specialization for arboreality, as in *Phyllomedusa*, *Chiromantis*, and some mantellids. Yet, opposable digits are also present in the aquatic hylid frogs of the genus *Pseudis* that have secondarily returned to an aquatic habitat. The presence of an opposable digit is strongly associated with grasping ability during locomotion. However, grasping ability varies across taxa (Fig. 1), such that some narrow-branch specialists demonstrate the greatest skilled forelimb and hand movements (*sensu* Iwaniuk & Whishaw, 2000).

In general, frogs with opposable digits seem to have finer motor control of hand and finger movements. The ability to execute these complex movements has been interpreted as an exaptation of the specialization of the forelimbs for arboreal locomotion (Gray *et al*., 1997). Arboreal frogs moving across narrow substrata not only move their arms independently from one another (in contrast to simultaneous

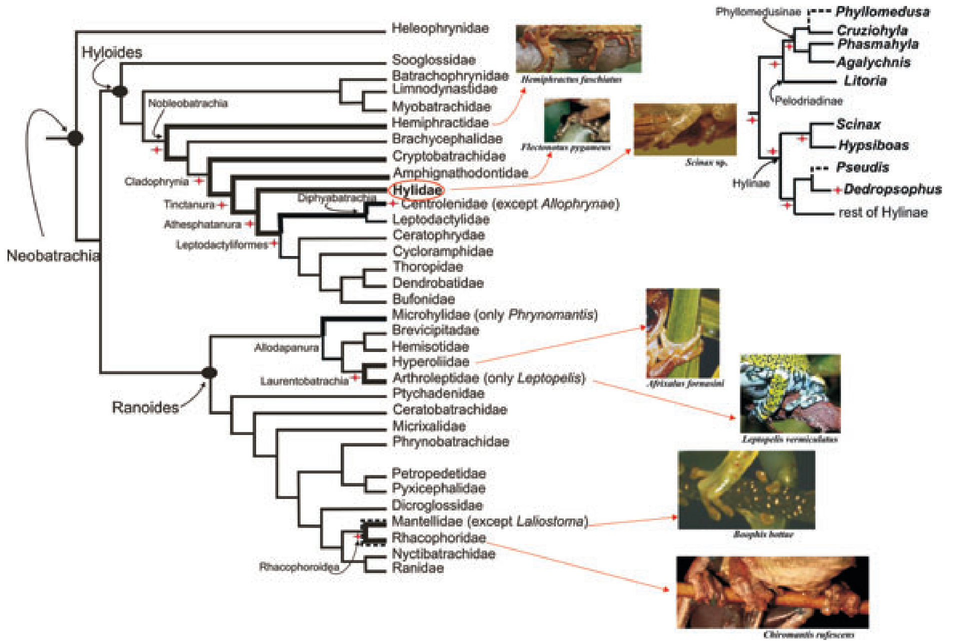

Fig. 1. Neobatrachian relationships, cladogram, and associated images reconstructed based on Frost *et al*. (2006) and Manzano *et al*. (2007). Thick lines (▬) indicate that branches were reconstructed as having intercalary elements. Stars (✦) symbolize the appearance of grasping and the arboreal mode of locomotion. Dashed lines (.........) indicate the presence of opposable digits. Photos of *A. fornasini* and *C. rufescens* modified from Wikimedia Commons; photos of *B. bottae*, *H. faschiatus* and *L. vermiculatus* courtsey of F. Andreone, M. Mirabello, and M. Menegon, respectively, *F. pygmaeus* obtained from Visual Photo LLC, and *Scinax* sp. by A. Manzano.

bilateral movements during landing or hopping), but also close the hand (i.e. execute a power grip *sensu* Napier, 1956) to generate a balancing torque while walking on branches narrower than their body. Frogs of the genus *Phyllomedusa* are mechanically capable of executing what is called a 'precision grip' [adduction of the thumb towards the digits such that the palmar surfaces of the thumb and digit touch each other (Napier, 1956)], known only from primates and characteristic of human manipulative skills (Landsmeer, 1962; Marzke *et al*., 1992; Manzano *et al*., 2008; Herrel *et al*., 2008*a*). In species of this genus, the forearm muscles are highly differentiated and appear to control each digit individually (Herrel *et al*., 2008*a*). Although the hand musculature of these frogs superficially resembles that of other tree frogs (a palmar aponeurosis being absent), there are some peculiarities that characterize this genus. These include: (*i*) a general elongation and increase in the size of the muscles, affecting speed and force of contraction, respectively, (*ii*) the presence of strong and long tendons (e.g. m. extensor brevis or m. adductor indicis longus), reflecting reduced compliance for greater control of more distal elements with increased tendon stress, and (*iii*) the presence of elongated and naked bony areas (i.e. not covered by muscle; Manzano & Lavilla, 1995) that likely do not have any specific functional role. The independence of the main flexor tendons (resulting in the ability of each digit to flex independently), and the presence of muscles with accessory branches (resulting in additional insertion sites; Manzano & Lavilla, 1995) are some of the features unique to *Phyllomedusa* that may be related to their increased dexterity (Manzano *et al*., 2008). For instance, there is a close anatomical and functional relationship between the m. palmaris profundus and the m. flexor digitorum communis longus as shown by stimulation experiments. Superficial tendons (main flexor tendons) originate from the branches of the m. flexor digitorum communis longus and are joined by a fascia that arises from the m. palmaris profundus. In the genus *Phyllomedusa* the m. palmaris profundus inserts directly onto the superficial tendon of the m. flexor digitorum communis longus, and upon contraction pulls it laterally 2–3 mm (Herrel *et al*., 2008*a*). This effectively increases the latter's moment arm, and actively assists in hand and wrist flexion that ultimately allows complete closure of the hand around a narrow substratum (Fig. 2D-F; Manzano *et al*., 2008).

(2) Functional implications and grasping performance

In vivo measurements of grasping force and the results of muscle stimulation experiments suggest that arboreal frogs actively adjust the position of the hands during locomotion and include a grasping type of support (Manzano *et al*., 2008). *Phyllomedusa bicolor* is capable of generating greater forces than the more generalized *Litoria caerulea*, which might improve its stability and allow it to move more securely on narrow substrata (Fig. 2G, H). *Phyllomedusa bicolor* is also able to generate large forces through the abduction of digits II, IV, and V. Interestingly, the combined stimulation of the mm. flexor indicis superficialis proprius II and lumbricalis IV in *Phyllomedusa bicolor* produced a pronounced adduction

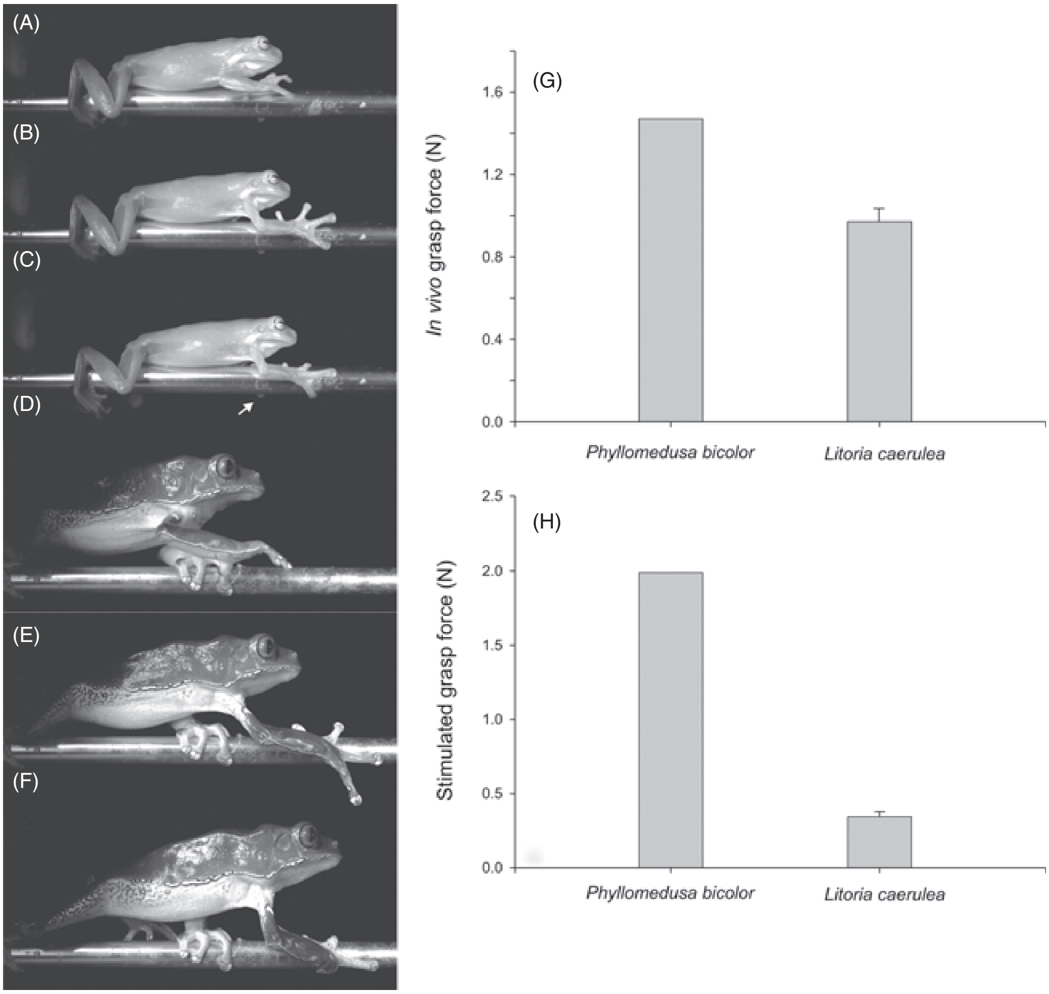

Fig. 2. Selected images from Manzano *et al*.'*s* (2008) high-speed recordings (100 frames/s) of walking on a narrow substratum in *Litoria caerulea* (A–C) and *Phyllomedusa bicolor* (D–F). Note the flexion of the hand and adduction of digit 2 during the swing phase (A, D) and extension and abduction of the digits just before substratum contact (B, E) in both species. During substratum contact, however, *P. bicolor* closes its fingers more completely and actively flexes the distal phalanx of each digit. *Littoria caerulea*, by contrast, cannot fully flex the distal phalanx (white arrow) when grasping a narrow substratum. (G) *In vivo* grasping forces and (H) maximal grasping forces obtained by electrical stimulation of muscles of *P. bicolor* and *L. caerulea* from Manzano *et al*. (2008). In both cases, *P. bicolor* generated relatively greater grasping forces, owing in part to their anatomical peculiarities (e.g. increased digital muscle size and individuated tendons) that provide them with greater digital dexterity and precision-grip capability. Bars represent mean ± S.D. ($N = 3$) of maximal forces recorded. Figure reprinted from Manzano *et al*. (2008) by permission of John Wiley & Sons, Inc.

of digits II and IV causing the extremes of the phalanges to touch each other, thus generating the precision grip observed in several primates. Hand movements in humans and other primates involve complex neuronal patterns and functions in areas of the fore- and hindbrain. Neuroanatomical variations among tree frogs show a trend towards increased cerebellum size (Taylor, Nol & Boire, 1995) that may be related to their increased manual dexterity, although this has yet to be tested explicitly in a phylogenetic framework. Given the complexity of forelimb movements observed in frogs and the fact that these evolved several times independently, frogs are an ideal system to understand better the ecological and behavioural contexts associated with the evolution of increased manual dexterity and grasping behaviour.

III. GRASPING IN LEPIDOSAURS

Studies of limb function in lizards have centred mostly on quadrupedal locomotion and running performance (e.g. Losos, 1990; Irschick & Garland, 2001), and to a lesser extent on clinging and climbing (e.g. Zani, 2000; Zaaf & Van Damme, 2001; Tulli *et al*., 2009; Tulli, Abdala & Cruz, 2011). Collectively, these studies underscore the ecological and functional diversity that lizards encounter in nature, and the selective forces operating on the evolution of limb morphology. Grasping in lizards appears to be driven largely by selection for navigating complex three-dimensional habitats, and plays less of a role in behaviours such as feeding or mating described for other tetrapods.

The best definition of the grip most commonly observed in lizards is that corresponding to a power grip as defined by Landsmeer (1962): objects are held in a clamp formed by the partly flexed fingers and the palm, with counter pressure applied by the thumb lying more or less in the plane of the palm. In the power grip the combined fingers form one jaw of the clamp with the palm as the other jaw. There is a general consensus that chameleons (perhaps the most specialized arboreal group of lizards) are the best graspers among lizards (Herrel *et al*., 2011). Data on chameleons show that in some species such as *Chamaeleo vulgaris*, the carpus has the central and distal bones fused forming one spherical bone (Renous-Lécuru, 1973). However, in other congeneric species no fusion is apparent (Herrel *et al*., 2012), and the role of the observed fusion in grasping remains unclear. Although it is often thought that these are the only lizards exhibiting any grasping ability, below we highlight three other lizard lineages that are capable of performing a power grip *sensu* Landsmeer (1962): geckos, *Polychrus*, and anolines, which have been examined much less extensively in this regard.

(1) The arthrology of lizard grasping

According to some studies (e.g. Abdala *et al*., 2009) a suite of anatomical traits in the hand of lizards can be linked to grasping ability. These particularities are more notable in relation to the tendinous and osseous aspects of the lizard hand, with the muscular design of the hand being rather conservative (Russell & Bauer, 2008; Abdala & Diogo, 2010; Diogo & Abdala, 2010). The tendinous pattern of the palm of the hand plays a key role in allowing the flexion of the metacarpo-phalangeal joints. This flexion is a main component of the power grip *sensu* Landsmeer (1962), which allows the hand to close around a perch or branch. Interestingly, the most widely distributed tendinous pattern among lizards is one that does not allow extensive metacarpo-phalangeal flexion. This pattern, known as the L-pattern (Moro & Abdala, 2004; Abdala *et al*., 2009), consists of a single tendinous plate that connects the biggest forearm muscle (m. flexor digitorum longus) with the digits through the digital flexor tendons (Fig. 3A–D). Embedded in this 'flexor plate' (Haines, 1950) are one or two palmar sesamoids. The connection between the forearm muscle and the digits through a single tendinous structure prevents the independent movement of the digits, which move together as a single unit. By contrast, in the 'P-pattern' (Moro & Abdala, 2004; Abdala *et al*., 2009), the flexor plate is reduced or absent, and the m. flexor digitorum longus connects to the digits through independent digital flexor tendons (Fig. 3E–G). Palmar sesamoids also tend to be reduced or absent. This P-pattern is recognizable in most anolines and other lizards such as *Polychrus*. A third pattern, the G-pattern, occurs in most geckos (Abdala *et al*., 2009). In this G-pattern the connection between the forearm muscle and the digits is through a flexor plate without embedded sesamoids (Fig. 3I, J).

Some experimental work showed that these different patterns correlate with hand movement capabilities and grasping performance (Abdala *et al*., 2009). Lizards exhibiting the L-pattern are not capable of flexing the metacarpo-phalangeal joint of the hand, which precludes execution of a power grip (Fig. 3M). Grasping abilities are thus restricted to lizards having P- and G-patterns, which appear to facilitate the flexion of the metacarpo-phalangeal joints (Fig. 3N). In the L-pattern a palmar sesamoid appears to obstruct tendon travel, thereby resulting in incomplete flexion of the digital joints. In humans, under certain circumstances proximal and distal interphalangeal (PIP and DIP, respectively) joint flexion precedes metacarpo-phalangeal (MCP) joint flexion, and substantially larger m. flexor digitorum profundus forces are required to effect similar flexion angles in the MCP as in the PIP and DIP (Nimbarte, Kaz & Li, 2008). However, Kamper, Hornby & Rymer (2002) demonstrated that contraction of the extrinsic flexor muscles (those that originate on the forearm and insert on the digits) resulted in simultaneous flexion of all the digital joints, but substantially less at the MCP. These results suggest that a greater tendon excursion is required for complete flexion of the digital joints, particularly the MCP joint, which the palmar sesamoid likely precludes in lizards possessing the L-pattern tendon configuration. Most data indicate that the intrinsic hand muscles (those that originate and insert within the manus) do not exhibit particular innovations related to the ability to move the hand in lizards. On the contrary, what seems to be of greater importance is the complexity and the distal insertion of the forearm muscles in those tetrapods having particularly skilled hand movements (Herrel *et al*., 2008*b*; Russell & Bauer, 2008; Abdala & Diogo, 2010; Diogo & Abdala, 2010).

Like tendon structure, the configuration of the wrist and hand bones also appears to correlate with grasping ability. In non-grasping lizards, the central carpal row typically consists of the central bone, embraced by the radiale and ulnare (Fig. 3C). This configuration provides restricted mobility, as the close contact between the proximal portions of the radiale and ulnare restricts wrist movement. The palmar sesamoid(s) also restrict digital flexion. These structures underlie most of the wrist bones and lock the articulation between the first distal carpal and metacarpal I, and between the second distal carpal and metacarpal II (Fig. 3B, C). Thus, the proximal hand essentially becomes a rigid structure, with the only possibilities of motion being flexion and extension of the distal-most phalanges (e.g. Fig. 3D). In those lizards capable of grasping (e.g. anolines and species of *Polychrus*), the centrale has shifted from the central row to the proximal one. Thus, it has penetrated the proximal row as a pivot between the radiale and ulnare (Fig. 3G), and has become more slender and elongated, whereas in most other lizards it is truncated and sub-spherical. Additionally, the first metacarpal has its proximal head located in a space bounded on one side by the lateral face of the radiale, proximally by the highly reduced distal carpal I, and on its lateral side by the distomesial side of the centrale. In the hand of most lizards, there is no differentiation into thenar and hypothenar regions. The shape and position of the centrale, and the reduction of the

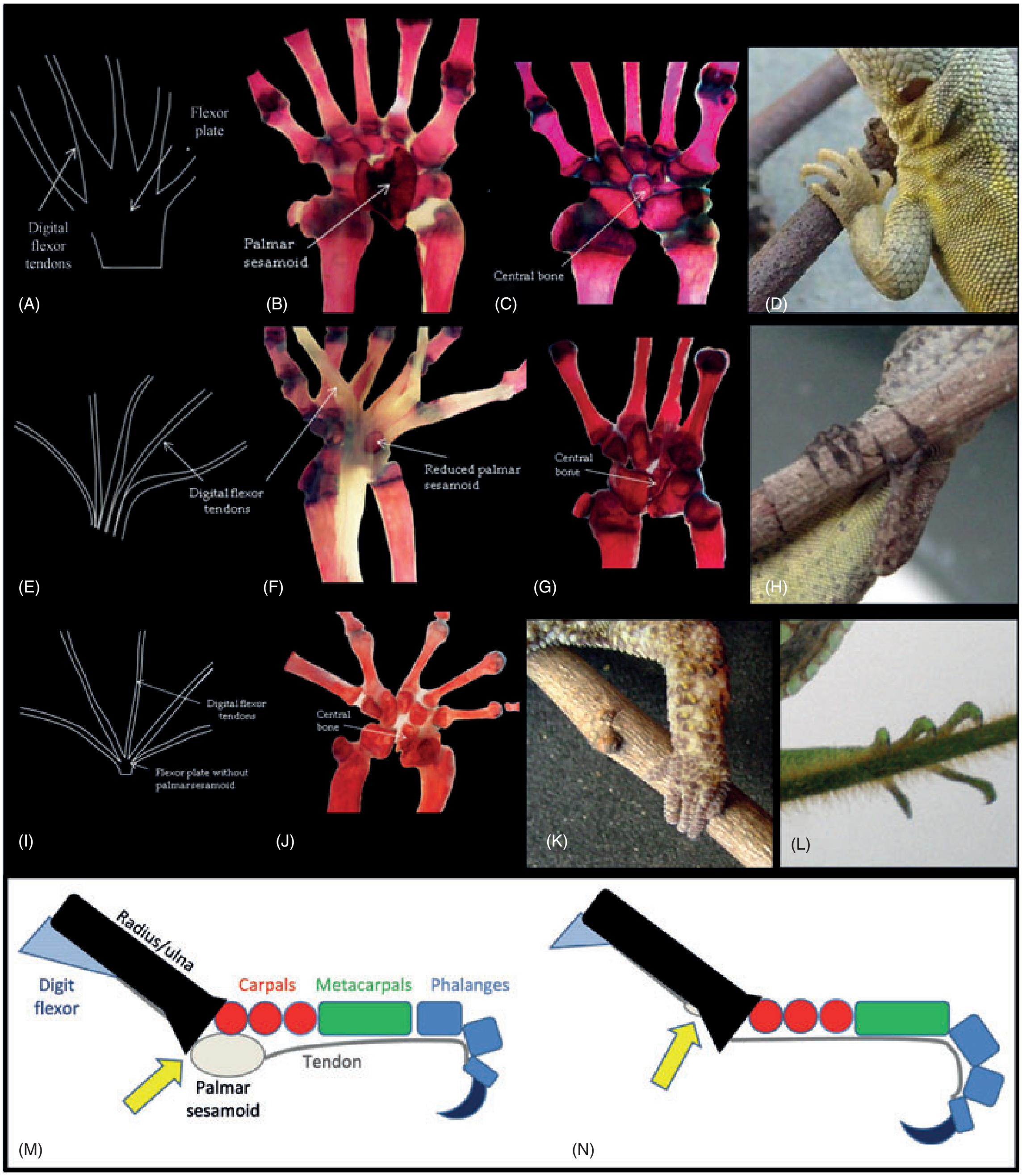

Fig. 3. (A–D) *Liolaemus cuyanus* right manus: (A) Schematic representation of the L-pattern (Moro & Abdala, 2004). (B) Ventral view showing the location of the palmar sesamoid. (C) Ventral view showing the carpal bones surrounding the central bone. (D) Dorsal view of *L. crepuscularis* left manus, showing partial digital flexion. (E–G) *Anolis cristatellus* right manus: (E) Schematic representation of a P-pattern (Moro & Abdala, 2004). (F) Ventral view showing the independence of the digital flexor tendons and the reduced palmar sesamoid. (G) Ventral view showing the shape and location of the central bone. (H) Ventral view of *A. cristatellus* right manus showing complete flexion of digits around branch. (I, J) *Bogertia lutzae* right manus: (I) Schematic representation of a G-pattern (Abdala *et al*., 2009). (J) Ventral view showing the completely flat surface of the palm, and the shape and location of the central bone. (K) Dorsal view of *Homonata fasciata* left manus showing complete digital flexion around branch. (L) Left manus of *Polychrus* sp. showing opposition of digits I and V about its long (proximo-distal) axis, that presumably results from the position and shape of the central bone depicted in (G). (M, N) Schematic representation of proposed action of palmar sesamoids. (M) L-pattern tendon with large palmar sesamoid that becomes obstructed (yellow arrow) and limits excursion of m. flexor digitorum tendon, and results in flexion of only proximal and distal interphalangeal joints. (N) P- or G-pattern tendon with reduced (P-pattern; yellow arrow) or no (G-pattern) palmar sesamoid, which allows complete excursion of the tendon and results in flexion of interphalangeal and metacarpo-phalangeal joints. Photos in D and K by G. Scrocchi; H by J. Daza, and L by A. Herrel; all others by M. J. Tulli. Tendon schematics reprinted from Tulli *et al*. (2012) by permission of John Wiley & Sons, Inc.

palmar sesamoid may thus provide regional differentiation and mobility within the hand by allowing digit I to be located in a more medial position. A similar displacement is present in relation to digit V in *Anolis* and *Polychrus*. This would provide the hand with an entirely new dimension for movement about the long (proximo-distal) axis of the palm (Fig. 3L) and may explain how these lizards are capable of grasping narrow branches.

(2) Pedal grasping in lizards

Although the morphology, kinematics, and ecomorphology of lizard hindlimbs and their role in locomotion have been studied intensively (Losos, 1990; Reilly & Delancey, 1997; Zaaf & Van Damme, 2001; Higham & Jayne, 2004; Kohlsdorf, Garland & Navas, 2001; Russell & Bauer, 2008), the topic of grasping feet in lizards has seldom been addressed (Brinkman, 1980; Russell & Bauer, 2008). However, the very same taxa that exhibit manual grasping abilities also show pedal grasping abilities: chameleons (Fischer, Krause & Lilje, 2010), varanids (Mendyk & Horn, 2011), anoles, and geckos (V. Abdala, personal observations). Contrary to what has been described in relation to manual grasping (e.g. Abdala *et al.*, 2009), the few accounts of the pedal tendon structures have shown great homogeneity among most lizards (Russell, 1993; Russell & Bauer, 2008), and no reports exist about differences in their complex plantar tendons related to particular functional abilities. The presence of a plantar sesamoid has seldom been reported (e.g. in the gecko *Ptenopus* spp. by Russell & Bauer (2008)), although its presence in frogs is well known (Ponssa, Goldberg & Abdala, 2010). Interestingly, *Ptenopus* spp. is secondarily terrestrial (Russell & Bauer, 2008), which may indicate that the anatomical constraints acting on manual morphology also might play a role in driving pedal morphology. Overall, the morphology of the lizard pes is conserved (Russell & Bauer, 2008). Some exceptions have been reported in the astragalocalcaneum of *Chamaleo* spp., which is different from any other astragalocalacaneum because it is depressed and curved. *Varanus* spp. presents an unusual structure of the mesotarsal joint with the development and orientation of the lateral process, and the structure of its distomesial border. The functional significance of these differences is unknown, however (Russell & Bauer, 2008). In accordance with this overall structural similarity, lizard lineages generally fail to exhibit pedal grasping capabilities. Pedal grasping in *Anolis* spp. appears to take place at the level of the distal interphalangeal joints (V. Abdala, personal observations).

(3) Ecological implications of lizard grasping performance

In most lizards, the hand forms an almost rigid plate whose flexibility seems to reside primarily in the distal digits and the claws (Zani, 2000; Tulli *et al.*, 2009). Claws are important for locomotion and claw height is a feature suggested to contribute to clinging ability on rough surfaces (Zani, 2000). Lizards that use vertical substrata (arboreal and saxicolous) tend to have shorter and especially deeper claws, whereas species utilizing open terrestrial habitats have longer and rather straight claws (Tulli *et al.*, 2009). Although these versatile claws allow lizards that cannot grasp to explore vertical substrata, they do not facilitate movement on narrow branches. This particular niche among arboreal habitats is likely restricted to lizards capable of grasping movements. Lizards that can close the hand around branches of small diameter can do so because their carpal joints are flexible, because they do not possess large sesamoids that prevent the hand from closing, and because they have independent flexor tendons from the forearm muscles to each digit that enhance their movements. Some work has compared the grasping performance of lizards possessing different tendinous patterns. Abdala *et al.*'*s* (2009) analysis of *in vivo* grasping forces indicated a tendency for grasping force to differ among species. Lizards such as *Pogona vitticeps*, which are unable to close their hands around a narrow substratum, had the weakest grasping forces on average. However, differences between species that are able to grasp were not significant despite grasping force being somewhat greater in *Anolis equestris* compared with *Gekko gecko* (mean ± S.D. [$N = 3$ for each]) $= 1.16 \pm 0.12$ N *versus* 0.62 ± 0.19 N). This difference is likely a result of the greater flexor muscle mass in *A. equestris* compared with *G. gecko*. More data across a variety of species could resolve the morpho-functional relationships among groups capable of grasping and provide insights into the fitness advantages conferred by the different tendinous patterns observed.

As mentioned previously, grasping ability in lizards is related to the specialized use of narrow branches. Mendyk & Horn (2011) demonstrated the ability of *Varanus beccari* to perform extractive foraging through grasping movements, constituting the first account of a lizard using its hands to take food and push it into the mouth. However, *V. beccari* is an arboreal lizard, further supporting the pervasive relationship between arboreality and enhanced hand movements. In this aspect, *V. beccari* converges on the condition in some frogs; the ability to free the hands from their role in substratum grasping and use them in a feeding context. This decoupling of the forelimb from substratum prehension is possible likely because of their grasping feet, which ensures the contact and stability of the lizard on the substratum, thus allowing the hands to be used in an entirely novel context of prey prehension. Apart from *V. beccari*, there are no reports of other taxa exhibiting pedal grasping that would allow free hands to be used in a feeding context. Thus, grasping feet may not suffice to explain the manual grasping tendencies of these lizards, which demonstrate comparatively high levels of behavioural complexity (Horn & Visser, 1997; Sweet & Pianka, 2007). Monitor lizards possess excellent memories and can be trained to respond to stimuli even after several weeks of latency (Mendyk & Horn, 2011). Thus, the possibility exists that the grasping ability of these lizards is associated with their cognitive abilities as much as with their grasping feet.

IV. GRASPING IN BIRDS

The vast majority of work on avian hindlimb form and function pertains to proximal limb morphology in relation to bipedal locomotion (e.g. Gatesy & Middleton, 1997; Hutchinson, 2004; Hertel & Campbell, 2007). Studies focusing on the avian pes account for relatively few, of which a small subset is devoted to the functional and evolutionary morphology of grasping. With the specialization of the forelimbs for flight throughout the evolutionary history of birds, the capacity for manipulating objects progressively became relegated to the hindlimbs (Fig. 4). This formulates an intriguing departure, in that a few birds have achieved comparable levels of digital dexterity in the pes as other tetrapods have in the manus, and consequently most birds are restricted to the execution of a power grip. The ability to grasp arboreal perches is a hallmark of avian evolution (Sereno & Chenggang, 1992; Middleton, 2001). Specifically when and how this evolved is subject to some debate (Middleton, 2003) that is unfortunately often overshadowed by that of the evolution of flight. Fowler *et al*. (2011) hypothesized that selection for grasping prey, as evidenced by claw and foot morphology of deinonychosaurian ancestors of Aves, might have formed the basis for arboreal perching, and possibly even flapping flight. One thing that is clear, however, is that the reversal and incumbency of the hind toe (hallux) to form an opposable digit was a fundamental precursor for grasping (Sereno & Chenggang, 1992; Feduccia, 1999; Middleton, 2001). Despite the apparent selection for perching early in the evolutionary history of birds (Sereno & Chenggang, 1992), the form and function of their feet were subjected to other, potentially conflicting, demands associated with feeding and locomotion (Feduccia, 1999; Middleton, 2001). Although many groups employ their feet in all of these functions to some extent, one function or another is relatively more important for certain groups compared to others (Fig. 5). Perhaps because of this, the avian pes has achieved a remarkable diversity of form and function in spite of having lost digit V (Bock & Miller, 1959; Fig. 4).

(1) Of toes and tendons: the functional anatomy of avian grasping

Bock & Miller (1959) described six major toe arrangements they presumed to have evolved from an ancestral anisodactyl (digits II–IV directed cranially, digit I directed caudally, Fig. 4) 'perching' foot, and Raikow (1985) described another six variations of these. These toe configurations have been taxonomic focal points in ornithology for centuries, though their utility for higher-order systematics is complicated by homoplasy. For instance, the zygodactylous toe arrangement (digits I and IV directed caudally, digits II and III directed cranially), is found in parrots (Psittacidae), cuckoos (Cuculidae), woodpeckers and allies (Piciformes), and facultatively in owls (Strigiformes) and the osprey (*Pandion haliaeetus*). The functional implications and whether or not this condition is derived are not clearly understood (Bock & Miller, 1959). Zygodactyly has traditionally been considered an adaptation for climbing. This is primarily because some Piciformes (woodpeckers) use their feet for climbing, but cuculids and other Piciformes generally perch/walk on the ground or in trees (Fig. 5). Bock & Miller (1959) proffered a variant of zygodactyly – the 'ectropodactyl' arrangement, in which the fourth toe is rotated to a lateral or anterior position – as the true 'scansorial' foot type possessed by woodpecker species they considered the most specialized for climbing. Owls and ospreys use their feet for food manipulation (killing and grasping prey); their facultative zygodactyly is presumed to enhance their prey-capture success by splaying the digits more symmetrically (thereby increasing foot area; Payne, 1962; Einoder & Richardson, 2007*b*), and digital flexion forces more equitably (Ward, Weigl & Conroy, 2002), which collectively increase the chances of achieving and maintaining foot-to-prey contact. Parrots use their feet both for food manipulation and climbing (see below). Thus, Bock & Miller (1959) concluded that although these toe arrangements ostensibly have phylogenetic bases, they represent different adaptive solutions to similar functional demands of maintaining a foothold. If variation in toe patterns indeed has important implications for grasping function, these have yet to be explored in a rigorous phylogenetic framework.

Besides the reversal of the hallux, another possible key feature for pedal grasping was the avian digital-tendon-locking mechanism (Quinn & Baumel, 1990). This mechanism was proposed to work both by way of flexion of the intertarsal joint to place the digital flexor tendons that run caudad to it into tension (Watson, 1869; Ward *et al*., 2002), and by virtue of the ratchet-like microstructure of the distal portions of the tendons and associated sheaths (Quinn & Baumel, 1990; Einoder & Richardson, 2006, 2007*b*). These two forms of the mechanism presumably work in combination to maintain digital flexion forces without the aid of continuous muscle contraction (Schaffer, 1903; Quinn & Baumel, 1990; Middleton, 2003; Einoder & Richardson, 2006). Galton & Shepherd (2012) actually tested this on European starlings (*Sturnus vulgaris*) that were anaesthetized while perched. They made nighttime observations of sleeping birds, specimen manipulations, and surgical interventions of tendon function, and demonstrated that there is no such 'automatic perching mechanism' (involving either mechanism, above). They suggested instead that the use of the toe flexors during perching is minimal and likely 'limited to an occasional readjustment of balance' (Galton & Shepherd 2012, p. 214). Its role in other functions (e.g. grasping prey, climbing, clinging, etc.), however, remains somewhat obscure, and attributes of the tendon-locking mechanism could play an important role for muscle contraction by placing flexors at more optimal lengths along their length-tension curves (Bock, 1965; cited by Galton & Shepherd (2012)).

Birds also possess a suite of muscle and tendon modifications to generate and transmit these digital flexion forces. The digit flexor musculature of birds is subdivided into

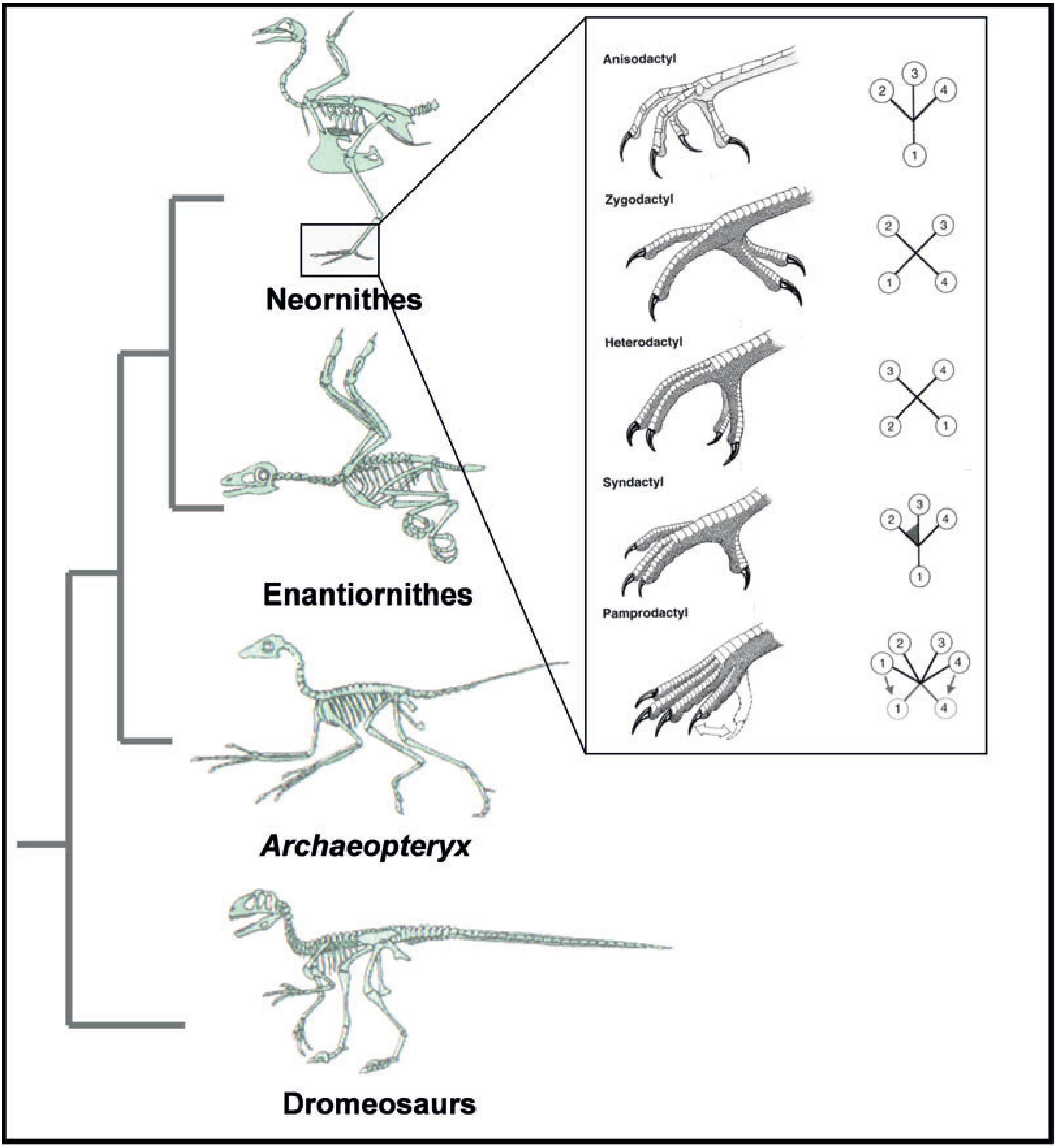

Fig. 4. Throughout their evolutionary history, the forelimbs of birds have become occupied for flight, thereby shifting the development of grasping capability onto the hindlimbs. The diversity of toe configurations within modern birds in part reflects this new role for the avian pes. Cladogram and associated images simplified from Pough, Janis & Heiser (2009) and foot type schematic adapted from Proctor & Lynch (1993), reprinted by permission of Pearson Education, Inc., and Yale University Press, respectively.

a series of superficial flexors (the mm. flexor perforans group) that insert on the proximal phalanges of digits II–IV, in addition to the two ancestral deep heads (m. flexors digitorum and m. hallucis longus) that insert on the ungual phalanges of digits II–IV and the hallux, respectively (Hutchinson, 2002). Although the functional significance of this is not entirely clear, other workers have suggested that increases in the number and attachment areas of the heads and/or increased fibre pennation of the digital flexors enhance flexion force (Raikow, Polumbo & Borecky, 1980; Berman &

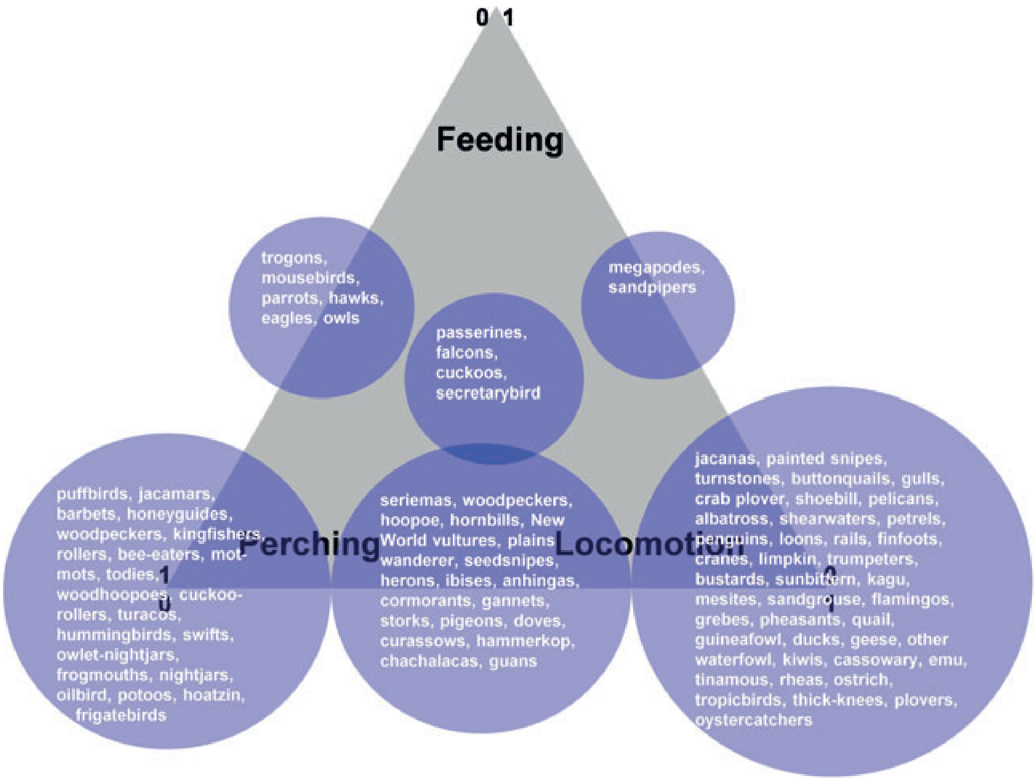

Fig. 5. Ternary-style diagram demonstrating major functional endpoints (feeding, terrestrial or aquatic locomotion, and arboreal perching) in the use of feet among avian taxa, based on Clark (1973; and references therein), Ross (1924) and Tozer & Allen (2004). Each group was scored for typical (1) or rare (0) use of feet for each behaviour, and proportions along each side were tallied based on a sum total of 3 (use of feet typical for all behaviours). Bubbles are centered on each of six possible proportional foot-use values, and sized relative to number of taxa. Taxa are from Hackett *et al.*'s (2008) phylogeny.

Raikow, 1982; Moreno, 1990). Aside from these qualitative modifications, quantitative characteristics also have been linked to an enhanced digital force production in birds. Among raptors, differences in the magnitude and scaling of the physiological cross-sectional area (PCSA; Ward *et al.*, 2002; Sustaita, 2008), mechanical advantage (Sustaita, 2008), and torque production (Goslow, 1972) of various digit flexor muscles underlie differences in their grip force capabilities and prey-handling behaviours.

Raikow (1985) summarized the eight main types of digit flexor tendon arrangements found in birds (after Gadow, 1896), which historically have been important in their classification; yet their functional significance remains obscure. In the most common (in terms of the number of families represented) Type I configuration, the tendon of m. flexor digitorum longus divides distally into three branches that insert onto digits II–IV, whereas that of m. flexor hallucis longus inserts directly onto digit I (Raikow, 1985). The tarsometatarsal portions of these deep flexor tendons are often connected together at some point along their lengths by a tendinous vinculum, and a single extensor (m. extensor digitorum longus) operates digits II–IV. Thus, in most plantar tendon arrangements the actions of the deep digital flexors are not independent, and contraction of the m. flexor hallucis longus assists in flexion of digits II–IV, but not *vice versa* (Raikow, 1985). However, in the Type VII flexor tendon arrangement characteristic of most passerines (songbirds), there is no vinculum between the deep flexor tendons, thereby enabling complete independence of flexion of digits II–IV from that of the hallux. Outside of the passerines, intrinsic muscles (those that originate from the tarsometatarsus and insert on the proximal phalanges) provide adduction, abduction, extension to digits II–IV, and extension and flexion to digit I (Raikow, 1982).

(2) The ecomorphology of avian grasping

Claw structure and function are other important components of avian grasping. Claw curvature increases from ground-dwelling, to arboreal perching and climbing, to predation (Feduccia, 1993; Pike & Maitland, 2004). Even within these broad functional groups, taxa can be distinguished along various metrics of claw shape (Csermely & Rossi, 2006). Furthermore, claw curvature (Fowler, Freedman & Scannella, 2009; Fowler *et al.*, 2011) and size (Einoder & Richardson, 2007*a*) have been associated with predatory behaviour and prey-type specialization, respectively. Although the biomechanical consequences of claw shape and size variation have yet to be tested explicitly, the correlations with locomotor and feeding behaviour are strongly suggestive of their roles in grasping by enhancing traction (Ramos & Walker, 1998; Fowler *et al*., 2009, 2011), and/or the probability of contact with prey items (Csermely, Bertè & Camoni, 1998). Further investigation into how these claw characteristics interact with grasping performance (below) should yield important insights.

Based on a comprehensive osteological data set of avian and non-avian theropods, Hopson (2001) demonstrated a pattern of increase in the proportional lengths of the distal phalanges of the third digit along an axis ranging from terrestrial cursorial (e.g. ostrich [*Struthio camelus*] and emu [*Dromiceius novaehollandiae*]), to arboreal perching (e.g. passerine songbirds), climbing (e.g. woodpeckers, woodcreepers), and predatory (e.g. hawks, falcons) bird species. This pattern was later reaffirmed by Kambic's (2008) multivariate analysis of avian and theropod pedal phalanx dimensions, which revealed additional aspects of phalangeal shape (e.g. width *versus* height, trochlear grooving) that provide finer discrimination among certain behavioural categories. Although the biomechanical consequences of variation in avian phalangeal length proportions remain elusive, Trinkaus & Villemeur (1991) demonstrated how differences in the proportional lengths of pollical phalanges between Neanderthals and modern Europeans resulted in differences in mechanical advantage across key interphalangeal joints that favoured power (Neanderthal) *versus* precision (modern European) grasping. The adaptive significance of grasping in birds has been associated primarily with climbing (e.g. Norberg, 1986). These studies have focused on the effects of toe arrangement (Bock & Miller, 1959) and musculoskeletal morphology (Raikow, 1994), to explain how internal and external forces are balanced to counteract gravity, and the role of claw shape for clinging to the substratum (Pike & Maitland, 2004).

Grasping in the context of feeding, i.e. 'the use of the feet in manipulating food' (Clark, 1973) is less common among birds but enjoys a fairly broad phylogenetic distribution (Ross, 1924; Scooter, 1944; Smith, 1971; Tozer & Allen, 2004). Clark (1973: 95) suggested that this behaviour 'extends the range of possible foods by enabling consumption of items too hard or too large to be handled by the bill alone'. Although feeding is most certainly an important selective force for grasping capability, on a larger evolutionary scale it is confounded with the adoption of an arboreal existence. Indeed, our test of correlated character evolution indicated a significant association between arboreality and pedal food manipulation (Fig. 6). Furthermore, a slightly greater transition rate parameter for the arboreal state change than that for pedal food manipulation suggests that arboreality occurred first, and therefore may have been exapted for pedal food manipulation. However, Fowler *et al*. (2011) suggested that grasping evolved much earlier in theropods for predation (i.e. for immobilizing their prey with their feet whilst suppressing it with their body weight), and was later co-opted for arboreal perching in birds. Although these authors conceded the difficulties in disentangling these potentially non-mutually-exclusive scenarios, they consider the predatory hypothesis more parsimonious given that the ancestors of birds were large-bodied carnivores that were likely non-arboreal. Overall, relatively few arboreal taxa handle food with their feet, suggesting that such 'repurposing' of grasping function may not necessarily be easy to accomplish. Raptors, parrots, and mousebirds (Coliidae), for instance, probably represent extremes in their tendencies for pedal food manipulation, and

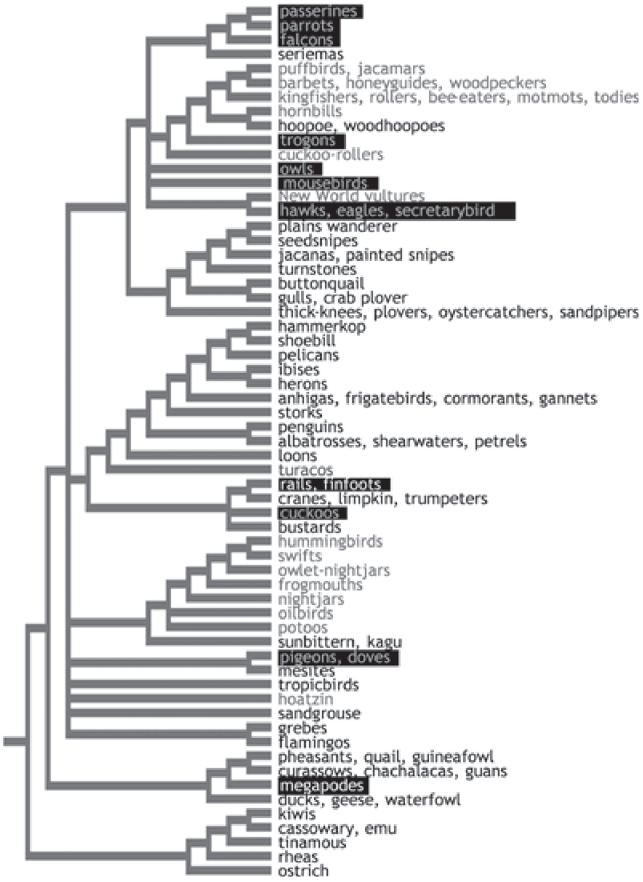

Fig. 6. Hackett *et al*.'s (2008) ordinal-level topology redrawn to illustrate clades that predominantly contain taxa with arboreal modes of existence (grey text), and those that are known to manipulate food with their feet [black highlighting; based primarily on Clark (1973; and references therein), Ross (1924), and Tozer & Allen (2004)]. The association between arboreality and pedal food manipulation was significant [Pagel's (1994) test of correlated character evolution; change in log-likelihood = 7.70 (after extra 10 searches), $P = 0.002$ (from 1000 simulation replicates)]. Although both appear to be relatively derived character states, the transition rate parameter for the presence of arboreality and absence of pedal food manipulation ($q_{13} = 1.08$) was slightly greater than that for the absence of arboreality and presence of pedal food manipulation ($q_{12} = 1.05$) (Pagel, 1994), implicating arboreality as a plausible exaptation for pedal food manipulation. Ancestral state reconstruction and correlation analyses were performed using MESQUITE (Maddison & Maddison, 2011) based on our recreation (not shown) of Hackett *et al*.'s (2008) fig. S1 maximum-likelihood phylogram containing 171 species and branch lengths.

possess different musculoskeletal modifications for enhancing grasping capability. Raptors appear to emphasize grip and talon force for seizing, subduing, and killing prey *via* digital flexor muscle hypertrophy and mechanical advantage (Goslow, 1972; Ward *et al*., 2002; Sustaita, 2008). Parrots and mousebirds tend to emphasize dexterity and fine motor control for accessing and manipulating hanging food items (Harris, 1989). This is achieved through greater diversification and development of intrinsic hindlimb digital muscles, such as the presence of an accessory insertion of the m. extensor hallucis longus pars distalis on the distal phalanx that provides cranial rotation of the hallux, and a branch of the m. extensor digitorum longus to the hallux (in addition to the three foretoes), which collectively are presumed to provide more 'delicate' control of the hallux (Berman & Raikow, 1982; Berman, 1984). Among parrots, other anatomical features thought to foster grasping ability, such as a medially directed metatarsus I (which articulates with the hallux) and robust digits III and IV, have evolved multiple times independently in the Psittaciformes, resulting in a complex series of character transitions leading to modern parrots (Ksepka & Clarke, 2012). However, the intricacies of grasping performance in modern parrots have been studied primarily in neuromotor contexts for investigating foot preferences during object manipulation and cerebral lateralization. Right, left, or ambidextrous foot preference varies within and among species (Harris, 1989; Brown & Magat, 2011). Brown & Magat (2011) found that larger-bodied species with greater tendencies for manipulating larger food items showed stronger left- or right-foot lateralization. Their ancestral state reconstructions indicated that lateralization (and loss thereof) in Australian parrot foot preference was driven by changes in body size and shifts in foraging mode, such that larger, strongly lateralized species consumed larger food items that required greater manipulation and foot-beak coordination, whereas smaller, non-lateralized species consumed small seeds and blossoms requiring little manipulation. Uses of the feet that are more peripheral to feeding, such as clinging to the substratum while probing flowers (e.g. hummingbirds; Feinsinger & Colwell, 1978) or manipulating food items (e.g. tits; Carrascal, Moreno & Valido, 1994), are much more widespread among birds. In hummingbirds, which are characterized by having disproportionately small hindlimbs and feet (Feinsinger & Colwell, 1978), there is a negative correlation between foot and bill dimensions (Yanega, 2007). This suggests that their feet are under selection for feeding, albeit indirectly through a complex interaction among the bill, feet, and floral food sources.

(3) Avian grasping performance: implications and opportunities

Measurements of realized performance are essential for understanding the functional, and ultimately ecological, consequences of a given morphology (Arnold, 1983; Wainwright, 1996). Among birds, raptors have been the focus of most (if not all) endeavours to quantify grasping strength. Most raptors use their feet to seize and subdue their prey, and many (save perhaps falcons, which also employ their bills; Cade, 1982; Hertel, 1995) rely more exclusively on their feet for killing prey with their toes and talons (Brown & Amadon, 1968; Csermely *et al*., 1998). Thus, grip strength directly affects predatory performance and as a result has been measured for several species to test functional (Harris, 1984; Csermely & Gaibani, 1998; Csermely *et al*., 1998), behavioural (Sustaita & Hertel, 2010), and ecological hypotheses (Marti, 1974; Ward *et al*., 2002). Grip force has been found to scale both allometrically (Ward *et al*., 2002) and isometrically (Sustaita & Hertel, 2010) with body mass within taxonomic groups. Thus, enhanced grasping capability has clear implications for raptor feeding ecology, either directly *via* grip force (Marti, 1974; Ward *et al*., 2002) or indirectly *via* prey size (Reynolds & Meslow, 1984; Schoener, 1984). Other metrics of prehensile capability (e.g. dexterity, precision, and coordination in reaching and grasping objects) that are more commonplace in kinesiology and exercise physiology (e.g. Zatsiorsky & Latash, 2004), and have become progressively more important in studies of non-human primates (e.g. Pouydebat *et al*., 2009), are lacking for birds. Aside from the speeds and forces they generate in their toes and talons, some groups, such as the African harrier-hawk (Accipitridae; Burton, 1978) and caracaras (Falconidae; Biondi, Bo & Vassallo, 2008), are particularly dexterous in reaching and manipulating objects with their feet.

Studies of neuromotor control of grasping in birds are limited and lag considerably behind those of mammals. Cutaneous (afferent) feedback from the digits can have profound implications for grasping performance (e.g. Shim *et al*., 2012). However, proprioception in birds has received very little attention in the avian somatosensory literature (Schwartzkopff, 1973), and most studies pertain to the bill, jaws, and feathered skin (Gottschaldt, 1985). Schwartzkopff (1949) discussed the presence of Herbst corpuscles in the proximal hindlimbs of bullfinches (*Pyrrhula* spp.) that are thought to play a role in detecting vibrations (Burns & Wight, 1970). The plantar surfaces of chicken feet possess concentrations of Herbst (Burns & Wight, 1970), and rudimentary Meissner-form corpuscles resembling those of arboreal primates (Winkelmann & Myers, 1961), suggesting potential roles for grasping function or for positioning the feet and maintaining balance. Lennerstedt (1975) also documented Herbst corpuscles in the foot pad papillae of parrot feet, indicating a touch function of the papillae presumably associated with their climbing and pedal food-handling habits.

There has been a recent surge of interest in avian grasping form and function in the vertebrate palaeontology community, as researchers have invoked grasping functional morphology of extant birds to infer attributes of behaviour and ecology of extinct birds (e.g. Pike & Maitland, 2004) and theropod dinosaurs (e.g. Manning *et al*., 2006; Fowler *et al*., 2009, 2011). Thus, birds formulate an important point of comparison for examining the evolutionary pathways by which pedal and manual dexterity are achieved in tetrapods.

V. GRASPING IN MAMMALS

Mammals display a great diversity of grasping form and function, which integrates several key features highlighted for other taxa. In mammals, grasping occurs extensively during food manipulation, while moving or standing on arboreal supports, and involves both manual and pedal grasping. Manual grasping is associated more with feeding behaviour, whereas pedal grasping is associated more with locomotor behaviours. Although many mammals have been studied in this regard, the literature on primates dominates this field of research. Relevant work on grasping behaviour and limb morphology in non-human primates abounds across the greater, synthetic field of Primatology. These studies span research from cognition, to locomotion, to evolution. Thus, it is impossible to canvass adequately all of these in the scope of this review. Instead, we attempt to address questions that we consider most pertinent for understanding the ecology and evolution of grasping among mammalian clades. In this context many questions arise: what are the demands and potential trade-offs associated with grasping in the context of these two behaviours? Can we retrace the evolutionary origin and investigate the selective pressures underlying the evolution of grasping? What is the relationship between arboreality and skilled food manipulation and forelimb movements? To answer these questions, we first review manual and pedal grasping for support during arboreal locomotion and for feeding, and then detail their underlying functional adaptations.

(1) Manual and pedal support grasping

Although a number of studies have focused on hand use during feeding or tool use, a much larger body of work exists exploring support grasping during locomotion, particularly in primates. Indeed, the capacity to grasp narrow branches remains at the centre of the debate on primate origins. Current hypotheses for primate origins propose that the use of fine terminal branches to exploit fruits, flowers, insects, and nectar may have constituted an important selective pressure driving the evolution of primate grasping. The evolution of specific hand and nail morphologies observed in primates might be related to the use of narrow terminal branches (Cartmill, 1974*a*; Sussman & Raven, 1978; Sussman, 1991). Comparative studies of other terminal-branch specialists have been used to test this hypothesis. Tree shrews (Tupaiidae; Sargis, 2001), some marsupials (Rasmussen, 1990; Rasmussen & Sussman, 2007), and chameleons (Cartmill, 1974*b*) have been shown to possess a hand and foot morphology that is functionally similar to that of primates, suggesting evolutionary convergence for grasping. For example, the woolly opossum (*Caluromys* spp.) is highly arboreal and uses the terminal small branches of the canopy (Rasmussen, 1990; Grelle, 2003). In association with this microhabitat use these animals have developed relatively long digits and a long opposable nail-bearing hallux (Szalay, 1994; Lemelin, 1999; Argot, 2002). These morphological characters form the basis for using *Caluromys* spp. as the adaptive analog of a terminal-branch feeder capable of a powerful hallucal grasp, a key feature that is thought to characterize primates (Hoffstetter, 1977; Youlatos, 2008). However, recent studies demonstrated that species lacking primate grasping adaptations, such as Eastern grey squirrels (*Sciurus carolinensis*) and European red squirrels (*Sciurus vulgaris*), also feed and forage on terminal branches (Samaras & Youlatos, 2010; Orkin & Pontzer, 2011). A study on the mouse lemur (*Microcebus murinus*) suggested that, more than an arboreal thin substratum, the frequent use of vertical supports may influence hand biomechanics toward ulnar deviation as observed for lorisids and indriids (Reghem, Byron & Poudebat, 2012). These studies suggest that selection for fine-branch foraging is not a sufficient condition for primate origins and that this hypothesis may oversimplify the evolution of primates by focusing on a small number of selective pressures. Primates display many morphological features that did not evolve concurrently suggesting a multitude of selective pressures (Dagosto, 2007; Sargis *et al*., 2007).

(2) Manual food grasping and manipulation

Although the ability to reach for food or prey, to hold it in a forepaw, or manipulate it with the digits exists in most tree-dwelling frogs (Gray *et al*., 1997), it is often considered to be most developed in mammals (Ivanco, Pellis & Whishaw, 1996; Iwaniuk, Nelson & Whishaw, 1999; Iwaniuk & Whishaw, 1999*a*, 2000; Endo *et al*., 2007; Sacrey, Alaverdashvili & Whishaw, 2009). It is unclear whether the use of the forelimb for grasping arose independently within each mammal lineage and represents convergent evolution of motor patterns (Lassek, 1954; Bracha *et al*., 1990), or if these patterns arose early in mammalian evolution (Whishaw, Pellis & Gorny, 1992) before being lost or elaborated upon in different lineages. To test these hypotheses, studies have focused on grasping in different taxa such as xenarthrans (sloths and anteaters; Taylor, 1985), pholidotes (pangolins; Grzimek, 1990), Scandentia (tree shrews; Bishop, 1964), Dermoptera (colugos; MacDonald, 1984), rodents (Whishaw, 1996; Whishaw, Sarna & Pellis, 1998), carnivorans (Boczek-Funcke *et al*., 1998; Iwaniuk *et al*., 1999), marsupials (Ivanco *et al*., 1996; Landy, 1997), and primates (Christel, 1993; Jones-Engel & Bard, 1996; Christel, Weiss & Bavar, 1998; Christel & Billard, 2002; Pouydebat *et al*., 2008, 2009, 2011).

The grasping pattern in mice and rats consists of several components (Whishaw *et al*., 1998). Food is detected by olfaction and then usually grasped with the mouth. Rodents then typically adopt a ‘sitting’ posture on their haunches and use their digits to manipulate the food in their mouth. The marsupial motor pattern based on data for the northern quoll (*Dasyurus hallucatus*), opossums, and gliders, shows a few characteristics in common with those of rodents (Schwensen, 1994; Ivanco *et al*., 1996; Landy, 1997). The food is detected by olfaction and in some cases by proprioception. Upon detection, food is initially grasped by the mouth, except in carnivorous marsupials (dasyurids) and didelphids

(Schwensen, 1994; Ivanco *et al*., 1996), or in phalangerid and petaurid species that ingest some animal matter (Landy, 1997). These species instead initially grasp the food between digits II and III ('scissor grip') as well as with the entire hand (power grip).

Among carnivorans, the motor pattern differs in several aspects. Most of them use olfaction to detect food, but the marsh mongoose (*Atilax paludinosus*), small-clawed otters (*Amblonyx* spp.), and the raccoon (*Procyon lotor*) detect their food both by visual and tactile means. After detection, raccoons essentially use their hands to grasp food and often opt for a bipedal posture (Iwaniuk & Whishaw, 1999*b*). In addition, as seen in carnivorous marsupials, raccoons use the scissor grip. Raccoons often roll the food between the palms of both hands, as do otters when manipulating food or other objects such as stones. Raccoons possess fine control of forepaw digits, whereas the kinkajou (*Potos flavus*; Pocock, 1917) and the olingo (*Bassaricyon* spp.; Ewer, 1973) grasp objects with a single-handed converging grip (Rensch & Ducker, 1969; McClearn, 1992). Other carnivorans are capable of fine manipulation of food, such as the giant panda (*Ailuropoda melanoleuca*), otters (*Aonyx* spp., *Lutrogale perspicillata*, and *Enhydra lutris*), the crab-eating and marsh mongooses (*Herpestes urva*, *Atilax paludinosus*; Ewer, 1973) and the African palm civet (*Nandinia binotata*; Estes, 1991). By contrast, the ringtail (*Bassariscus astutus*) and coatis (*Nasua* spp.) seem to be less dexterous, having little fine control of digit movements (Ewer, 1973; McClearn, 1992). It is noteworthy that coatis and raccoons mostly forage on the ground, suggesting that postures and the use of their forepaws during feeding are potentially adaptations to terrestrial conditions. Coatis are excellent diggers and shredders so their lack of fine control of digit movements and associated musculoskeletal correlates might prevent complex grasping ability and terminal-branch feeding as seen, for example, in kinkajous (McClearn, 1992). Thus, a relation between arboreality and dexterous food manipulation in carnivorans might be expected. However, food manipulation in semi-aquatic mustelids cannot be explained by arboreality and is likely associated with their omnivorous diet.

In primates, food detection occurs by a mixture of visual, olfactory, and auditory stimuli in most strepsirrhines (lemuriforms and lorisiforms; Siemers *et al*., 2007; Piep *et al*., 2008), and mainly visually in haplorhines (Martin, 1990). Stepsirrhines appear to take static foods first with the mouth and show no digital individualization (Petter, 1962; Bishop, 1964; Reghem *et al*., 2011). By contrast, when grasping mobile prey, as well as during manipulation, the hand seems to be used first. For example, the specialized aye-aye (*Daubentonia madagascariensis*) is known to use the third finger to pry insects from holes in trees (Erickson, 1991; Milliken, Ward & Erickson, 1991; Erickson *et al*., 1998). In addition, Cheirogaleidae and several lorisiforms catch insects with one or both hands (Martin, 1972; Oates, 1984; Lemelin, 1996; Nekaris, 2005). In contrast to strepsirrhines, haplorhines use their hands to grasp static foods and in so doing employ a great variety of hand and digit postures (Napier, 1956; Bishop, 1964; Christel, 1993; Spinozzi, Truppa & Lagana, 2004; Pouydebat *et al*., 2008). The various grip types used by chimpanzees (*Pan troglodytes*) and other great apes when grasping static foods are highly comparable to those used by humans (Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Byrne & Corp, 2001; Pouydebat *et al*., 2011). Several primates (i.e. great apes, capuchin monkeys [*Cebus* spp. and *Sapajus* spp.]) partially use the scissor grip, as do several marsupials and carnivorans (Pouydebat *et al*., 2009). The power grip may be one of the most common in mammals because it is used by animals with opposable (great apes), pseudo-opposable (i.e. without a complete rotation of the first carpo-metacarpal joint as in platyrrhines), and non-opposable thumbs (carnivorans and marsupials). However, the hand of haplorhines is capable of a diversity of movements, partly a result of the independent movement of the digits. The saddle-shaped carpo−metacarpal joint of the thumb allows their thumb to oppose the other digits (Napier & Napier, 1985), but pad-to-pad surface area contact with the other digits is limited to the distal tips (Marzke, 1997). The amount of force that the chimpanzee thumb can apply in a precision grip is lower than in humans, primarily a result of shorter (average) thumb muscle moment arm lengths (Marzke *et al*., 1999). These morphological differences might explain why the chimpanzee 'precision grip' is different from that of humans, and why they almost never use pad to pad grips (Pouydebat *et al*., 2011). The human hand presents many derived musculoskeletal traits relative to the hands of other apes (Lewis, 1989; Tocheri *et al*., 2008). Human digits have derived features compared with apes, with long robust thumbs, relatively larger joint surfaces, and hypertrophic thenar muscles; these features might have evolved in the context of making and using stone tools (Marzke, 1997; Susman, 1998). Longer digits require relatively less muscle force to stabilize digital joints, and are exposed to relatively lower joint contact stresses during stone tool use, in part because of an increase in the robusticity of metacarpals and phalanges. This is reflected in the differences in humans relative to chimpanzees (Rolian, Lieberman & Zermeno, 2011). On the contrary, Williams, Gordon & Richmond (2012) reported that manual normal forces and pressures acting on the hand during Oldowan stone tool production showed that peak normal force, pressure, impulse, and the pressure/time integral are significantly lower on the thumb than on digits II and/or III. These results challenged the assumptions linking modern human thumb robusticity specifically to load resistance during stone tool production. The hand of haplorhines (especially in apes and capuchins) seems to be the most dexterous among mammals, but whether the ability to perform skilled manipulation and forelimb movements is linked to their arboreal origins remains to be examined in a phylogenetic framework (e.g. Fig. 7).

(3) **Functional adaptations and ecological consequences**

The morphology of the mammalian hand reflects adaptations functionally related to support prehension and foraging

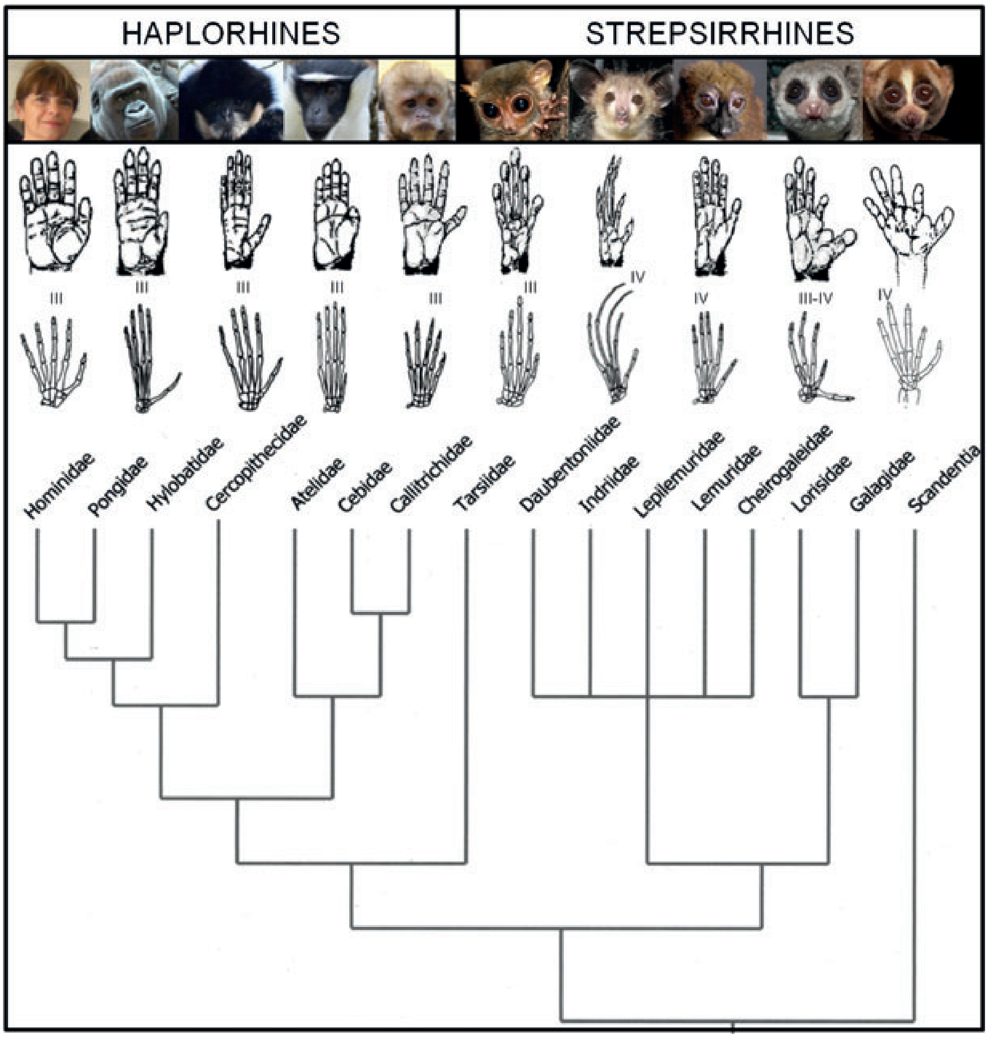

Fig. 7. Phylogenetic branching patterns showing morphological and functional differences of the hand in primates. Modified and adapted from Schultz (1972; hand skeleton figures), Hershkovitz (1977; hand skeleton figures), and Chiu & Hamrick (2002; phylogenetic topology). Photos courtesy of A. Bardo (Hylobatidae and Cercopithecidae), D. Haring (Tarsiidae, Daubentoniidae, Cheirogaleidae, Galagidae); all others by E. Pouydebat.

strategies (Hamrick, 2003). A considerable effort (e.g. Jouffroy & Lessertisseur, 1979; Van Valkenburgh, 1987; Norberg, 1994; Szalay, 1994; Hamrick, Rosenman & Brush, 1999; Lemelin, 1999; Hamrick, 2001*c*) has been devoted to the study of potential adaptive variation in the mammalian hand skeleton and the integumentary structures in relation to foraging behaviours (e.g. Thewissen & Etnier, 1995; Rosenberg & Rose, 1999; Lemelin, 2000; Hamrick, 2001*a*, *b*). Climbing mammals such as primates, tree shrews, and burramyid marsupials have developed papillary ridges on their fingers that improve their ability to grasp arboreal supports (Whipple, 1904; Le Gros Clark, 1936; Cartmill, 1974*a*, 1985; Hamrick, 1998; Rosenberg & Rose, 1999; Lemelin, 2000). Other marsupials such as koalas (*Phascolarctos cinereus*) and gliding phalangers (*Petaurus breviceps*) have sharp and keeled claws to cling to large-diameter substrata, whereas pygmy possums (Burramyidae) have thin and flat nails, better suited for climbing on narrow branches (Iwaniuk & Whishaw, 2000). Napier (1993) claimed that claws are incompatible with prehensile hands because they overgrow the fingertips, and hence obstruct the grasping process. However, the claws of tree kangaroos (*Dendrolagus* spp.) help facilitate one-handed grasping of food objects (Iwaniuk *et al*., 1998), clawed rodents are capable of one-handed feeding (Whishaw *et al*., 1998), and arboreal tupaiids (*Ptilocercus lowii* and *Tupaia minor*) are capable of grasping (Sargis, 2001). Colugos (Dermoptera) lack epidermal ridges on their fingers yet use arboreal substrata (Lemelin, 2000). Some bats (e.g. *Thyroptera tricolor*) have adhesive pads on their hands and feet to enhance friction with smooth arboreal supports (Wimsatt & Villa, 1970; Thewissen & Etnier, 1995). Bats (e.g. Quinn & Baumel, 1993), dermopterans (Simmons & Quinn, 1994), and some climbing rodents (Haffner, 1996) possess intrinsic digital tendon-locking mechanisms that maintain flexion forces with no additional muscular effort. However, these mechanisms differ among groups in form and function; whereas bats and birds possess a micro-anatomical ratcheting mechanism composed of tendon tubercles and tendon sheath plicae (Quinn & Baumel, 1990, 1993), rodents possess ventral tendon thickenings that provide resistance to tendon passage upon digital flexion (Haffner, 1996).

Adaptive changes in the integumentary structures of the hand in mammals might have been essential in the diversification of foraging strategies. Comparative studies of limb anatomy and function among extant mammals have shown a link between the ecological niche and the evolution of specific limb proportions (Hamrick, 2001*c*). For example, primates and marsupials foraging for fruits and insects on thin branches have relatively short palms, long fingers, and reduced claws (Jouffroy, Godinot & Nakano, 1991; Hamrick *et al*., 1999; Lemelin, 1999).

Primates and other mammals possess pedal grasping adaptations that may have contributed to the evolution of manual dexterity in a manner comparable to those observed in lizards; that is, by using the pes to grasp the substratum for support, thereby liberating the manus for other functions (e.g. Mac Neilage, Studdert-Kennedy & Lindblom, 1987). *Caluromys* spp., arboreal marsupials, are capable of 'powerful' pedal grasping (Sargis *et al*., 2007), having longer digits, a widely divergent hallux, and a developed hallucal eminence and pad (Argot, 2002; Lemelin, Schmitt & Cartmill, 2003). A grasping foot with opposable hallux is one of the shared derived features in primates other than humans (Cartmill, 1972; Martin, 1990), and is thought by some to precede the evolution of manual grasping (Byron *et al*., 2011 and references therein). Lemurid strepsirrhines possess a relatively large adductor hallucis allowing hallucal grasping by pinching the substratum between the first and second digits (Cartmill, 1985; Szalay & Dagosto, 1988; Gebo, 1993; Lemelin, 1999; Boyer *et al*., 2007), and an active m. peroneus longus during grasping behaviours, contributing to hallucal grasping (Kingston *et al*., 2010). An opposable hallux even occurs in the molossid bat *Cheiromeles* spp. (Vaughan, Ryan & Czaplewski, 2011). Finally, several studies on great apes (see Congdon, 2012 for review) have suggested that pedal phalangeal curvature may be indicative of increased grasping during suspensory and climbing behaviours in addition to the well-developed hallux in *Pan* spp. (Nakatsukasa *et al*., 2002).

To conclude, the ability to grasp with the feet and hands has been proposed as one of the defining features of primates (Le Gros Clark, 1959; Martin, 1990). Although many terrestrial vertebrates use their hands to grasp and manipulate food for eating, mammals appear to be the most dexterous (Ivanco *et al*., 1996; Iwaniuk & Whishaw, 2000). Some authors believe that skilled reaching movements in rodents and primates are similar (Bishop, 1964; Jeannerod, 1988; Whishaw, 1996) and suggest this implies an ancestral origin of skilled forelimb movements, or homology (Sacrey *et al*., 2009). However, the great variability of postures and behavioural data (repositioning, success *versus* error, body posture, etc.) reported for primates suggest that more observations of additional non-primate species are needed to distinguish whether grasping behaviour is homologous or homoplastic. Furthermore, the diversity in grasping patterns among primates shows the importance of taking into account the species, specific task (Pouydebat *et al*., 2006, 2010), properties of the food (size, mass, texture, form), position of the food, posture of the animal, its morphology, and finally its social context, in order to understand fully realized grasping capabilities.

VI. SYNTHESIS AND PROSPECTUS

We have described grasping form and function in the context of each major tetrapod clade where it is known to occur. Here we summarize our major findings and construct a synthesis of the developmental, morphological, and behavioural traits that collectively affect grasping performance in terms of force and precision. Different aspects of grasping form and function have been emphasized in different groups. This is partly a result of individual research biases, and the fact that certain groups formulate better models for illustrating particular principles and patterns underlying grasping ability. Nevertheless, it is likely that all aspects play important roles in all groups. For instance, grasping ability and underlying forearm musculature are fairly well conserved among most tetrapod clades (Iwaniuk & Whishaw, 2000; Abdala & Diogo, 2010). Digital muscle and tendon complexity may limit, or enhance, digital independence, which could have important implications for grip force production and/or digital dexterity. Several mammals employ both manual and pedal grasping, ostensibly driven by selection for both food manipulation and substratum use. However, there are also important differences in the morphological underpinnings and selective contexts among groups.

(1) Anatomical underpinnings to tetrapod grasping

We suggest at least two prevailing common anatomical threads among tetrapods that grasp. The first feature of obvious significance is the presence of opposable digits. Although grasping may be accomplished without opposable digits (e.g. scissor grasping between digits II and III as described above for many marsupials, raccoons, and some primates), frogs with opposable digits demonstrate greater dexterity and finger mobility than frogs without opposable digits. Although truly opposable digits have not been reported in lizards other than chameleons, our data show that digit I is sometimes more (e.g. *Polychrus* spp.) or less (e.g. *Liolaemus cuyanus*) differentiated from the others, thereby forming an incipient basis for opposability among squamates. In birds, the transition to an opposable hallux from an anterior- or medially directed one characteristic of their theropod ancestors (Middleton, 2001) was an essential step, one that has progressed evolutionarily into several different toe patterns that consistently involve one or two digits placed in opposition to the rest (e.g. Raikow, 1985).

The second common thread is in the relative development of the digital extensor and flexor muscles. Grand (1977) suggested that despite the diversity of locomotor strategies that have evolved to exploit the same supports, certain features of the forest canopy select for similar tissue proportions. Arboreal mammals tend to have relatively more muscle mass devoted to the forearms and shanks, and less to the epaxial musculature (Grand, 1983). For most terrestrial tetrapods, the flexors and extensors are activated in alternation during stance and swing phases during locomotion (Liem *et al*., 2001). For those that tend to cling and climb, however, the flexors might play a relatively more important role for counteracting the force of gravity. Myatt *et al*. (2012) reported that the digital flexors of chimpanzees, bonobos, gorillas, and orangutans had the largest PCSAs of all of the distal forelimb muscles. Moreno (1991) and Raikow (1994) demonstrated that in scansorial birds (e.g. woodcreepers) the distal hindlimb flexors (those that act to bring the centre of gravity closer to the substratum) are relatively more developed than their antagonists. Similarly, we could reasonably hypothesize that in graspers there should be greater development of the digital flexors relative to the extensors (in terms of PCSA) compared to non-graspers. A comparison among a few species of mammals and birds for which such data are available suggests that this is so. In grasping mammals such as gibbons (Hylobatidae), the ratio of the PCSAs of the primary forelimb digital flexors [m. flexors digitorum superficialis (FDS2) and digitorum profundus (FDP1)] to extensors [m. extensors digitorum communis (EDC) and pollicis longus (EPL); Michilsens *et al*., 2009] averages 6.7 across four species, compared with a ratio of 2.2 for homologous muscles in digitigrade, cursorial dogs (i.e. 'superficial digital flexor' plus three humeral, radial, and ulnar heads of the 'deep digital flexor', divided by the 'common digital extensor' plus 'lateral digital extensor', averaged across four individuals; Shahar & Milgram, 2005). Grand's (1977) work demonstrated that these patterns hold with respect to muscle mass as well. For instance, in the potto (*Perodicticus potto*) and slow loris (*Nycticebus* spp.), the m. flexor digitorum tibialis is equal to, or twice, the mass of the distal hindlimb extensors, respectively. In macaques (*Macaca* spp.), finger flexors and wrist deviators, and toe flexor and ankle deviators, comprise the greatest mass of muscles below the elbow and knee joints, respectively (Grand, 1977). Among birds, the primary flexor (m. flexor digitorum longus) and extensor (m. extensor digitorum longus) of the fore-digits for a 'grasping' passerine, the black-billed magpie (*Pica pica*; Verstappen, Aerts & Vree, 1998), is 4.6, compared with 2.1 for a 'non-grasping' cursorial ratite, the ostrich (Smith *et al*., 2006). Surprisingly, the same ratio for raptors (averaged over several individuals and species of *Accipiter* hawks and falcons; Sustaita, 2008, and associated unpublished data) is only 1.5. However, the average ratio of the primary hind-digit flexor (m. flexor hallucis longus) to extensor (m. extensor hallucis longus) is 15.6 from the same data set. Not only does this highlight the importance of a powerful hallux for raptors (Goslow, 1972), but this also suggests a greater role for their digital extensors. Perhaps these counteract their pronounced flexor tendon-locking mechanisms (Einoder & Richardson, 2006, 2007*b*), or otherwise facilitate greater power for disengaging the talons and opening the digits between bouts of grasping and kneading prey (Fowler *et al*., 2009).

Despite these and other anatomical similarities that favour grasping, such as increased size of digit flexor muscles, complexity of their origins, and the lengths of distally inserting tendons (Tulli *et al*., 2012), avian (pedal) and non-avian tetrapod (manual and pedal) grasping morphologies differ in a few important ways. One is the involvement of the metapodials (e.g. palm, thenar, and hypothenar regions of the manus) in the 'power grasp' of non-avian tetrapods (described above for *Anolis* and *Polychrus* lizards). This means that the proximal phalanges of bird feet assume the role that the metapodials play in the appendages of other grasping tetrapods in providing a base for the phalanges to close against when grasping an object (*cf*. Landsmeer, 1962; Marzke *et al*., 1992; Pouydebat *et al*., 2008). In birds this effectively reduces the degrees of freedom (and contact points) in the digits available for grasping relative to other tetrapods, and could have implications for their grasping kinematics and performance in terms of precision.

The ability to move the digits independently might contribute to differences in grasping capability, particularly in precision gripping (Schieber, 1991). Schieber (1995) noted that, among mammals, the ability to individuate finger movement increases from ancestral to derived taxa, and is reflected to some extent in species-level differences in muscle structure. For instance, in macaques digits I, II, and V are controlled by relatively fewer multi-tendoned muscles, whereas in humans (and gibbons; Myatt *et al*., 2012; Diogo, Richmond & Wood, 2012) they tend to be operated by separate mono-tendoned muscles (partly a result of a separate m. flexor pollicis longus belly), resulting in a greater degree of digital independence (Schieber, 1995). In certain frog genera, the forearm muscles are highly differentiated and appear to control each digit individually (e.g. Herrel *et al*., 2008*a*). The independence of hand and digit muscles and tendons of several squamates (and even freshwater turtles) are thought to foster a greater range of hand motion (Abdala, Manzano & Herrel, 2008). That performance of selected digit movements requires 'additional control to individuate motion or force' (Schieber & Santello, 2004: 2293), suggests that, across taxa, increases in the number of actuators may be associated with increased digital dexterity. Nevertheless, the number of actuators that control digital movements is similar among non-mammalian tetrapods. Abdala & Diogo (2010) described 8–11 homologous forelimb digital muscles across six major amphibian and reptilian clades (including Aves) based on patterns of innervation, function, structure, and phylogeny. By comparison, prosimian primates possess 30–36, anthropoid monkeys and apes possess 20–27, and humans possess 21 hand muscles (Diogo & Wood, 2011).

Vereecke *et al*. (2005) described approximately 17 hindlimb digital muscles that insert on the metatarsals or phalanges in gibbons and bonobos, both known to use their feet extensively for grasping. Avian hindlimbs have evolved a digital flexor group with several subdivisions (Hutchinson, 2002), and most lineages possess up to 21 flexors, extensors, adductors, and abductors that primarily operate the digits (Raikow, 1985). However, the largest and most derived lineage, the Passeriformes, which is characterized in part by the loss of most (if not all) of the seven intrinsic digital muscles (Raikow, 1982), seems to have converged upon a more simplified system of digit actuation more typical of other tetrapods. Abdala & Diogo (2010) suggested the complexity of extrinsic hand musculature (in conjunction with more distal insertions of some components) evolved in a few derived tetrapod taxa in association with greater digital dexterity. However, the functional significance of these various degrees of digital muscle complexity is not entirely clear. A single, multi-tendoned muscle can activate multiple digits, and conversely multiple muscles can operate a single digit, but usually complex interactions among multiple muscles dictate individual or collective movements of the digits (Schieber, 1995). For instance, because of mechanical coupling and/or neuromotor synchronization, surprisingly few statistically distinguishable kinematic patterns are required to reconstruct a large variety of human hand postures (Schieber & Santello, 2004). Such patterns, however, have yet to be quantified for non-primate tetrapods.

Tendon morphology also varies considerably within and across groups. Although variation in tendon length among Neotropical iguanian lizards appears to be driven more by phylogeny than habitat use (Tulli *et al*., 2012), tendon configuration may impart a functional signal in association with muscle actuation and digital individuation. Among lizards and birds, several different tendon patterns allow varying degrees of mobility of the manus and/or pes and individual digits. Lizards that possess tendon patterns that afford greater interdigital independence and flexibility of the tendon plate (P- and G-patterns, respectively) tend to be those with greater grasping capabilities (Abdala *et al*., 2009). In birds it is unclear how tendon patterns correlate with grasping function (Raikow, 1985). The Passeriformes, which are characterized by having a derived perching foot, possess the Type VII tendon arrangement that affords independence between the foredigits and hallux (Raikow, 1985). However, other groups, such as raptors, parrots, and mousebirds, also renowned for their grasping capabilities, possess other arrangements with more or less limited independence between opposing sets of digits (Types III, I, and V, respectively; Berman & Raikow, 1982; Raikow, 1985). Among mammals, some forearm and hand muscle (e.g. m. extensor carpi radialis longus, m. extensor carpi radialis brevis, and m. flexors carpi radialis and ulnaris) tendons insert more distally onto the metacarpals, compared to the plesiomorphic radial/ulnar or carpal insertions exemplified by most tetrapod lineages; this is thought to enhance digital movement capabilities (Abdala & Diogo, 2010). Clearly there is not a one-to-one mapping of grasping form to function (e.g. Wainwright *et al*., 2005), neither within nor among tetrapod groups. Although multiple digital musculoskeletal morphologies underlie grasping capability, the extent to which different configurations yield similar levels of performance awaits quantification (e.g. Alfaro, Bolnick & Wainwright, 2005).

(2) The role of ecology in grasping morphology

Iwaniuk & Whishaw (2000) provided a phylogeny-based overview of skilled forelimb movements [‘movements of the limbs, paws, and digits for catching, holding, and manipulating objects’ (Whishaw, 2003, p. 33)] among tetrapods, indicating that behaviours associated with forelimb dexterity evolved early in tetrapod evolution. The ubiquity of skilled forelimb movements in the context of feeding among tetrapod clades (Whishaw, 2003) bolsters the role of feeding in selection for grasping performance, and grasping enhances overall feeding performance. For instance, although rats typically grasp food with their mouth upon detecting it, when hunting live crickets they use a single forepaw to grasp and immobilize them, followed by the tips of their digits to hold and manipulate the crickets for ingestion (Whishaw, 2003). However, it seems that the crux of tetrapod fore- and hindlimb prehension is the arboreal context within which more complex forms of grasping are presumed to have arisen (e.g. as in birds, above). Adaptations for grasping in association with arboreality present important exaptations for other uses of grasping in the contexts of feeding (prey capture and handling), reproduction (e.g. amplexus or nest-building in frogs), and tool use (e.g. primates). However, to maintain traction and balance for climbing and perching in arboreal habitats does not preclude other potential causes for the development of grasping capability. For instance, Cartmill (1974*b*, p. 442) contested the idea that arboreality selected for primate grasping extremities, and instead suggested that they evolved ‘because they facilitate cautious well-controlled movements in pursuit of prey on slender supports’. As a case in point, Cartmill (1974*b*, p. 440) reasoned that claws, characteristic of ancestral primates and other arboreal animals, but reduced to flattened nails in more derived primates, may be advantageous for arboreal locomotion under most circumstances, but would actually impair the abilities of a ‘bush-dwelling animal that grasps slender twigs by opposition of preaxial and postaxial digits’ to approach their insect prey cautiously. Recent studies of squirrels (Samaras & Youlatos, 2010; Orkin & Pontzer, 2011) indicated that the presence of functional (keeled) claws does not preclude medium-sized species from using terminal branches, warranting further investigations into the effects of claws on grasping, and more generally, how grasping morphology maps onto patterns of substratum use (Samaras & Youlatos, 2010).

A potentially important corollary to the selective context of grasping among tetrapods is the decoupling of fore- and hindlimb apparatuses from one another, and from the task of locomotion. Many animals effect this behaviourally; for instance, rats sit on their haunches when they manipulate food items with their forepaws (Whishaw, 2003). Similarly, frogs and lizards that are known to manipulate food manually (see above) support themselves extensively with their hind feet. A more integral decoupling occurs in modern birds, in that the hindlimbs are thought to comprise a separate locomotor module from that of the wings and tail (Gatesy & Dial, 1996). A similar form of wing and hindlimb decoupling has also been proposed for bats and pterosaurs (Bell, Andres & Goswami, 2011). Incidences of such decoupling exist in terrestrial quadrupeds, but are less clear cut. Sylvester (2006) suggested that decoupling of the fore- and hindlimbs in early hominins may have facilitated the evolution of bipedalism, by allowing effective terrestrial and suspensory capabilities simultaneously. In other primates, however, the fore- and hindlimbs are used simultaneously during locomotion, and may comprise a single locomotor module (Sylvester, 2006). Thus, the extent to which such locomotor-module decoupling occurs in other tetrapods is unclear. A more common, perhaps subtler, variation of this decoupling is a shift of weight-bearing responsibilities from the fore- to the hindlimbs (Sylvester, 2006; Youlatos, 2008; Kivell, Schmitt & Wunderlich, 2010). Lower peak vertical substratum reaction forces on the forelimbs relative to hindlimbs during quadrupedal walking have been observed for other primates and at least one other arboreal quadrupedal mammal (woolly opossum; Schmitt & Lemelin, 2002). This pattern of weight distribution is thought to reflect a shift in forelimb function from support to greater mobility and grasping ability (Schmitt & Lemelin, 2002, and references therein). Thus, a comprehensive, phylogenetically explicit examination of fore- and hindimb loading patterns between grasping and non-grasping tetrapods may be useful for testing the incidence and evolutionary importance of fore- and hindlimb decoupling for grasping capability.

(3) The role of grasping in tetrapod evolution

We hope that we have convinced readers that tetrapod grasping form and function is a contemporary and vibrant research avenue. We acknowledge that our review does minimal justice to the depth and detail achieved in this area by workers of various sectors of zoology, anthropology, and medicine. Nevertheless, based on what we have gathered from juxtaposing independent investigations of grasping form, function, and evolution in each major tetrapod clade, we present a series of priorities for enhancing research programs dedicated to the functional and evolutionary morphology of grasping. Grasping performance might play a more critical role in tetrapod evolution than currently understood. Among the tetrapod clades considered here, groups characterized by enhanced grasping capabilities are among the most speciose of their respective clades. Naturally, species diversity may be attributable to a variety of other factors potentially correlated with grasping capability. Nevertheless, the capacity to grasp has been posed as a 'critical adaptive innovation' for arboreal primates (Kivell *et al.*, 2010) and a 'key feature' of primate evolution (Ravosa & Dagosto, 2007). We suggest that in order to perform a thorough, phylogenetically explicit analysis of the role of grasping in tetrapod evolution, more information needs to be gathered with respect to the presence and absence of grasping behaviour across a wider range of tetrapod taxa. Furthermore, though it is often treated as such, grasping is not necessarily a discrete behaviour, warranting the development of an objective and universal metric for grasping propensity. For the purpose of our review we have qualified grasping performance rather broadly as realized manual and/or pedal digit prehensile capabilities. However, in our previous work and that of others presented herein, grasping has been quantified in a number of ways, from measurements of force (e.g. Ward *et al.*, 2002; Abdala *et al.*, 2009; Manzano *et al.*, 2008; Sustaita & Hertel, 2010; Rolian *et al.*, 2011; Williams *et al.*, 2012), to scores of the numbers of different types of grasps used on different objects during behavioural observations (Pouydebat *et al.*, 2008, 2009, 2011), to differentiating between the two principal roles of precision *versus* force. In the human performance literature, grasping capability has been quantified using a variety of other kinematic and kinetic techniques. This in part reflects the diversity of goals for quantifying grasping capability within and across disciplines. For instance, quantifying dexterity, or precision grasping, often involves different techniques than those used for quantifying strength, or power grasping. Morphofunctional attributes that promote grasping strength can conflict with those that promote digital speed and dexterity, resulting in potential trade-offs (Sustaita, 2008). Thus, we suggest that research endeavours that aim to quantify attributes of both grasping strength and precision would be particularly insightful for testing such trade-offs. Furthermore, it seems to us that experiments should be conducted in unconstrained environments (i.e. forelimb free to move) and under comparable conditions (i.e. same items and environment) to truly judge the movement potential in different taxa. In addition, where grasping is extensively involved in feeding and locomotion (e.g. birds and mammals) food grasping should be compared with substratum grasping in the context of locomotion to understand better the behavioural and functional precursors for food-grasping abilities. Finally, we suggest that analyses of fore- and hindlimb loading patterns and kinematics, such as those cited above, will contribute substantially to evaluating the importance of fore- and hindlimb decoupling from one another, and the task of locomotion, in the development of grasping ability.

The study of tetrapod grasping performance has much broader implications. Grasping in birds has been a topic of interest in neuroanatomical and behavioural fields. Research on handedness in birds has shed interesting insights into eye-foot coordination and cerebral lateralization (Harris, 1989; Csermely, 2000; Izawa, Kusayama & Watanabe, 2005; Brown & Magat, 2011), and the study of grasping ability has generated profound insights into sensory control and brain function in mammals (Whishaw, 2003). Outside the realm of vertebrate biology, avian grasping performance has been a source of bioinspiration and biomimicry, as mechanical engineers have explored the efficacy of the avian foot ‘design’ for robotics applications (e.g. Ramos & Walker, 1998; Doyle *et al*., 2011). In turn, guiding principles of robotics, such as coupled and underactuated mechanisms (e.g. Dollar & Howe, 2011), may help explain the anatomical complexities and versatility of the avian foot (S. Backus, D. Sustaita & A. Dollar, in preparation). Thus, we suggest that a broader application of current techniques to the study of grasping capabilities in non-human tetrapods may yield important and mutually beneficial insights for both applied and academic endeavours.

VII. CONCLUSIONS

(1) Grasping behaviour plays an essential role in locomotion, feeding, and reproduction in a great diversity of tetrapod vertebrates, but has received relatively little attention outside of the anthropological and biomedical literature. Although the ability to reach for food or prey, to hold it in a forepaw, or manipulate it with the digits exists in most tree-dwelling frogs, it is often considered to be most developed in mammals. Grasping modalities may differ from group-to-group, but they share common musculoskeletal bases and selective pressures.

(2) Among lissamphibians, anurans demonstrate the greatest complexity of forelimb movements, which have evolved several times independently. Features such as relatively long forelimbs, intercalary elements of the hand skeleton, adhesive sub-digital pads, and opposable digits facilitate their abilities to perform both power and precision gripping, that ultimately enhance their arboreal locomotion and feeding abilities.

(3) Grasping in lizards appears to be driven largely by selection for navigating complex three-dimensional habitats, and plays relatively less of a role in other behaviours such as feeding. The tendinous pattern of the palm of the hand plays a key role allowing the flexion of the metacarpo-phalangeal joints. Lizards exhibiting the L-pattern (a single tendinous plate from the m. flexor digitorum longus to the digits, with embedded sesamoids) are not capable of flexing the metacarpo-phalangeal joint, and complete power grasping abilities are restricted to those exhibiting the P- (reduced or absent flexor plate) or G-patterns (flexor plate with reduced sesamoids). Like tendon structure, the configuration of the wrist and hand bones also appears to correlate with grasping ability. Those taxa, such as chameleons, anoles, geckos, and varanids, that exhibit varying degrees of manual grasping abilities, also exhibit pedal grasping abilities.

(4) With the evolution of flight in birds, the capacity for manipulating objects progressively became relegated to the hindlimbs, resulting in enhanced pedal grasping abilities relative to other tetrapods. An important precursor to the evolution of grasping in birds was the reversal and incumbency of the hind toe (hallux) to form an opposable digit. Digital flexor muscle size and complexity, and tendon-locking mechanisms likely play important roles for producing and maintaining grip forces. The functional significance of other features of the avian pes, such as the various toe and digital flexor tendon configurations, proportional phalanx lengths, and claw size and shape is not explicitly clear, but these features are likely also involved in enhancing grasping capability. Although feeding is most certainly an important selective force for grasping capability, on a larger evolutionary scale it is confounded with the adoption of an arboreal existence.

(5) In mammals, grasping occurs extensively during food manipulation, while moving or standing on arboreal supports, and involves both manual and pedal grasping. The vast majority of work in this vein pertains to primates. Current hypotheses for primate origins propose that the use of fine terminal branches to exploit fruits, flowers, insects, and nectar may have constituted an important selective pressure driving the evolution of primate grasping. The power grip may be one of the most common in mammals because it is used by animals with opposable, pseudo-opposable, and non-opposable thumbs. Adaptive changes in the integumentary structures of the hand in mammals might have been essential in the diversification of foraging strategies. Primates and other mammals possess pedal grasping adaptations that may have contributed to the evolution of manual dexterity.

(6) Grasping ability and underlying forearm musculature are fairly well conserved among most tetrapod clades. The presence of opposable digits and the relative development of the digital extensor and flexor muscles appear to underlie the grasping abilities of most tetrapods. Digital muscle and tendon complexity may limit, or enhance, digital independence, which, in turn, could have important implications for grip force production and/or digital dexterity. There is not a one-to-one mapping of grasping form to function, neither within nor among tetrapod groups; however, the extent to which different configurations yield similar levels of performance awaits quantification. Despite the role of feeding in selection for grasping performance, the crux of tetrapod fore- and hindlimb prehension appears to be the arboreal context within which more complex forms of grasping are presumed to have arisen. A potentially important corollary to the selective context of grasping among tetrapods is the decoupling of fore- and hindlimb apparatuses from one another, and from the task of locomotion. Grasping performance might play a more critical role in tetrapod evolution than currently understood. However, more comprehensive data on grasping behavior and functional morphology, from a greater diversity of taxa, are required to test this in a rigorous phylogenetic framework.

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