

Fascinating Life Sciences

Vincent Bels · Anthony Patrick Russell *Editors*

Convergent Evolution

Animal Form and Function

This volume presents a series of case studies, at different levels of inclusivity, of how organisms exhibit functional convergence as a key evolutionary mechanism resulting in responses to similar environmental constraints in mechanically similar ways. The contributors to this volume have selected and documented cases of convergent evolution of form and function that are perceived to be driven by environmental abiotic and/or biotic challenges that fall within their areas of expertise. Collectively these chapters explore this phenomenon across a broad phylogenetic spectrum. The sequence of chapters follows the organizational principle of increasing phylogenetic inclusivity, rather than the clustering of chapters by perceived similarity of the phenotypic features or biomechanical challenges being considered. This is done to maintain focus on the evolutionary phenomenon that is the primary subject matter of the book, thereby providing a basis for discussion among the readership about what is necessary and sufficient to justify the recognition of functional convergence. All chapters stress the need for integrative approaches for the elucidation of both pattern and process as they relate to convergence at various taxonomic levels.



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 Springer

ISBN 978-3-031-11440-3



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Chapter 12

Convergent Evolution of Manual and Pedal Grasping Capabilities in Tetrapods



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Abstract Grasping behavior and manipulation using the hand and/or foot is widespread among tetrapods and can be used in various contexts in the daily life of many species. Activities such as feeding and movement through the environment may be assisted by grasping. Well-defined digits and digital musculature are synapomorphies of the tetrapod clade and from this foundation other features, such as opposable digits and tendon configurations, have evolved independently in many lineages. The evolutionary transitions leading to grasping and manipulative behaviors are complex and require better understanding. Here we survey the evolution of grasping autopodia and their forms and functions across four major tetrapod clades, revealing that the underlying morphological bases and ecological factors may differ among tetrapods. Further interdisciplinary approaches, including eco-ethology,

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morphology, biomechanics, ontogeny, and even genetics, relating to grasping form and function within and among tetrapods must be developed for a better understanding of the role that object/substrate/food grasping abilities play in the evolutionary success of several tetrapod lineages.

Keywords Grasping · Manipulation · Tetrapods · Dexterity · Feeding · Locomotion

12.1 Introduction

The ability to grasp and manipulate substrates and/or objects is fundamental from an evolutionary point of view (Sustaita et al., 2013). Indeed, these actions are involved in locomotion, postural stabilization, food acquisition and processing, social interactions and have contributed to the evolutionary success of many groups of vertebrates. Thus, grasping is fundamental to the behavioral repertoires (i.e., locomotion, feeding, and reproduction) of many vertebrates, and has implications for fitness. Nevertheless, data relating to this are scarce other than those relating to human biomechanics, kinesiology, medicine and physical anthropology (e.g., Susman, 1998; Marzke & Marzke, 2000; Pouydebat et al., 2014; Feix et al., 2015). Many studies have analyzed the evolution of structural variation of the hominid hand with regard to prehensile capabilities, emphasizing how grasping capabilities were involved in the origins and use of tools (Napier, 1956; Marzke et al., 1992; Marzke, 1997; Susman, 1998; Kivell et al., 2011; Borel et al., 2016; Vigouroux et al., 2018; Bardo et al., 2020). Nevertheless, grasping behavior is much more widespread. Defined as the application of functionally effective forces by an appendage to an object for a task, grasping can be accomplished by the limbs, the tail, the trunk, the tongue, the teeth, or other animal parts (Mackenzie & Iberall, 1994; Lefeuvre et al., 2020). When focusing on the autopodia (hands and feet), grasping involves orientating and positioning of the digits along with appropriate displacement of the limb to accomplish the correct location of the grasping structure in space (Mackenzie & Iberall, 1994). Gripping suggests a static posture, but grasping is achieved by the dynamic development of a posture (Malek, 1981). Napier (1956) described the power grasp that is used for stability and security. He defined it as a primary grasp that provides the ability to resist slipping. He distinguished it from the precision grasp that is used for dexterity and sensitivity, whereby the digits are able to sense and monitor small changes in force and position. Specialists in robotics have expanded these definitions and have distinguished several grasping types within the power vs. precision grasping dichotomy (Cutkosky & Wright, 1986; Cutkosky, 1989; Cutkosky & Howe, 1990). Thus, they have identified nine types of power grasp that are characterized by “large areas of contact between the grasped object and the surfaces of the fingers and palm and by little or no ability to impart motions with the fingers” (Cutkosky, 1989, p. 272). These nine types differ according to whether

they result in wrapping (i.e., for a prismatic object), or employ radial symmetry (i.e., for a circular object), and include the lateral pinch (i.e., bringing into opposition the first digit [generally the thumb] and the other digits which act as one gripping surface) and the non-prehensile grasp (i.e., a flat platform holding the object). With regard to the precision grasp (the object being held with the tips of the digits and thumb), Cutkosky (1989) identified seven different types according to the pattern of radial symmetry adopted (i.e., disk, sphere, or tripod [only three digits participating in grasping]), or with opposition occurring between the thumb and other, more laterally-situated, digits (i.e., for prismatic objects). Even though these definitions and categorizations are based on human hands, they have been applied to other primates (Pouydebat et al., 2009, 2011; Bardo et al., 2016, 2017) and can be applied to other groups of tetrapods. Indeed, frogs and lizards have also evolved significant forelimb grasping capabilities (e.g., Manzano et al., 2008; Abdala et al., 2009; Anzeraey et al., 2017). Iwaniuk and Whishaw (2000) suggested that ‘rudimentary skilled forelimb movements’, including grasping and manipulating with the digits, likely originated at the base of the tetrapod clade. These types of movements are probably homologous in frogs and mammals, and various losses of these abilities across taxa may have occurred independently. The examination of the forelimb musculature of tetrapods that ultimately underlies these movements demonstrates a large number of homologies across clades (Abdala & Diogo, 2010; Kardong, 2011), revealing six relevant ‘muscular complexes’ of the hand and forearm (ulnar extensors/flexors, radial extensors/flexors, and digital extensors/flexors). Thus, skilled movement behaviors made by the hands and/or feet seem to be phylogenetically conserved in tetrapods, from tree frogs to the first stone tool users, but also exhibit strong selective versatility.

We already know that the ability to grasp with the hand is often presumed to result from selective pressures associated with arboreal locomotion (e.g., Grillner & Wallen, 1985; Bracha et al., 1990) and/or prey capture (Iwaniuk & Whishaw, 2000). It seems that both arboreal locomotion (e.g., Gebo, 1985; Feduccia, 1999; Youlatos, 2008) and food acquisition (e.g., Fowler et al., 2011) are also implicated in the evolution of grasping with the foot in tetrapods. However, compared to manual grasping behavior and its associated anatomy, data on pedal grasping abilities are scarce. Here, we review grasping behavior as the ability to grasp and manipulate objects or substrates through voluntary movements of the hand and/or foot by exerting force (Sustaita et al., 2013). Our objective is to explore the form, function, ecology, and evolution associated with autopodial grasping in the context of each major extant tetrapod clade: Lissamphibia, Lepidosauria, Aves, and Mammalia. We hope to improve our understanding of the phenotypic variation exhibited by grasping autopodia and the selective forces that have shaped the evolution of grasping ability by exploring contemporary approaches incorporating measurements of grasping performance (i.e., force and precision). This review presents the opportunity for clarifying both the functional and ecological consequences of variation in musculo-skeletal morphology and behavioral patterns of grasping and highlighting patterns of convergence among disparate tetrapod clades.

12.2 Grasping in Lissamphibians

Anurans are characterized by the absence of discrete caudal vertebrae and a truncated axial skeleton. Girdles and paired appendages develop at larval stages and integrate with the axial skeleton simultaneously with tail regression (Rocčková & Rocěk, 2005; Handrigan & Wassersug, 2007; Pugener & Maglia, 2009; Manzano et al., 2013; Fabrezi et al., 2014). With this derived morphology many locomotor modes develop, such as jumping, which is considered the primary locomotor activity from which the other modes of locomotion of anurans, such as hopping, walking, swimming and climbing (Emerson & Koehl, 1990; Gomes et al., 2009; Manzano et al., 2018), derive (Příkryl et al., 2009).

Swimming, walking, burrowing to construct refugia, building nests, spreading substances on their skin, or even grasping objects such as branches, each associated with a different behavior and ecological context, are reflected in anatomical adaptations (Robovska-Havelkova et al., 2014; Liao et al., 2015; Manzano et al., 2017; Hill et al., 2018; Frýdlová et al., 2019) (Fig. 12.1a–c). Those adaptations are mainly found in the autopodia (hands and feet), which exhibit extensive variation highlighting the ecological importance of the manus and pes (Duellman & Trueb, 1986; Irschick et al., 1996; Zaaf & Van Damme, 2001; Rothier et al., 2017). For example, anuran manus bear four digits and their pedes carry five, and these digits may vary in

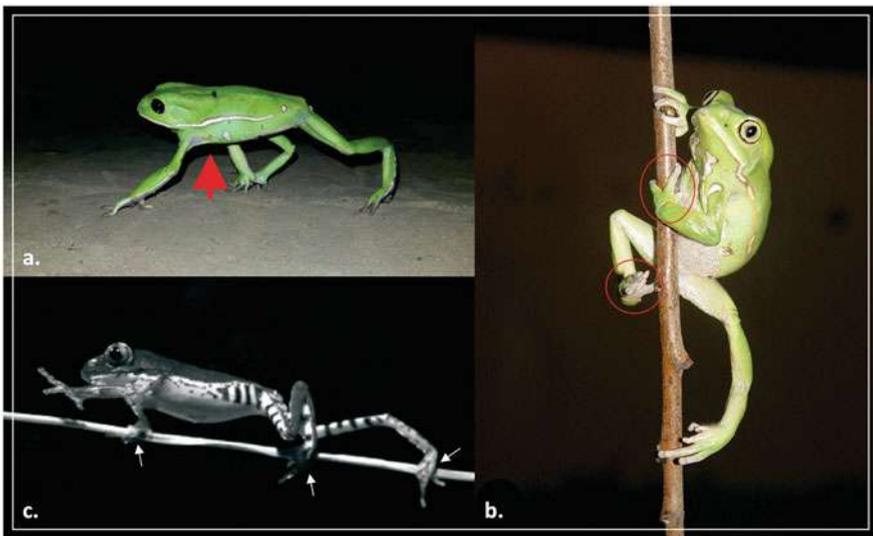


Fig. 12.1 Species of *Phyllomedusa* moving on different substrates. (a) *P. sauvagii* elevates its body during walking (modified from www.inaturalist.org/observations/22510236). Red arrow indicates body elevation during locomotion; (b) *P. sauvagii* adjusts its wrists and ankles to permit grasping during vertical locomotion on a narrow perch (modified from Manzano et al., 2017); (c) Grasping of *P. azurea* on an inclined, thin branch [modified from Herrel et al. (2013a)]. White arrows indicate the point of hand-perch contact during the grip on an inclined substrate

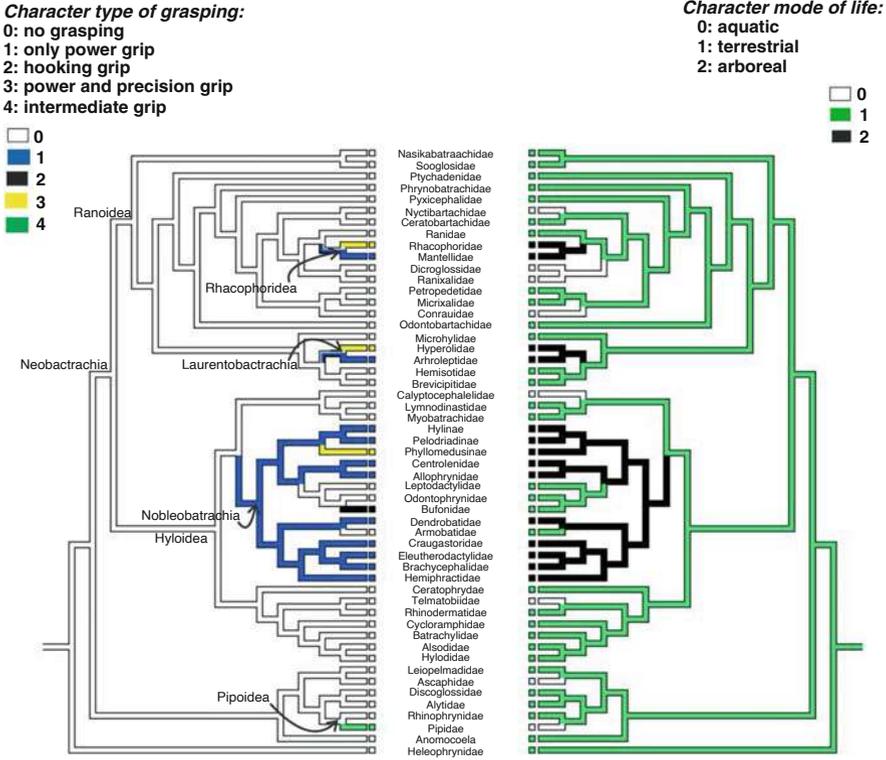


Fig. 12.2 Ancestral reconstruction of characters related to grasping capabilities in anuran amphibians using parsimony with Mesquite 2.7 (Maddison & Maddison, 2019), based on Jetz and Pyron (2018) and Feng et al. (2017). The comparison of grasping types (Table 12.1) and mode of life suggests that ancestral anurans lacked grasping abilities. The ability to grasp appeared at least three times within the Neobatrachia: Nobleobatrachia, Laurentobatrachia, and Rhacophoroidea. The precision grip specialization occurs within the groups Phyllomedusinae, Rhacophoridae, and Hyperoliidae (in yellow). All frogs with a precision grip share an arboreal mode of life. The case of Pipidae could be interpreted as a novelty because they exhibit a different type of grip employed in its aquatic mode of life (Napier, 1956; Anzeraey et al., 2017). The hooking grip has been described only for Bufonidae and this manifests only as a behavior pattern

length due to reduction or loss of phalanges, or an acquisition of additional structures such as intercalary elements (additional connective tissue, bony or cartilaginous structures occurring between the penultimate and ultimate phalanx in the digits of many anurans; Duellman & Trueb, 1986; Manzano et al., 2007). Intercalary elements are considered to be an adaptation for climbing. Some frogs may also have sesamoid bones embedded in the flexor plate of hands and feet (Ponssa et al., 2010), the functional implications of which are unclear (Fig. 12.2a, b). All such adaptations of their limbs involve bone-muscular-ligament system modifications.

Table 12.1 Descriptions of the types of grip according to the position of digits and the forces exerted on an object

Grip type	Definition	Author
Power	The object is held in a clamp, involving the partially flexed fingers and the palmar and plantar surfaces. The arm and the leg exert the forces on the object.	Napier, (1956), Feix et al. (2016), Manzano et al. (2018)
Precision	The objects are held with the tips of the fingers, which oppose each other. The opposing forces exerted between the fingers on the object are weak, but they provide dexterity to the hand or feet.	Napier (1956), Feix et al. (2016), Manzano et al. (2018)
Intermediate/scissor	The objects are held by the medial and lateral sides of two adjacent digits. Forces are intermediate between those of the above-described grips.	Napier (1956), Anzeraey et al. (2017), Vassallo et al. (2021)
Hooking	The distalmost phalanges of each digit hold the objects. Forces that are exerted do not require strong muscle contraction and are prolonged.	Napier (1956), Vassallo et al. (2021)

Despite adaptations for performing specific tasks some generalist frogs, such as *Rhinella marina* and *Rhinella arenarum*, also practice other skills, such as climbing, to escape when in danger or for exploring while foraging (Hudson et al., 2016; Vassallo et al., 2021) without any specific specializations. Their abilities involve strategies of behavior through the development of a hooking grip that allows them to achieve their objective. The hook-shaped terminal phalanges, combined with the action of the flexor tendons, enable them to climb occasionally to escape from an environment that presents obstacles (Vassallo et al., 2021), although—unlike tree frogs—, they cannot climb on smooth surfaces.

Climbing exclusively in arboreal environments has been considered to be the primary driver of the evolutionary development of skilled movements of the limbs, such as grasping (Manzano et al., 2008, 2018; Hildebrand, 1995; Gray et al., 1997; Cartmill, 1985). The limbs of many arboreal anuran species are relatively long, and intercalary skeletal elements and digital adhesive pads are often present on the hands and feet (Manzano et al., 2007), these being integrated with a muscle-ligament system to prevent the animal from falling (Hanna & Barnes, 1991) from smooth surfaces (Endlein et al., 2017). Additionally, in many arboreal frogs extensive divergence of the angles between the digits, such as those associated with opposability, are present on the hands or feet, or both (Fontanarrosa & Abdala, 2016; Manzano et al., 2018). In species of highly specialized arboreal frogs, such as *Phyllomedusa*, *Chiromantis*, and *Pseudis*, one or two digits have become rotated to lie opposite the others. These characteristics have been related to arboreality and, more specifically, to locomotion among thin branches in complex three-dimensional habitats (Herrel et al., 2013a).

Forelimbs are historically considered to be conserved among frogs and support the body during standing or walking, being *de facto* decoupled from a role in the generation of power for propulsion. Studies in this regard have focused mainly on

the unique saltatory locomotion of anurans (Gans & Parsons, 1966; Lutz & Rome, 1994; Shubin & Jenkins, 1995). The forelimbs also, however, play an essential role in absorbing the impact of forces generated during landing (Nauwelaerts & Aerts, 2006; Akella & Gillis, 2011; but see Essner et al., 2010). Iwaniuk and Whishaw (2000) described specific forelimb movements of tetrapods as skilled movements associated with abilities to hold, reach, and manipulate objects, such as food.

During reproduction, anuran forelimbs play a fundamental role in amplexus: the male embraces the female while the eggs are deposited and fertilized. However, the hands are not particularly modified for the amplexus grasp, except for the presence of some epidermal calluses present on the ventral face of the hands of males. Sexual dimorphism is evident in the development of the muscles of the forearms and in the hands of the males, with the calluses (called nuptial pads) that are present, which help to hold the female during amplexus (Duellman & Trueb, 1986).

In general, the hands are not involved in feeding or even in the search for prey, except for some frogs with grasping hands that have been documented to hold the prey (Anzeraey et al., 2017; Manzano et al., 2018).

Historically, skilled forelimb movements were thought only to be encountered in the primate lineage (Napier, 1956, 1993; Landsmeer, 1962; Marzke et al., 1992; Susman, 1994), but it is now recognized that they are common among tetrapod taxa and probably share a common origin in early tetrapods. Skilled forelimb abilities in taxa other than hominids, primates, and mammals have been documented (Iwaniuk & Whishaw, 2000) and an increasing number of papers have noted the skilled limb abilities exhibited by anurans (e.g., Blaylock et al., 1976; Gray et al., 1997; Vaira, 2001; Sheil & Alamillo, 2005; Manzano et al., 2008; Herrel et al., 2013a; Anzeraey et al., 2017).

Most frogs with the ability to grasp with their hands exhibit similar pedal capabilities. However, studies of the feet of frogs are scarce and have focused mainly on toe pad anatomy and associated sticking abilities (Hanna & Barnes, 1991; Hill et al., 2018) and on 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 using both the hands and feet to grasp branches, even those arrayed at different angles (Herrel et al., 2013a; Hill et al., 2018); see Fig. 12.1. Possible amphibian skills using manual and pedal movements, other than those related to locomotion, deserve more attention.

The hind feet can also display movements other than those associated with grasping during locomotion. The most complex limb movements involving the hands and feet occur during the “wiping behavior” observed in frogs with opposable digits, such as *Polypedates maculatus* and species of *Phyllomedusa* (Lillywhite et al., 1997; Barbeau & Lillywhite, 1999). During wiping frogs spread lipid substances all over their body using their hands and feet (Blaylock et al., 1976). Several arboreal frogs also use their hands and feet to build leaf nests into which their eggs are deposited (Kenny, 1966; Biju, 2009). These frogs also belong to arboreal groups that possess divergent opposable digits (Rhacophoridae, Hyperolidae, and Phyllomedusinae) (Fig. 12.2). Nevertheless, the opposability of digits is not always a characteristic of both the hands and feet.

Frogs capable of exercising skilled wrist movements that use their hands to reach for prey, grasp it and move it into or out of the mouth (Gray et al., 1997) do not, however, appear to use their feet to do this (except for *Phyllomedusa*; Manzano et al., 2018). Surprisingly, the grip used during locomotion in *Phyllomedusa bicolor* was described as being accomplished with a high level of dexterity (Manzano et al., 2008; Herrel et al., 2013a). It was also recorded that species of *Phyllomedusa* can perform power and precision grips (Table 12.1), taking prey by surrounding it with their hand (Manzano et al., 2018). Anzeraey et al. (2017) reported on an intermediate grip (Table 12.1) in the aquatic *Xenopus* (described as the ‘scissor grip’), which is used to hold the prey item but that does not allow the hand to close around it. In addition, the aquatic *Pseudis*, a hylid frog genus with opposable digits on the hands, has fully webbed feet and limited digital movements. They use their hands mainly to float over the vegetation and no grasping has been reported; the feet are used for propulsion during swimming or jumping (Manzano & Barg, 2005).

12.2.1 Anatomical Bases of Grasping and the Precision Grip

As mentioned above, intercalary elements form an integral unit of the limbs of frogs that evolved independently of the phalanges and have been integrated into the developmental program of the forelimb and, in some groups, the hindlimb also (Manzano et al., 2007). The distalmost phalanges, intercalary elements, muscles, and digital adhesive pads act as integrated units to enhance climbing ability (Noble, 1931; Emerson & Diehl, 1980; Mcallister & Channing, 1983; Paukstis & Brown, 1987, 1991; Burton, 1996, 1998a, b). However, the presence of well-developed intercalary elements or digital pads is not always associated with the arboreal mode of life (Manzano et al., 2007). Regardless, they constitute parts of a successful device for preventing falls from slippery surfaces (Hill et al., 2018). Furthermore, the presence of widely divergent angles between digits, such as occurs with opposable digits or some degree of zygodactyly, is believed to reflect specialization for living in an arboreal environment, as can be seen in *Phyllomedusa*, *Chiromantis*, and some mantelids (Manzano et al., 2018). The opposability of one or two digits implies the ability to rotate them so that they face the other digits, with the possibility of their tips being able to touch each other, thereby exerting sufficient oppositional forces on the object to execute a precision grip (Table 12.1). Opposability of anuran digits has been reported (Sheil & Alamillo, 2005; Manzano et al., 2008; Sustaita et al., 2013), but the connection between opposing fingers and the capability of gripping are not always clear. An example of this is encountered among the members of the pseudine group (secondarily aquatic hylid frogs) that are unable to grasp objects with their hands or feet because their digits are practically immobile due to the presence of complete interdigital webbing. The immobile, cylindrical and mineralized intercalary elements of species of *Pseudis* (Hylidae) (Manzano et al., 2007) limit the mobility of the fingers and also their flexion, along with that of the palm, around objects. No reports mention their ability to grasp or climb. Selective pressure has seemingly been

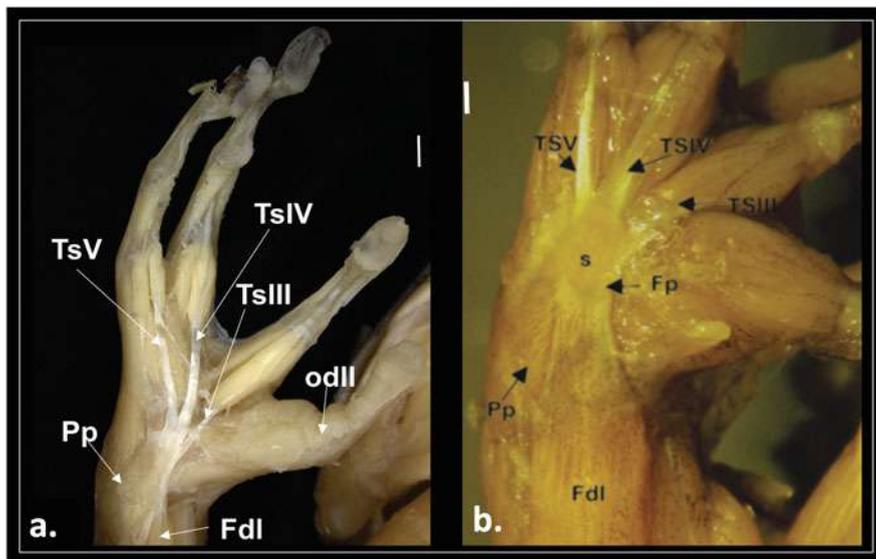


Fig. 12.3 Ventral view of the manus of (a) *Phyllomedusa iheringii* showing the m. palmaris profundus attached to the flexor tendons of digits IV and V. No flexor plate or sesamoid are present. (b) Ventral view of the manus of *Rhinella fernandezae* showing the sesamoid embedded within the flexor plate; the digital tendons arise from it. Abbreviations: *Pp* m. palmaris profundus (“m. flexor accessorius” according to Blotto et al., 2020); *TsII-V* superficial tendons of digits II, III, IV and V, respectively; *odII* opposable digit II; *Fdl* m. flexor digitorum longus; *s* sesamoid; *Fp* flexor plate. Scale: 1 mm

focused on the feet and their role in swimming, rather than on their hands which tend to remain immobile.

When present, grasping ability varies from taxon to taxon, and some specialists for walking on narrow branches demonstrate the most highly derived forelimb and hand movements (*sensu* Iwaniuk & Whishaw, 2000). Species of frogs with fully mobile, opposable fingers appear to have the finest motor control of movements of the hands and fingers. The presence of opposable digits has been associated with the ability for a precision grip (Table 12.1) (Napier, 1956) because as the contact of the tips increases so does the dexterity of finger movement. Even in those species reported to execute manual movements with a high degree of skill, such as *Phyllomedusa sauvagii*, the toe pads do not appear to be highly developed (Manzano et al., 2008) (Fig. 12.3a). They avoid slipping through the power and precision of their grip, with dexterity essentially being used during wiping behavior or other tasks, such as the grasping of narrow branches (Blaylock et al., 1976; Lillywhite et al., 1997).

When tree frogs move on narrow substrates they move their arms independently of one another (as opposed to simultaneous bilateral movements during landing or jumping), and also close their hands (i.e., execute a grip, *sensu* Napier, 1956) to resist rolling torques while walking on branches narrower than the width of their

body (Hill et al., 2018). In the case of *Phyllomedusa* the body can also be raised during walking (Fig. 12.1a, c) and the wrist can be manipulated to ensure the grip (Fig. 12.1b) (Manzano et al., 2017). In species of this genus, the forearm muscles are highly differentiated and appear to be able to control each finger individually (Herrel et al., 2008a). The musculature of the hand of these frogs superficially resembles that of other tree frogs (there is no palmar sesamoid or aponeurosis) but seems to have more complex architecture (Fig. 12.3a). Manzano et al. (2008) mentioned a general increase in the length and cross-sectional area of the muscles, affecting the speed and force of contraction respectively. Also, the presence of strong and long tendons, such as those of the m. extensores breves and m. adductor indicis longus, reflect reduced compliance for greater control of the more distal elements as a result of increased tendon stress. Additionally, the main flexor tendons are independent, resulting in the ability of each finger to be able to be flexed independently (Fig. 12.3a). The presence of muscles with accessory branches (which result in additional insertion sites; Manzano & Lavilla, 1995) are some of the unique characteristics of *Phyllomedusa* that may be related to its greater manual dexterity (Manzano et al., 2008).

For example, there is a close anatomical and functional relationship between the m. palmaris profundus (“m. flexor accessorius” *sensu* Blotto et al., 2020) and the m. flexor digitorum longus as shown by stimulation experiments (Manzano et al., 2008) (Fig. 12.3a). Generally, in frogs (and also in other tree frogs, such as *Tripurion petasatus*; see Blotto et al., 2020) the superficial tendons (the major flexor tendons) originate from the branches of the m. flexor digitorum longus or from a flexor plate and are united by a fascia to the m. palmaris profundus (“m. flexor accessorius” *sensu* Blotto et al., 2020) (Fig. 12.3a, b). In the genus *Phyllomedusa* the m. palmaris profundus attaches directly to the superficial tendon that arises from the medial branch of m. flexor digitorum longus, and when contracted it pulls that tendon laterally 2–3 mm (Manzano et al., 2008), thereby effectively increasing the moment arm of the latter. This actively assists in flexing the hand and wrist, ultimately allowing complete closure of the hand around a narrow perch (Manzano et al., 2008).

The ability to execute complex actions by the limbs, such as grasping, has been interpreted to be an exaptation of the specialization of the forelimbs and hindlimbs for arboreal locomotion (Manzano et al., 2008). However, Anzeraey et al. (2017) demonstrated that the aquatic frog *Xenopus laevis* can perform a complex repertoire of grasping and handling tasks, thus challenging perspectives on the ecological origin of grasping within anurans (Fig. 12.3). The hooking grip performed by the terrestrial generalist *Rhinella* shows unexpected functional capacities that could allow a species to colonize new niches (Vassallo et al., 2021).

12.2.2 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 (Fig. 12.1b) (Manzano

et al., 2008, 2018; Herrel et al., 2013a). *Phyllomedusa bicolor* can generate greater grasping forces than the more generalized *Litoria caerulea*, which may assist in enhancing its stability and allow it to move more securely on narrow substrates. *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 of *Phyllomedusa bicolor* produced pronounced adduction of digits II and IV, causing the extremities of the digits to touch one another, this being required for the generation of a precision grip (Napier, 1956; Feix et al., 2016). Species of *Phyllomedusa* can use both the hands and feet in the same skillful way.

Herrel et al. (2013a) demonstrated that in *Pithecopus azureus* (also a phyllomedusine), hand positions and grip types are highly dependent on the substrate. The substrate can vary in texture, size, diameter and inclination, interfering with the animal's stability during locomotion (Lammers & Zurcher, 2011). In these cases the animals change their grip to optimize interactions with the substrate (Fig. 12.1b, c). Primates can also vary their grip according to the substrate (Lemelin & Schmitt, 1998; Reghem et al., 2012). The effects of the diameter and inclination of the substrate on the grip type and kinematics, at least for primates and lizards, suggest that locomotor mechanics associated with movement on narrow substrates drive movement kinematics independently of morphology and phylogeny (Herrel et al., 2013a; Manzano et al., 2018).

12.2.3 Brain Correlates

Hand movements in humans and other primates involve complex neuronal patterns and functions in the fore- and hindbrain areas. The main center of movement coordination in tetrapods is the cerebellum, with organized layers of cells that regulate coordination of impulses, such as a granular layer of round and small cells and specialized Purkinje cell layers. Despite the conservative organization of the brain among tetrapods, neuroanatomical variation is evident among frogs (Ten Donkelaar, 1998; Manzano et al., 2017). A functionally-related trend towards increased cerebellum size is evident (Taylor et al., 1995). Indeed, Manzano et al. (2017) showed an increasingly complex network of Purkinje cells in the cerebellum of species of *Phyllomedusa* compared to other arboreal and terrestrial species of frogs. This was related to the generation of complex or subtle movements and their associated increased manual dexterity. Purkinje cells are inhibitory cells of the vestibular system that mature during frog metamorphosis and are involved in the cerebellum's sensory process (Gona & Uray, 1980; Llinàs et al., 1967; Ten Donkelaar, 1998).

Although Manzano et al. (2008) experimentally demonstrated the precision grip capacities of the hands and feet of these frogs, the coordination between the movement of the hands and the visual perception of the frogs seems to be limited. During locomotion, visual coordination for controlling landing is essential (Drew,

1991), as Cox et al. (2018) demonstrated. An experimental procedure of labyrinthectomy and ablation of the optic nerves, with the addition of bilateral transection of the sciatic and femoral nerves responsible for proprioception in cane toads, shows that vision is essential for fine-tuning this behavior (Cox et al., 2018). A combination of vision and proprioceptive postural behavior (Lambert & Straka, 2012) may be more highly developed in those frogs that must move in a three-dimensional environment, such as tree branches. In fact, in aquatic frogs, such as *Xenopus*, postural compensation and recovery after damage (the unilateral ablation of the endorgans of the vestibular system) are not possible whereas, for example, in terrestrial frogs they are (Lambert & Straka, 2012). Manipulation other than prehensility to avoid falling from a branch would arise as an exaptation from locomotion favoring increased size and complexity in those structures that allow arboreal locomotion. However, climber-walkers (see also Taylor et al., 1995), hopper-walkers and burrowing frogs have a large cerebellum, suggesting that these abilities, developed with the paired limbs in different locomotor contexts, would have implications for the evolution of the cerebellum in anurans, with the arboreal environment being a driver of more profound cerebellar modifications.

Given the complexity of limb movements observed in frogs and the fact that these evolved independently several times (Fig. 12.2), frogs provide an excellent taxon for better understanding the neurological context associated with the evolution of increased manual dexterity and grasping behavior.

12.3 Grasping in Non-avian Reptiles

The recorded non-avian reptilian species that exhibit manual or pedal grasping abilities are restricted to the lepidosaurs (Abdala et al., 2009; Herrel et al., 2011; Sustaita et al., 2013). The most recent synthesis of prehensility in lepidosaurs is that of Sustaita et al. (2013), wherein it was noted that most studies of limb function in lizards have focused 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, 2011). These studies highlight the ecological and functional diversity that lizards face in nature and the forces driving limb morphology evolution. Lizards use grasping mostly to accommodate locomotion in complex three-dimensional habitats that present discontinuities and gaps between perches. In general terms, feeding or mating behaviors play a lesser role in shaping the grasping skills of lizards than they do in other tetrapods, such as some anuran species (Anzeray et al., 2017; Manzano et al., 2018).

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”. Chameleons (one of the most

Fig. 12.4 Chameleon hand showing the “super-digits” generated by the syndactylous complexes formed by manual digits 1–3 and 4–5. Each complex constitutes a single functional unit (Molnar et al., 2017)



specialized arboreal groups of lizards) are considered the most adept graspers among lizards (Herrel et al., 2011). Chameleons exhibit zygodactylous manus (Fig. 12.4) and pedes and a fully prehensile tail. Some species, such as *Chamaeleo vulgaris*, possess a carpus in which the centrale and distal bones are fused, forming a single spherical element (Renous-Lécuru, 1973). However, in other congeneric species no fusion is evident (Herrel et al., 2013b). The role of this fusion of elements with regard to grasping remains unclear. Interesting data on the development of these autopodial specializations are provided by Diaz Jr. and Trainor (2015). They stressed that chameleons lack an astragalus-calcaneum complex typical of amniotes; additionally, phylogenetically derived chameleons exhibit an ankle structure convergent with that of amphibians (Diaz Jr. & Trainor, 2015). Remarkably, most of the muscles usually present in the hands and feet of chameleons are present in the same configuration as they are in other lizards (Mivart St., 1870; Ribbing, 1913; Gasc, 1963; Molnar et al., 2017). Some peculiarities are, among others, the broad, V-shaped plantar and palmar aponeuroses and the muscle orientation of the superficial short flexors originating from these aponeuroses, which contribute to the functioning of the “super digits” described for this group (Fig. 12.4, Molnar et al., 2017).

Until relatively recently it was thought that chameleons were the only lizards that exhibited autopodial prehensility, but the list has grown with more recent studies. Three other lizard lineages are capable of performing a power grip *sensu* Landsmeer (1962): geckos, *Polychrus*, and anolines (Abdala et al., 2009; Sustaita et al., 2013; Fontanarrosa & Abdala, 2014, 2016), although these have been examined much less extensively in this regard. Interestingly, prehensility in non-chameleon lizards is performed with a hand without the extreme modifications shown by chameleons. Recently, it has been demonstrated that grasping skills of the hands, feet, and tail seem to be affected by the amount of friction the animal can generate between its feet and the perch (Luger et al., 2020).

12.3.1 The Anatomy of the Hands and Feet of a Grasping Lizard

Several anatomical traits of the hand of lizards can be linked to grasping abilities (Abdala et al., 2009; Fontanarrosa & Abdala, 2014, 2016). These specializations are evident in relation to the tendons and bones of the lizard hand and the rather conservative intrinsic muscles of the hand (Russell & Bauer, 2008; Abdala et al., 2009; Abdala & Diogo, 2010; Diogo & Abdala, 2010). Three patterns of the tendons of the palm of the hand have been described: L, P and G (Fig. 12.5). These play a crucial role in the flexion at the metacarpo-phalangeal joints, which provides the main input for the power grip *sensu* Landsmeer (1962). The power grip allows the

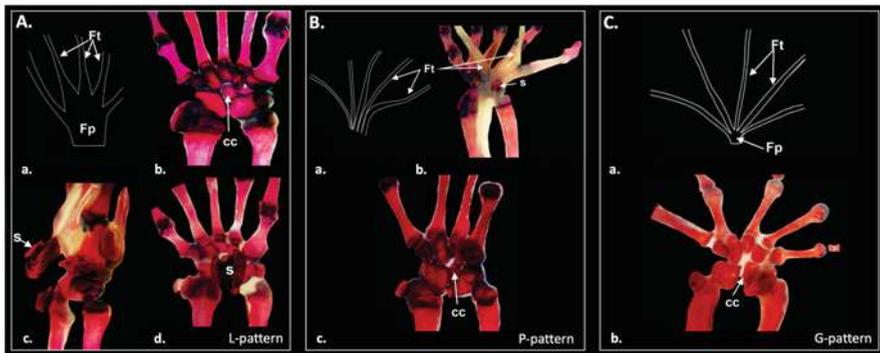


Fig. 12.5 (A) Hand of *Liolaemus cuyanus* showing the L-pattern of palmar tendons with (a) a schematic of the flexor plate and the digital flexor tendons; (b) the centrale located at the center of the palm of the hand; (c) lateral and (d) ventral view of the hand showing the location of the palmar sesamoid. (B) Hand of *Anolis cristatellus* showing the P-pattern of palmar tendons. (a) schematic of the independent flexor tendons to the digits and the reduced palmar sesamoid; (b) digital flexor tendons and the sesamoid embedded in a flexor plate; (c) elongated centrale. (C) Hand of *Homonota horrida* showing the G-pattern of palmar tendons. (a) schematic of the independent flexor tendons serving the digits and the flexor plate lacking the palmar sesamoid; (b) elongated centrale. cc centrale, Fp flexor plate, Ft digital flexor tendons, s sesamoid. Redrawn from Sustaita et al. (2013)

hand to close around a narrow perch or branch. The most widely distributed tendinous pattern within lizards is the L-pattern (Moro & Abdala, 2004; Abdala et al., 2009), consisting of a single tendinous plate that does not allow for extensive metacarpo-phalangeal flexion (Fig. 12.5A). The plate is associated with the *m. flexor digitorum longus*, the largest forearm muscle, and serves the digits through the digital flexor tendons. One or two sesamoids—the palmar sesamoids—are generally embedded in this ‘flexor plate’ (Haines, 1950; Abdala et al., 2009; Regnault et al., 2016). This single tendinous structure prevents independent movement of the digits and instead they move together as a single unit. However, the flexor plate may enhance the flexion of the distal phalanges thereby improving, for example, the grip provided by the claw (pers. obs. VA). Contrastingly, the P-pattern (Moro & Abdala, 2004; Abdala et al., 2009) has a small or no flexor plate and the *m. flexor digitorum longus* serves the digits with independent digital flexor tendons. Palmar sesamoids also tend to be small or absent (Fig. 12.5B). Most anolines and other lizards, such as *Polychrus*, exhibit the P-pattern. Finally, a third pattern, the G-pattern, is present in most geckos (Abdala et al., 2009), the flexor plate of which lacks embedded sesamoids (Fig. 12.5C). Experimental work was conducted showing that the different patterns (L, P, and G) correlate with hand movement capabilities and grasping performance (Abdala et al., 2009). Similar anatomical patterns are recognized in anurans, for example (see Fig. 12.3a, b), but this promising area of research has not been pursued recently. It would be interesting to evaluate experimentally, and with more ecological data from more tetrapod species, the consequences of having a flexor plate in relation to the possibilities for colonizing new niches in, for example, forest trees.

Lizards with a sesamoid embedded in the tendon of the *m. flexor digitorum longus* are not capable of flexing the metacarpophalangeal joints of the hand and therefore cannot execute a power grip. Although the function of sesamoids, even the palmar sesamoid, are still speculative, it can be inferred that the palmar sesamoid allows flexion of the distalmost phalanges through the tension transmitted by the digital flexor tendons, this allowing for a more accurate interaction with the perch (see, e.g., Vassallo et al., 2021). Absence a sesamoid or sesamoids in the palm of the hand appear to facilitate the flexion of the metacarpophalangeal joints, as exhibited by lizards with the P- and G- patterns. It can be inferred that lizards possessing a palmar sesamoid limit tendon movement, thereby resulting in incomplete flexion at the digital joints. In certain cases, however, the pressure of the palm of the hand against the perch combined with a gentle flexing of the terminal phalanges of the hand can generate a form of prensility in lizards with the L pattern of palmar tendons (Fig. 12.6).

Interestingly, a human clinical condition, “trigger-wrist,” can provide clues about the impairment produced by the palmar sesamoid. Humans lack palmar sesamoids but in some circumstances a tumor or nodule occurs on the flexor tendon and/or tendon sheath. This passes through the carpal tunnel and may prevent the sliding of the tendons through this conduit (Förstner & Schaefer, 1998) (Fig. 12.7a). It may be that the tendon of the *m. flexor digitorum longus*, reinforced with a palmar sesamoid as in the L pattern, would have considerable difficulty sliding through the carpal

Fig. 12.6 A gentle flexure of the terminal phalanges of the hand produce a version of prensility in *Iguana* which has the L pattern of palmar tendons. Picture available in the royalty free photos released under public domain license site Pikist.com



tunnel (Fig. 12.7b). Moreover, in humans, under certain circumstances, proximal and distal interphalangeal (PIP and DIP, respectively) joint flexion precedes metacarpophalangeal (MCP) joint flexion, and substantially greater m. flexor digitorum profundus forces are required to effect similar flexion angles at the MCP joints, as is the case for the PIP and DIP (Nimbarde et al., 2008). Kamper et al. (2002) showed that contraction of the extrinsic flexor muscles simultaneously with flexion of all the digital joints generated substantially less flexion at the MCP. It can be thus deduced that a greater tendon excursion is required for complete flexion of the digital joints, especially the MCP joint, and the palmar sesamoid probably prevents this in lizards with an L pattern of palmar tendons.

Many studies have shown that the intrinsic hand muscles (those that originate and insert within the hand) do not exhibit particular innovations related to the ability to move the hand in lizards. The distal insertion of the forearm muscles in those tetrapods having particularly skilled hand movements seems to be of greater importance (Herrel et al., 2008b; Russell & Bauer, 2008; Abdala & Diogo, 2010; Diogo & Abdala, 2010; Sustaita et al., 2013).

Some studies have shown that the configuration of the wrist and hand bones of lizards also correlate with grasping ability. The osseous structures of the hand and their characteristics associated with grasping abilities have been analyzed by Fontanarrosa and Abdala (2014, 2016). Collectively these studies surveyed the anatomy of the carpus of 278 specimens distributed among 24 genera and 13 squamatan families qualitatively (Fontanarrosa & Abdala, 2014) and quantitatively (Fontanarrosa & Abdala, 2016). In addition to the potential for the palmar sesamoid to impede grasping they highlighted other characters, such as an elongated centrale (Figs. 12.5B, C) (as previously noted by Sustaita et al., 2013), which

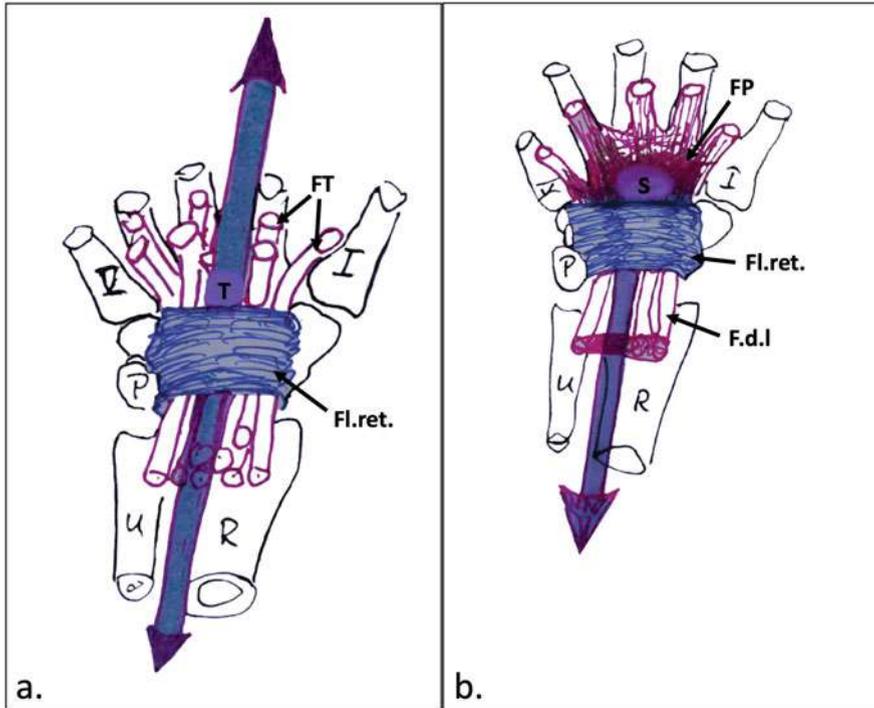


Fig. 12.7 (a) Anatomical structure of the human right hand in palmar view showing a tumor or nodule occurring on the flexor tendon and/or tendon sheath, preventing the sliding of the tendons in the carpal tunnel. (b) The same structures projected onto a “lizard hand in palmar view”: the tendon of the m. flexor digitorum longus is reinforced with a palmar sesamoid, exhibiting the L pattern of palmar tendons. Here the tendons have considerable difficulty in sliding in the carpal tunnel and flexion of the wrist and fingers and their free extension are hampered. *U* ulna, *R* Radius, *P* pisiforme, *I–V* metacarpals, *FT* Flexor tendons, *Fl.ret.* flexor retinaculum, *F.d.l.* m. flexor digitorum longus, *S* sesamoid, *T* tumor or nodule, *FP* flexor plate. Drawings from H. Förstner

facilitate grasping. The centrale is the only element in the lacertilian middle carpal row (Russell & Bauer, 2008). In non-grasping lizards it is usually flanked by the radiale and ulnare (Fig. 12.5A). This pattern imposes restricted mobility because the close contact between the proximal portions of the radiale and ulnare prevents wrist movement. The palmar sesamoid(s) also prevents flexion of the digits. These one or two sesamoids lock the articulation between the first distal carpal and metacarpal I, and between the second distal carpal and metacarpal II. The proximal region of the hand becomes a rigid structure with the only possibilities of motion being flexion and extension of the distalmost phalanges. In those lizards capable of grasping (e.g., *Anolis* and *Polychrus*), the centrale has shifted positionally from the central row to the proximal one (Fig. 12.5B). Thus, it has become, functionally, a proximal carpal, acting as a pivot between the radiale and ulnare, and it is now more slender and elongate rather than being truncated and sub-spherical as it is in most other lizards.

Additionally, the proximal head of the first metacarpal is located in a space bounded medially by the radiale, proximally by the highly reduced distal carpal I, and laterally by the distomesial side of the centrale. In the hand of most lizards there is no differentiation into thenar and hypothenar regions. The altered shape and position of the centrale and the reduction of the palmar sesamoid may thus provide regional differentiation and mobility within the hand by allowing digit I to be located in a relatively more medial position. A quantitative analysis of the hand bones of lizards indicated that grasping is a functional consequence of the centrale's width and the proximodistal length of the palmar sesamoid (Fontanarrosa & Abdala, 2016). A similar displacement is present in relation to digit V in *Anolis* and *Polychrus*. This provides the hand with an entirely new dimension for movement about the long (proximo-distal) axis of the palm and may explain how these lizards are capable of grasping narrow branches. Moreover, a grasping hand exhibits a relatively narrower first metacarpal and a greater divergence angle between digits one and five (Fontanarrosa & Abdala, 2016) than is the case in lizards that lack grasping abilities. Finally, a grasping hand depends on the relative lengthening of its long bones, a feature shared by almost all arboreal tetrapods (Fontanarrosa & Abdala, 2016).

12.3.2 *Pedal Grasping in Lizards*

The morphology, kinematics, and ecomorphology of lizard hindlimbs and their role in locomotion have been intensively studied (Losos, 1990; Reilly & Delancey, 1997; Zaaf & Van Damme, 2001; Higham & Jayne, 2004; Kohlsdorf et al., 2001; Russell & Bauer, 2008). However, the topic of grasping feet in lizards has seldom been addressed (Brinkman, 1980; Russell & Bauer, 2008; Abdala et al., 2014). Remarkably, taxa that exhibit manual grasping abilities also show pedal grasping skills: this being evident in chameleons (Fischer et al., 2010), varanids (Mendyk & Horn, 2011), anoles, and geckos (Abdala et al., 2014). Contrary to what has been described in relation to manual grasping (e.g., Abdala et al., 2009), the few accounts of pedal tendon structure have revealed great homogeneity among most lizards (Russell, 1993; Russell & Bauer, 2008; Abdala et al., 2014), and no reports exist of differences in their complex plantar tendons that relate to particular functional abilities. The presence of a plantar sesamoid (Abdala et al., 2019) has seldom been reported (e.g., in the gecko *Ptenopus* spp. by Russell & Bauer, 2008). *Ptenopus* is secondarily terrestrial (Russell & Bauer, 2008), which seemingly suggests that the anatomical constraints acting on manual morphology may also play a role in driving pedal morphology. Overall, the morphology of the lizard foot is conserved (Russell & Bauer, 2008; Abdala et al., 2014). Some exceptions have been reported for the astragalocalcaneum of *Chamaleo*, which is different from all other lizard astragalocalcanea in being depressed and curved. *Varanus* presents an unusual structure of the mesotarsal joint through the elongation and orientation of the lateral process of the astragalocalcaneum and the structure of its distomesial border. The functional significance of these differences is, however, unknown (Russell & Bauer,

2008). In accordance with this overall structural similarity, lizard lineages generally fail to exhibit pedal grasping capabilities, except for those taxa mentioned above that exhibit manual grasping abilities. Pedal grasping in *Anolis* spp. appears to take place at the level of the distal interphalangeal joints (Robinson, 1975; V. Abdala, personal observations).

Abdala et al. (2014) analyzed the anatomy of the crus and pes of several lizard families in a phylogenetic context to relate them to grasping abilities. Once again, no particular anatomical trait was discovered that was found to be related to grasping. Most of the skeletal elements evaluated showed a strong phylogenetic signal. Even taxa such as *Polychrus* and *Anolis*, which can actively grasp using the pedal digits and curl them around narrow branches, lack any particular set of osteological attributes associated with this ability. Thus, phylogeny seems to be the best predictor of most osteological traits of the lizard foot, with ecological particularities playing a lesser role in shaping anatomy. Contrastingly, most of the K values, the metric indicating phylogenetic signal (Blomberg et al., 2003), for the variables based on muscle and tendon morphometric characters, indicated weak phylogenetic signal, suggesting that their variation cannot be explained by phylogeny alone. Perhaps it is in these soft tissues of the foot that the ability to adjust the grip resides.

12.3.3 Lizard Grasping Performance

Claws are a vital aspect of locomotion, with claw height contributing to clinging and climbing on rough surfaces (Zani, 2000). In most lizards, the hand forms an almost rigid plate, whatever flexibility there is seeming to occur primarily in the distal regions of the digits and at the claws (Zani, 2000; Tulli et al., 2009). Arboreal and saxicolous (moving on rocks) lizards use vertical substrata and tend to have shorter and significantly more highly curved claws. Contrastingly, species utilizing open terrestrial habitats have longer and relatively straighter claws (Tulli et al., 2009). A more extensive analysis of the major traits of claws in lizards has recently been published and assesses convergent evolution of these structures (Baeckens et al., 2020). Versatile claws allow lizards that cannot grasp to negotiate vertical substrates but do not facilitate movement on narrow branches. It should be noted, however, that some facility for grasping can be achieved by using flexure at the metacarpophalangeal (MP) joints, such as in the arboreal *Iguana* (Fig. 12.6), as explained above. The few studies of grasping performance of lizards reveal a tendency for grasping forces to differ among species (Abdala et al., 2009). The weakest grasping forces recorded are for *Pogona vitticeps*, which is unable to close its hands around narrow substrata (Abdala et al., 2009). Species able to grasp exhibited no significant difference in grasping force, although it was somewhat greater in *Anolis equestris* compared to *Gekko gecko* (Abdala et al., 2009). More data recorded from a wider variety of species are needed to enhance our understanding of the morpho-functional relationships among grasping species and provide insights into the advantages conferred by the different palmar tendinous patterns observed (Abdala et al.,

2009). A recent study (Feiner et al., 2020) analyzed the locomotor performance of some *Anolis* lizards and suggested that differences in structural habitats promote different styles of locomotion and perching behavior in this genus.

In summary it can be stated that lizards that can close the hand around branches of small diameter are able to do so mainly because their carpal joints are flexible, they lack large palmar sesamoids that would otherwise prevent them from closing the hand, and they exhibit flexor tendons emanating from the forearm muscles that serve each digit independently, enhancing their ability to move. These morphological traits are expected to facilitate the hand movements needed to exploit niches characterized by narrow branches.

Varanus beccarii is one of the few lizards reported to be able to perform extractive foraging through grasping movements (Mendyk & Horn, 2011) by using its hands to take food and push it into its mouth. Interestingly, *V. beccarii* is an arboreal lizard, further supporting the pervasive relationship between arboreality and skilled hand movements. As for some frogs, *V. beccarii* can free its hands from their role in locomotion and support in order to use them in a feeding context. It could be proposed that this decoupling is enabled by their grasping feet which ensure stability of contact with the substratum while performing manually-assisted foraging and feeding. In general, hands can only be employed in an entirely novel context, such as prey prehension, if they are able to be temporarily released from their roles in locomotion and substrate prehension. *V. beccarii* is the only lizard species for which pedal grasping that enables it to free its hands for use in a feeding context has been reported. Additionally, it should be noted that these lizards exhibit high levels of behavioral complexity (Horn & Visser, 1997; Sweet & Pianka, 2007). It is possible that the grasping hands and feet of this species, coupled with their cognitive abilities (Manrod et al., 2008; Cooper et al., 2020), account for their remarkably skilful activities.

12.3.4 What About Other Reptilian Groups: Turtles and Crocodiles?

The subject of the capability of grasping has been scarcely, if ever, investigated for turtles. Forelimb abilities of aquatic, fresh-water turtles have been reported by Manzano et al. (2015). Pleurodires are capable of complex and subtle hand movements that are associated with locomotion and certain grooming behaviors (Manzano et al., 2015). Several YouTube videos of copulating aquatic turtles reveal that the males of *Phrynops* hold the females by grasping their shells and curving the distalmost extremities of their digits around the border of the carapace. In sea turtles the male exerts pressure on the female's shell using the distal ends of its pectoral and pelvic flippers. Females of both *Phrynops* and sea turtles swim during the entire copulatory processes. Although the general anatomy of turtles is relatively conservative, some aquatic turtles exhibit specializations related to their grasping

capabilities (Abdala et al., 2008), although there are no data about hand grasping abilities in any of the more than 400 species. Recently Fujii et al. (2018) documented evidence of marine turtles using both hands to catch prey, and suggested that such forelimb use could have originated in ancestral turtles approximately 70 million years ago (Fujii et al., 2018). As can be seen, much work remains to be conducted about turtles for this underrated issue.

Seemingly, the only record of skilled forelimb movements in crocodiles is that furnished by Iwaniuk and Whishaw (2000), although unfortunately it is based upon unpublished observations. Data on the wrist movements of alligators indicate that the crocodylian wrist mechanism functions to automatically lock their semi-pronated palms into a rigid column (Hutson & Hutson, 2014). Thus, it is possible that this inhibits the development of other skilled attributes of the hands of this group. Interestingly, YouTube videos show that crocodiles can use their almost rigid hands to assist females to receive the male during mating. Unfortunately, we were unable to locate any literature pertaining to the role of grasping during mating in turtles and crocodiles, indicating that much more work is required in the exploration of this subject. Crocodiles exhibit almost all locomotor modes present in quadrupedal mammals, with an impressive locomotor repertoire (Hutchinson et al., 2019). Thus, it can be inferred that locomotion was the primary function driving the evolution of the limbs in crocodiles.

12.4 Grasping in Birds

With the specialization of the forelimbs for flight throughout the evolutionary history of birds, the capacity for grasping, such as in perching, resides solely with the pes. The climbing of substrates, handling of food items and the manipulation of nesting materials, progressively became relegated to the hindlimbs. This poses distinct challenges for the development of grasping ability in birds because the feet are subject to a variety of functional demands beyond grasping, such as terrestrial and/or aquatic locomotion, preening, fighting, and thermoregulation (Lovette & Fitzpatrick, 2016). Despite the specializations exhibited by many groups of birds for one or few of these functions, many birds employ their feet, to varying extents, for several of these functions (Sustaita et al., 2013; Morrison 2018). Perhaps because of this, the avian foot has achieved a remarkable diversity of form and function despite having lost digit V (Bock & Miller, 1959). Possibly because of these potential constraints, most birds that perform pedal grasping are restricted to the execution of a ‘power grasp’ (as opposed to a ‘precision grip’), as exemplified most dramatically by birds of prey (hawks, falcons, and owls) for seizing, and to some extent, killing, prey. Parrots, mousebirds, tits, and even crows (Melletti & Mirabile, 2010; Katzner, 2016) are able to hang upside down with acrobatic mastery. Nevertheless, some birds, such as parrots, have achieved comparable levels of digital dexterity to other tetrapods whose limbs are far more specialized for grasping (Sustaita et al., 2013). Thus, birds have independently converged on grasping form and function found in other groups

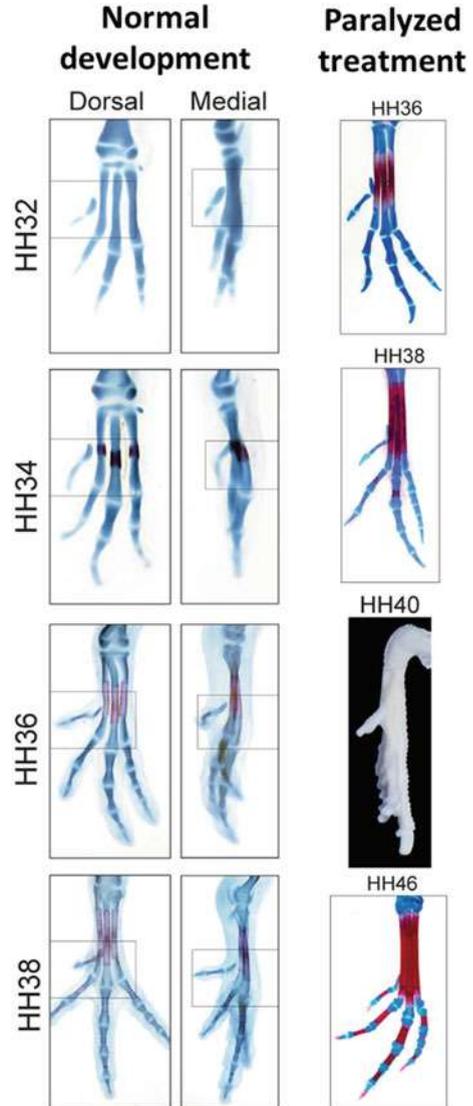
of tetrapod vertebrates principally along four main avenues: (1) opposability of digits, (2) the presence of toe pads and claws, (3) modification of certain aspects of musculoskeletal morphology, and (4) through behavioral repertoires. Below, we consider each of these avenues in turn, highlighting how birds have attained similar grasping abilities to those of other tetrapods, albeit by different means. In doing so, we provide several new insights that have emerged since Sustaita et al.'s (2013) review of the topic.

12.4.1 *Opposability of Digits*

Digital opposability is a key feature of manual and pedal grasping among tetrapod lineages (Sustaita et al., 2013), particularly for arboreal lizards (e.g., chameleons) and mammals (e.g., primates). The ability to grasp arboreal perches is a hallmark of avian evolution (Sereno & Chenggang, 1992; Middleton, 2001). The reversal of the hallux has been associated with the ability to perch; as such, specifically *when* this ability evolved is subject to some debate, as the orientation of the hallux in the putative ancestor of modern birds, *Archaeopteryx*, is somewhat equivocal (Middleton, 2001, 2003; Fowler et al., 2011; Hattori, 2016). Conventional wisdom suggests that hallucial reversal evolved with arboreality in birds for grasping perches (Feduccia et al., 2007), but Fowler et al. (2011) suggest that reversal of the hallux might have been selected for predatory purposes in the terrestrial dromaeosaurid lineages leading to birds. Regardless, it is clear that the reversal and incumbency of the great toe (hallux) to form an opposable digit was a fundamental precursor of grasping (Sereno & Chenggang, 1992; Feduccia, 1999; Middleton, 2001; Fowler et al., 2011). Furthermore, we now have a better understanding of *how* digital opposability might have evolved in birds (Fig. 12.8). Pharmacological paralysis experiments performed on developing embryonic birds have shown that torsion of the cartilaginous immature first metatarsal, resulting from muscle activity, is the primary cause of hallucial reversal at an early developmental stage (Botelho et al., 2015a; Fig. 12.8). Degrees of this form of plasticity may have existed in ancestral lineages, leading to the various stages of hallucial reversal observed in fossil avialian taxa.

Digit opposability in birds occurs in different ways, such that digit I (hallux) opposes the other three, or different combinations of digits II, III, IV cluster with the hallux in opposition to the others (Fig. 12.9). Abourachid et al. (2017) highlighted how the “pincer-like” foot structure of arboreal birds, comprising different combinations of these forward- and rearward-facing toes, converges upon that of many other arboreal/climbing tetrapods, particularly chameleons and primates. Previously it was thought that the six typical toe arrangements found among avian taxa (zygodactyl, heterodactyl, syndactyl, anisodactyl, pamprodactyl, ectropodactyl) evolved from an ancestral anisodactyl (in which the caudally-directed hallux opposes toes II–IV) ‘perching’ foot (Bock & Miller, 1959). However, recent developmental studies suggest that the zygodactyl toe arrangement (in which the

Fig. 12.8 Alcian/Blue Alizarin Red-stained feet of developing quail and chicken embryos at selected Hamburger and Hamilton (HH) developmental stages. HH32-HH38 for normally developing quail embryos show the progressive reorientation of the hallux. Lack of reorientation is evident in paralysed chicken embryos during stages HH36-HH46. Modified with permission from Botelho et al. (2015a), Scientific Reports, www.nature.com, Creative Commons CC-BY 4.0



caudally-directed toes I and IV oppose toes II and III), found in parrots, cuckoos, woodpeckers and allies, and facultatively in owls, some kites, and the osprey (Bock & Miller, 1959; Raikow, 1985; Tsang, 2012), may in fact represent the ancestral condition for crown-group birds (Botelho et al., 2014; Botelho et al., 2015b). Botelho et al. (2014) provided compelling evidence regarding the role of asymmetrical degeneration of the intrinsic muscles controlling digit IV for generating the zygodactyl configuration in budgerigars, similar to the process of hallucial reversal (Fig. 12.8). They further suggested that the loss of the abductor of digit IV in

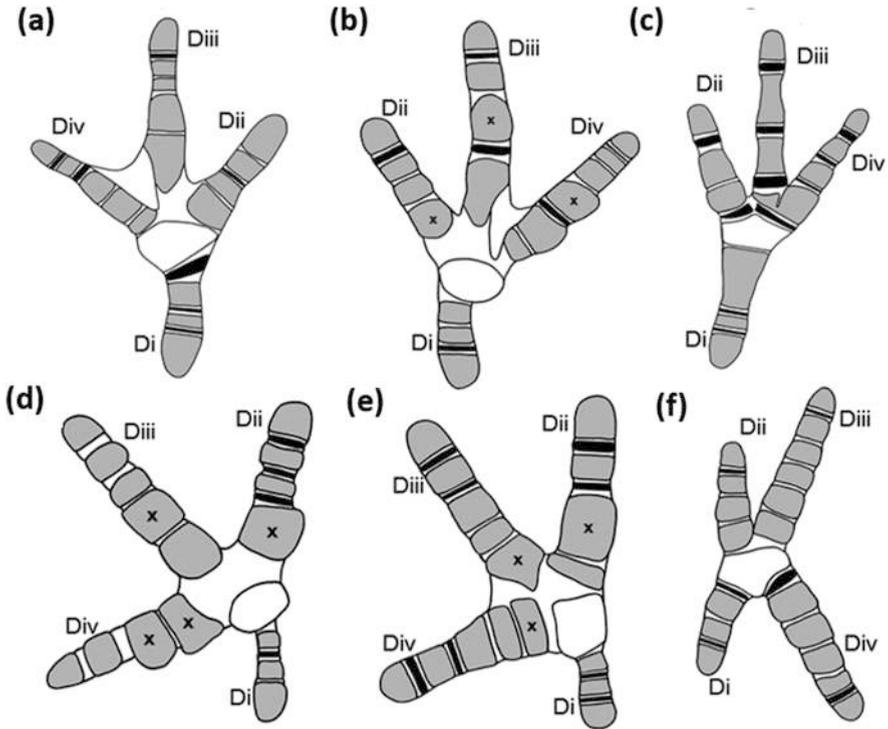


Fig. 12.9 Drawings of the plantar surface of the feet of various representatives of predatory and non-predatory avian taxa, left (L) or Right (R) as indicated: (a) *Aquila audax* (R); (b) *Falco cenchroides* (L); (c) *Corvus coronoides* (L); (d) *Ninox boobook* (R); (e) *Tyto alba* (R); (f) *Eolophus roseicapilla* (L). The drawings illustrate varying degrees of toe divarication among anisodactylous (a–c) and zygodactylous (d–f) taxa, as well as variation in the sizes, shapes, and distribution of toe pads (gray), furrows (black), and folds (white). Protrusional pads are marked with an “X.” *Di* Digit I, *Dii* Digit II, *Diii* Digit III, *Div* Digit IV. Modified with permission from Tsang et al. (2019a), *Journal of Morphology*, Wiley

passeriforms resulted in their ‘secondarily’ anisodactyl configuration (Botelho et al., 2014, 2015b).

The functional significance of the various toe arrangements is not precisely clear. Many climbing specialists, such as woodpeckers, have zygodactyl (or “ectropodactyl” *sensu* Bock & Miller, 1959) feet. Parrots, which both climb and manipulate food and other objects with their toes, are strongly zygodactylous. Trogons are heterodactylous (with toes I and II opposing toes III and IV; Bock & Miller, 1959) and mostly use their feet for perching, whereas mousebirds that do a lot of climbing, hanging, and manipulation of food items, can assume toe configurations that range from anisodactyl, to zygodactyl, to pamprodactyl (Berman & Raikow, 1982). Perhaps these arrangements distribute the forces more evenly to enhance the grasping of vertical substrates (Bock & Miller, 1959). However, roadrunners are also zygodactylous, but are primarily cursorial. Moreover, owls and ospreys are

semi-zygodactylous and use their feet for killing and grasping prey. The zygodactyl arrangement (Fig. 12.9) is thought to distribute the toes more symmetrically (Payne, 1962; Einoder & Richardson, 2007b; Tsang & McDonald, 2018), and the digital flexion forces more equitably (Ward et al., 2002), thereby enhancing prey-capture success. Indeed, based on an analysis of publicly available internet images and videos, Sustaita et al. (2019) found that semi-zygodactylous ospreys disproportionately use the zygodactylous toe arrangement when grasping (Fig. 12.12c). Facultative zygodactyly is characteristic of few, but phylogenetically disparate, taxa (Tsang, 2012; Botelho et al., 2015b). Tsang and McDonald (2018) showed that semi-zygodactylous taxa can assume a wide array of toe divarication angles (Fig. 12.9). They also showed how the raptorial foot morphotype is considerably more flexible than previously understood in its ability to assume a variety of toe divarication angles, particularly among prey generalists.

12.4.2 *Toe Pad and Claw Morphology*

Since Lennerstedt's (1974, 1975a, b) and Stettenheim's (2000) classic works on the topic, recent studies have reinvigorated the roles that keratin plays in avian foot form and function. Höfling and Abourachid (2020) recently described aspects of podothecal morphology that might also play an important role in grasping, such as the sharp, pointed and overlapping ventral scales of predatory or climbing species, thought to afford them greater traction. These authors also reported a greater prevalence of syndactyly (the partial fusion of certain foretoes) among bird taxa possessing each of the main toe configurations (anisodactyl, zygodactyl, and heterodactyl). They suggested that syndactyly may play roles in increasing the size of the sole for increasing friction with the substrate, and cite its potential advantage for perching by keeping the toes parallel and restricting their forces to those acting at a right angle to the branch (Höfling & Abourachid, 2020). Tsang et al. (2019a) found that the morphology of the ventral toe pads varied considerably among raptors, as well as between predatory and non-predatory taxa, and even among digits within individuals (Fig. 12.9). This variation in toe pad morphology is not unlike that displayed by the volar and plantar pads (or tubercles) on the paws of mammals, that are particularly well-developed in climbing and scansorial species (Cartmill, 1985; Barbera et al., 2019). They highlighted how, in predatory taxa, the toe pads are more pronounced and typically located at the interdigital joints, whereas in non-predatory taxa the folds between the pads are situated at the joints and the pads themselves are relatively smaller and flatter. Furthermore, toe pads are more protrusive in bird-eating raptors, presumably to aid in gaining purchase on more highly elusive prey, and more uniform, well-developed toe pads are characteristic of accipitrids that tend to pursue ground-dwelling prey (Tsang et al., 2019a).

Claw shape has obvious implications for grasping capability and many advancements have been made in our understanding of how claw shape varies among taxa and functional groups (Fig. 12.10a). Previous studies have reported significant

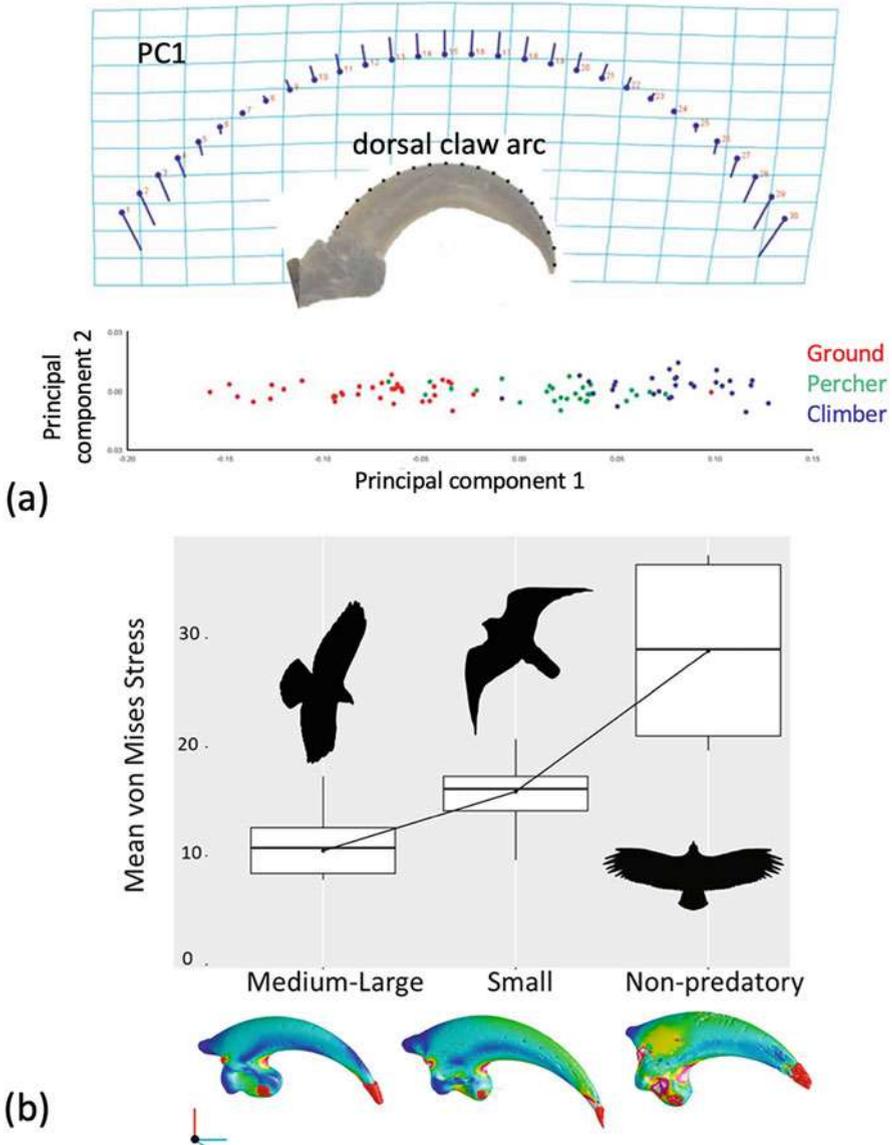


Fig. 12.10 (a) Variation in claw shape, measured using contemporary methods of geometric morphometrics, showing variation within and among “ground,” “percher,” and “climber” groups of taxa. Modified with permission from Tinius and Russell (2017), *Journal of Morphology*, Wiley. (b) Effects of claw shape on functional performance based on finite element analysis, among predators of medium-large and small prey, compared to non-predatory taxa. The warmer colors indicate regions of higher stress when subjected to external forces at the tips. Modified with permission from Tsang et al. (2019b), *Scientific Reports*, www.nature.com, Creative Commons CC-BY 4.0

differences in claw shape among functional groups (e.g., ground-dwellers, climbers, predatory birds), such that claw curvature is greater among arboreal perching/climbing and predatory than among ground-dwelling forms (Feduccia, 1993; Pike & Maitland, 2004). Glen and Bennett (2007) took their analysis in a different direction by testing for differences among foraging categories at the ordinal level, and found that claw curvature increases with degree of arboreal foraging. However, Birn-Jeffery et al. (2012) found that at the broadest taxonomic scales, including other tetrapods such as lizards, and after correcting for body size and phylogeny, claw shape differences only really separate ground-dwelling birds from other groups. These results were largely corroborated by recent studies based on geometric morphometric analyses of claw shape (Tinius & Russell, 2017; Hedrick et al., 2019) that failed to recover clear, discrete ecological groupings, but rather found claw shape to vary on a continuous scale and that this is confounded by body size (Fig. 12.10a). Nevertheless, taxa can be distinguished along various metrics of claw shape within functional groups. For example, among predatory birds Csermely and Rossi (2006) and Csermely et al. (2012) found clear differences in claw shape along phylogenetic lines. Furthermore, claw curvature (Fowler et al., 2009, 2011) and larger size (Einoder & Richardson, 2007a) have been associated with differences in prey immobilization technique (e.g., hawks and eagles use their highly curved talons to pin prey down during feeding) and prey-type specialization (e.g., piscivorous and mammal-eating raptors have long and robust talons, respectively). More recently the biomechanical consequences of claw shape and size have been explicitly tested with finite element modeling. Tsang et al. (2019b) argued that prey size profoundly influences claw shape and mechanical performance (Fig. 12.10b). They found that non-predatory species—and, to some extent, predatory species that pursue relatively small prey—have talons that are shorter, less curved, blunter, and experience higher von Mises stresses; the latter of which suggests a greater likelihood of structural failure (Fig. 12.10b). Conversely, the talons of predators that take relatively large prey are highly curved, with enlarged flexor tubercles, and experience lower von Mises stresses along their curvature (Tsang et al., 2019b).

Naturally the claws do not function in isolation from the rest of the foot and for scansorial/climbing species in particular, the arrangement of the toes (Bock & Miller, 1959), the hindlimb muscles and their moment arms, and the posture of birds play vital biomechanical roles in their abilities to cling, climb, and hang (Winkler & Bock, 1976; Norberg, 1979, 1986; Moreno & Carrascal, 1993; Zeffer & Norberg, 2003). Below we describe some additional musculoskeletal modifications related to grasping that birds share with other tetrapods.

12.4.3 Musculoskeletal Modifications for Grasping

Bird feet show a variety of adaptations for grasping deep to the skin and claws, exhibiting skeletal, muscular, and tendinous modifications. With regard to skeletal elements, Hopson (2001) demonstrated how the proportional lengths of the distal

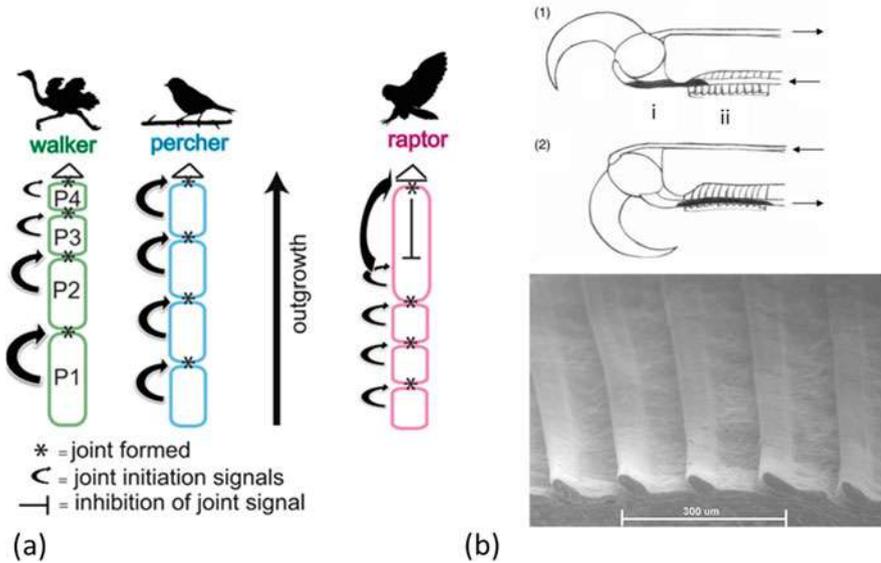


Fig. 12.11 (a) Variation in phalanx proportions among functional groups, showing how each phalanx signals the development of the next joint, such that in raptors the distal phalanx signal is inhibited, resulting in a long penultimate phalanx. Modified with permission from Kavanagh et al. (2013), *Proceedings of the National Academy of Sciences*, Highwire. (b) Raptor digit tendon-locking mechanism. Top panel shows engagement of the mechanisms (i = tubercle pad, ii = plicated sheath) from extended (1) to flexed (2). Modified with permission from Einoder and Richardson (2006), Ibis, British Ornithologists' Union. Lower panel shows a scanning electron micrograph of a longitudinally-sectioned tendon sheath of a barn owl, demonstrating the arrangement of plicae. Modified with permission from Einoder and Richardson (2007b), *Emu*, Royal Ornithologists Union, Csiro Publishing

phalanges of the third toe tend to be longer in arboreal climbing/perching/predatory birds and shorter in terrestrial cursorial birds. This same pattern has more recently been confirmed by others (Kavanagh et al., 2013; Backus et al., 2015; Abourachid et al., 2017; Fig. 12.11a). Kavanagh et al. (2013) took the analysis a step further by uncovering the developmental basis of this pattern, thereby identifying a critical source of convergence among vertebrates. These authors indicated that the development of phalanges is modular, and this form of development restricts phalanx proportions in birds in the same way that it does in other vertebrate taxa. However, in birds the penultimate phalanx enjoys some developmental independence, and it is this phalanx that appears to show the greatest range of variation among grasping (relatively longer) and walking (relatively shorter) forms (Fig. 12.10a).

Interestingly, many arboreal and digging mammals demonstrate a similar pattern of increased distal phalangeal lengths (e.g., Ji et al., 2002), but seem to have arrived at this situation differently, through fusion of normally condensed phalanges and/or Fgf signaling (Kavanagh et al., 2013).

Other interesting osteological modifications in birds thought to foster grasping ability occur in parrots, such as a medially directed metatarsal I (which articulates with the hallux) and robust digits III and IV (Ksepka & Clarke, 2012). Furthermore, aspects of unguis phalanx morphology, reflective of the forces generated and incurred by the distal regions of the toes, vary in concert with substrate use and predatory behavior, such that the sizes of the articular surfaces and the digital flexor tubercles are relatively larger in arboreal and predatory birds (Mosto & Tambussi, 2014; Abourachid et al., 2017). The digital flexor musculature of birds is subdivided into a series of superficial flexors that insert on the proximal phalanges of toes II–IV, and two deep flexors that insert on the unguis phalanges; one onto those of toes II–IV, and another onto the unguis phalanx of the hallux (Hutchinson, 2002). The number and distribution of these flexor muscles, particularly in more derived passeriform taxa that have lost the intrinsic pedal muscles (Raikow, 1985), results in an ‘underactuated mechanism’ with fewer muscles and tendons relative to the degrees of freedom along the toe joints (Backus et al., 2015). Backus et al. (2015) performed a series of simulations, taking into consideration variation in phalangeal proportions and object sizes, to model the effects of multiple (superficial and deep) flexors vs. a single (just deep) flexor on grasping performance. Their results suggested that, hypothetically, a single deep flexor tendon serving the distal (unguis) phalanges is sufficient to oppose the (downward) weight of an object, and indeed, these deep digital flexors tend to be relatively larger than the superficial flexors in taxa that grasp objects. However, the addition of more proximally-inserted superficial flexors improves grasping performance with upwardly-directed (reaction) forces experienced during perching or walking. Here again, birds that tend to use their feet primarily for perching or walking have relatively more well-developed superficial flexors than deep flexors (Backus et al., 2015). Parrots and mousebirds enjoy a greater diversification and development of the intrinsic hindlimb digital muscles (e.g., m. extensor hallucis longus pars distalis and a branch of the m. extensor digitorum longus), which collectively provide for more ‘delicate’ control of the hallux (Berman & Raikow, 1982; Berman, 1984) for accessing and manipulating hanging food items (Harris, 1989). The neuromuscular coordination of grasping forces has not been extensively studied. Cutaneous (afferent) feedback from the digits can have profound implications for grasping performance (e.g., Shim et al., 2012). Lennerstedt (1975a, b) found 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.

With regard to tendon morphology, Raikow (1985) summarized the eight main types of digit flexor tendon arrangements found in birds. In the most common (in terms of the number of families represented) Type I configuration, the tendon of the m. flexor digitorum longus divides distally into three branches that insert onto toes II–IV, whereas that of the m. flexor hallucis longus inserts directly onto the hallux (Raikow, 1985). The tarsometatarsal portions of these deep flexor tendons are often connected together at some point along their lengths by a tendinous vinculum. 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

toes II–IV, but not vice versa (Raikow, 1985). Perhaps the most striking tendon modification is that of the digital tendon-locking mechanism (Quinn & Baumel, 1990), which is highly convergent with a similar mechanism in the toes of bats (Bennett, 1993; Quinn & Baumel, 1993; Simmons & Quinn, 1994). This mechanism works by virtue of the ratchet-like microstructure of the distal portions of the tendons and their associated sheaths (Quinn & Baumel, 1990; Einoder & Richardson, 2006; Fig. 12.11b). An additional mechanism has been proposed to work by way of flexion of the intertarsal joint, which places the digital flexor tendons that run caudad to it into tension (Ward et al., 2002; Einoder & Richardson, 2006). These two mechanisms presumably work in combination to maintain digital flexion forces during perching without the aid of continuous muscle contraction (Quinn & Baumel, 1990; Middleton, 2003; Einoder & Richardson, 2006). Incidentally however, Galton and Shepherd's (2012) surgical intervention experiments on European starlings (*Sturnus vulgaris*) demonstrated that they were still able to perch without these tendons being intact. Perhaps this mechanism is more important in forms of grasping other than perching.

12.4.4 Behavioral Repertoires

Birds perform grasping in a few major contexts: landing, perching, climbing, hanging, and handling/manipulating food and other objects (e.g., nesting materials). None of these tasks are particularly unique to birds and many other tetrapods regularly perform these forms of grasping, even with their feet as do birds. However, landing arguably presents different challenges from those experienced by most (non-flighted) tetrapods, and to some extent even bats [which land upside down! (Riskin et al., 2009)]. Bonser's (1999) extensive studies of the locomotor mechanics of perching revealed convergences in take-off and landing behavior between primates and birds. Specifically, landing forces are significantly lower than take-off forces in both, although interestingly perch compliance decreases landing forces in primates but not in birds. Provini et al. (2014) found that the hindlimbs of zebra finches and diamond doves reduced landing velocity by 60% and thereby contributed substantially to the absorption of kinetic energy during touchdown. Furthermore, they described how birds coordinate the use of the wings and hindlimbs to control landing speed, by producing higher wingbeat forces in the final stages prior to touchdown (Provini et al., 2014). Roderick et al. (2019) showed how foot, toe, and claw kinematics are also coordinated during landing in parrotlets (Fig. 12.12A). The foot 'pre-shapes' to the perching substrate ~30 milliseconds prior to making contact, which is thought to enable the grasp to be secured more quickly (Roderick et al., 2019; Fig. 12.12A). At the point of contact the claws curl around the perch until the toe pads and claw tips achieve the requisite amount of friction to prevent slippage, thereby minimizing the amount of squeezing that needs to be accomplished by the toes. This "overcompensation then relax" strategy is thought to balance safety and the reduction of energy expenditure during landing/grasping. Roderick et al. (2019)

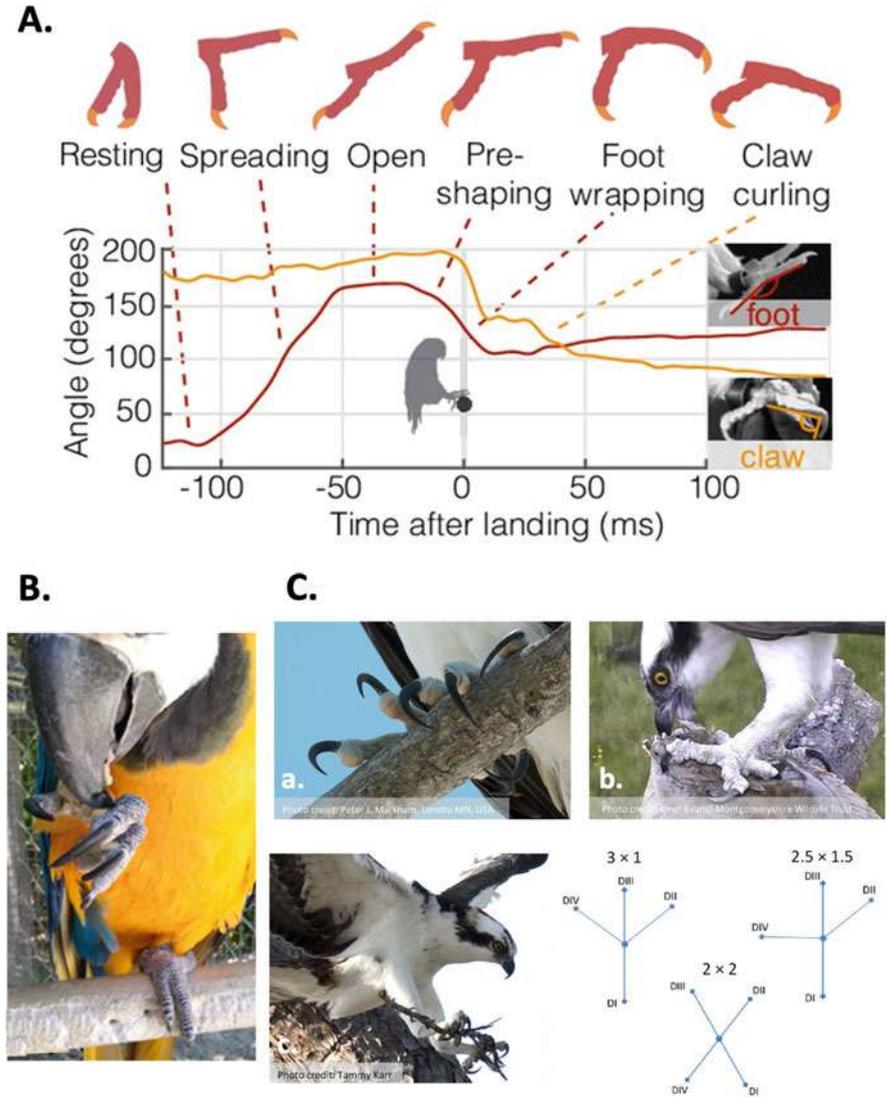


Fig. 12.12 (A) Changes in foot and claw angles before, during, and after landing in parrotlets. Modified with permission from Roderick et al. (2019), eLife, [elifesciences.org](https://doi.org/10.1101/2019.03.01.282828), Creative Commons CC-BY 4.0. (B) Close-up of a blue and yellow macaw using its right foot to handle food during feeding (photo by D. Sustaita). (C) Different contexts of foot use in ospreys, showing the versatility in toe configuration, from anisodactyly (3×1 ; (a) left foot) to zygodactyly (2×2 ; (b) left foot and (c) left and right foot); a transitional configuration (2.5×1.5) being visible on the right foot in (a). *Di* Digit I, *Dii* Digit II, *Diii* Digit III, *Div* Digit IV. Modified with permission from Sustaita et al. (2019); PeerJ, Creative Commons CC-BY 4.0

indicated that while the coordinated wing, leg, and foot dynamics are largely stereotyped, the claw kinematics change with respect to perch diameter and substrate properties, and move remarkably rapidly to accommodate to the substrate after contact is made.

Pedal grasping in the context of handling and manipulating of objects, such as food (Clark, 1973; Fig. 12.12B) and/or nesting material (Sustaita et al., 2019; Fig. 12.12C), is less common among birds but enjoys a fairly broad phylogenetic distribution (Scooter, 1944; Smith, 1971; Tozer & Allen, 2004). Although feeding is likely to impose an important selective force for grasping capability in birds, on a larger evolutionary scale it appears to be confounded with arboreality (see Sustaita et al., 2013). Despite its broad phylogenetic representation, however, relatively few arboreal taxa regularly handle food with their feet, suggesting that such 'repurposing' of the grasping function may not necessarily be easy to accomplish. Raptors, parrots, tits (Moreno & Carrascal, 1993), and mousebirds (Berman & Raikow, 1982), for instance, probably represent extremes in their tendencies for pedal food manipulation. At one extreme raptors (hawks, falcons, and owls) are clearly adapted for generating high grasping forces (Goslow Jr., 1972; Csermely & Gaibani, 1998; Ward et al., 2002; Sustaita, 2008; Sustaita & Hertel, 2010).

At the other extreme parrots seem to exert finer control over their grasps for handling and manipulating food items (Berman, 1984; Fig. 12.12B), often with a predilection for using the right, left, or either foot, depending on the individual and species (Harris, 1989; Brown & Magat, 2011). In fact, some raptors have demonstrated similar lateralization (Csermely, 2004), and others, such as the African harrier-hawk (Burton, 1978) and the caracara (Biondi et al., 2010), are also particularly dexterous in reaching for and manipulating objects with their feet.

12.4.5 *Summary and Prospects*

The grasping behavior of birds is convergent with that of other tetrapods on several phenotypic levels. Birds share the propensity to grasp with other tetrapods for a variety of reasons; for maintaining stability and support on vertical and horizontal substrates, and for seizing, handling, and manipulating food items and other objects (Iwaniuk & Whishaw, 2000). As for other tetrapods, grasping in birds is affected by some combination of opposable digits and in climbing/scansorial species this conforms to similar morphological rules, such as the presence of relatively long distal phalanges. In addition, birds share other adaptations of the tendons, toe pads and claw morphology with several other scansorial/climbing tetrapod taxa. Nevertheless, there are unique aspects to their grasping capabilities that are explained by their commitment to a volant, and typically arboreal, lifestyle. The primary differences in grasping between birds and other tetrapods is that in birds grasping is restricted to the feet, albeit often with the aid of the bill. As a result, birds likely experience more conflicting demands on their foot form and function, since they cannot partition the roles of weight-bearing and object manipulation between the hind- and forelimbs as

mammals do (Iwaniuk & Whishaw, 2000; Sustaita et al., 2013). In addition, birds experience the added complexity of landing, which we argue differs from the types of landing performed by gliding and other volant tetrapods, principally in the greater requirement for coordinating functions across wing/tail and hindlimb locomotor modules (Gatesy & Dial, 1996). Specifically, how this might constrain the evolution of bird feet is a subject of considerable interest. Identifying the trade-offs in foot form and function in light of competing demands is not only important for uncovering evolutionary pathways but is also of great utility for the bioinspired robotic design of grasping implements.

12.5 Grasping in Mammals

Mammals exhibit a great diversity of grasping forms and functions (see Fig. 12.13), which includes several key features described above. As soon as they are born, some young mammals actively grasp the parental fur when being carried, while others can grasp the same locomotor substrates that adults move on. Later during life, grasping, both manual and pedal, occurs extensively during food manipulation. Manual grasping is associated most prominently with feeding behavior, even if it is largely also involved in the grasping of arboreal substrates during locomotion. Pedal grasping is associated more with locomotor behaviors, even if the feet can also be used for grasping objects or food, according to species. Although many mammals



Fig. 12.13 Grasping in different contexts—locomotion, foraging and social interactions—in the young olive baboon (*Papio anubis*). (a) Gripping the fur when clinging to the mother. (b, c) Grasping during social interactions: grooming and play. (d) Fine precision grip of a small item between the thumb and the side of the index finger. (e) Bimanual grasping of a large food item. (f) Grasping of arboreal substrates during locomotion. Photograph credit: G. Boulinguez-Ambroise

have been studied with regard to their grasping abilities and its associated limb morphology, the literature on primates is by far the most extensive.

Given the number of studies on primates, we cannot be exhaustive here. On the other hand, we address questions that we consider the most relevant for understanding the ecology and evolution of grasping among mammals: what are the demands and potential trade-offs associated with food and substrate grasping? Can we trace the evolutionary origin and explore the selective pressures that underlie grasping evolution? What is the relationship between arboreality, complex manipulative skills and forelimb movements? To answer these questions, we first examine manual and pedal grasping abilities during arboreal locomotion and food acquisition and subsequently describe their underlying functional adaptations.

12.5.1 *First and Early Grasping Experiences*

Ultrasound scans have demonstrated that limb movements emerge during fetal life. From 14 weeks of gestation human fetuses already show exploratory hand movements such as pushing the uterine wall (also flattening and sliding the palm against it); they grasp and manipulate the umbilical cord, and even repeat hand-mouth contacts (Sparling et al., 1999). Fetal limb movements have also been observed in chimpanzees, with frequent forelimb contact with the head (Takeshita et al., 2006). After birth, in many primates—including strepsirrhine and haplorrhine species—juveniles are carried by the parents, usually the mother (see Fig. 12.13a). In some species, especially in New-World primates like titi monkeys (*Callicebus moloch*), the juvenile is almost exclusively carried by the father (Fragaszy et al., 1982; Mendoza & Mason, 1986). When clinging to the parental fur (using both the hands and the feet), young primates commonly press each finger toward the adjacent ones (i.e., involving a close contact between digits) while the fingertips are pressed toward the palm (Bishop, 1962; Peckre et al., 2016). This fur-grasping grip (see Fig. 12.13a) involves different hand surface areas and contacts than those recruited when grasping branches during arboreal locomotion (i.e., the whole palm and all palmar parts of the fingers, see Fig. 12.13f; Reghem et al., 2012; Peckre et al., 2016). Peckre et al. (2016) compared oral-carrying with fur-clinging strepsirrhine species and found that species that cling to parental fur have greater manual dexterity. The authors thus suggested, with regard to fur-grasping, that “such focus of control on the touch-pads is a likely forerunner of fine control of the hand” (Bishop, 1962, p. 329; Peckre et al., 2016). In olive baboons (*Papio anubis*) young individuals cling to their mother’s fur using both the fore- and hind limbs, being almost exclusively cradled during the first 3 weeks (i.e., clinging to the belly) and are then carried dorsally for several months (Nash, 1978). At the juvenile stage, relatively wider and thicker manual and pedal phalanges (see Fig. 12.14)—compared to those of adults—allow young baboons to strongly grasp the maternal fur (Boulinguez-Ambroise et al., 2021) while the mother is free to walk, run, climb, or leap (i.e., exhibits the full locomotor repertoire). Well-developed grasping abilities thus appear to be

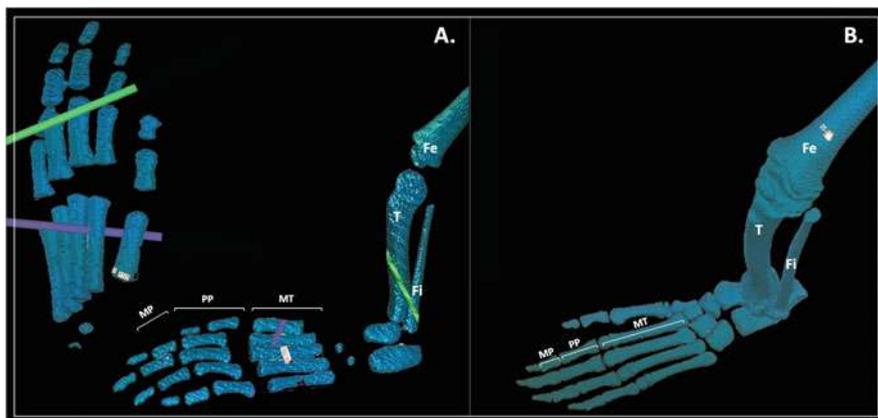


Fig. 12.14 Illustrations of hindlimb bone segments in juvenile and adult olive baboons (*Papio anubis*; 3D surface models segmented from CT-Scans; Photo courtesy of Gilles Berillon). (a) The juvenile morphology (with non-ossified epiphyseal plates) is best characterized by relatively wider phalanges and digit joints, compared to those of adults, while (b) length and thickness of the long bones and metapodia best characterize the adult morphology (Boulinguez-Ambroise et al., 2021). *MP* middle phalanges, *PP* proximal phalanges, *MT* metatarsals, *Fe* femur, *T* tibia, *Fi* fibula

fundamental to the survival of young baboons, whose grasping performance (first year of life) reaches 200% of the adult performance relative to body mass (Boulinguez-Ambroise et al., 2021).

Regarding marsupial neonates, the immature altricial young leaves the uterus and reaches the maternal pouch, where it will be carried and complete most of its development attached to the teat. Precociously developed forelimbs with separated digits and claws allow the tiny neonates to climb to the pouch at a stage in development in which the hindlimbs are still rudimentary buds (Lyne, 1964; Cooper & Stepan, 2010; Ashwell & Shulruf, 2014; Schneider & Gurovich, 2017). As in other mammals, marsupial neonates display forelimb movements even before birth; in the case of the tammar wallaby (*Macropus eugenii*) fetus, climbing movements have been reported about 3 days before birth, in preparation for those required for climbing to the pouch (Drews et al., 2013).

12.5.2 Manual and Pedal Substrate Grasping

In primates, a large number of studies have focused on hand use during food acquisition, and the grasping of objects or tools. However, an even greater number of studies have explored substrate grasping during locomotion. Indeed, the ability to grasp narrow branches safely and forcefully remains at the center of the debate on primate origins. Current hypotheses suggest that the use of narrow terminal branches to exploit fruits, flowers, insects and nectar may have been an important selective



Fig. 12.15 (a–e) Autopodial grasping configurations in young mouse lemurs (*Microcebus murinus*) on vertical and horizontal substrates. Configurations differ according to the position of the digits relative to the substrate: (a) Mesaxonic manual grasp with the axis running along digit 3; (b) Schizaxonic manual grasp between digits 2 and 3; (c) Pedal secure grasping; (d) Powerful telaxonic manual grasp: the thumb is fully opposed to the lateral digits; (e) Entaxonic manual grasp with the axis running along digit 2. Photograph credit: G. Boulinguez-Ambroise

pressure that led to the evolution of primate grasping (Cartmill, 1974; Godinot, 1991; Sussman, 1991). The evolution of specific hand and nail morphologies observed in primates might thus be linked to the use of thin terminal branches. Interspecific comparative studies in primates have been used to test this hypothesis. A study on the mouse lemur (*Microcebus murinus*) suggested that, more so than an arboreal thin substratum, the frequent use of vertical supports may influence hand biomechanics toward ulnar deviation (see Fig. 12.15), as observed for lorises and indriids (Reghem et al., 2012). The different types of grips employed in substrate grasping can be described according to the general posture of the hand/foot (midline) relative to the forearm's/leg's midline, the digits involved in substrate grasping (see Fig. 12.15), and the hand/foot areas that are in contact with the substrate (for a description, see Toussaint et al., 2020).

More generally, Lemelin and Schmitt (1998) observed that the use of ulnarly-deviated hand postures was associated with substrate preference in six haplorhine species. The highly arboreal species displayed the most deviant manual postures both on poles and on the ground, whereas highly terrestrial species displayed only small deviations. The adaptations to the challenges of arboreal locomotion should be greater in very young arboreal primates, whose balance is not yet fully developed. Indeed, in young mouse lemurs the use of manual secure grasps—the most ulnarly deviant gripping postures (see Fig. 12.15d)—decrease during development, being greatly used shortly after birth on vertical and narrow substrates (Boulinguez-Ambroise et al., 2020a). Comparative studies of other terminal-branch specialists

have tested the fine-branch hypothesis. Toussaint et al. (2020) compared 11 primate species (6 strepsirrhines and 5 platyrrhines) and 11 non-primate arboreal species (1 scandentian, 3 rodents, 3 carnivorans, and 4 marsupials) and found the possession of a grasping pollex and hallux to be crucial for climbing small vertical substrates. This study also revealed that carnivorans and rodents show a smaller repertoire of grasping postures than primates and marsupials, with primates having the greatest capability for postural adjustment (Toussaint et al., 2020). Tree shrews (Tupaïidae; Sargis, 2007) and some marsupials (Rasmussen, 1990; Rasmussen & Sussman, 2007) possess a hand and foot morphology that is functionally comparable to that of primates. In addition, the highly arboreal woolly opossum (*Caluromys* spp.) uses the terminal narrow branches of the canopy (Rasmussen, 1990; Grelle, 2003) and has developed relatively long digits and a long opposable nail-bearing hallux (Szalay, 1994; Lemelin, 1999; Argot, 2002). Such attributes provide the reasons for considering *Caluromys* the adaptive analog of a terminal-branch user capable of a powerful hallucal grasp, a key feature that is supposed to characterize primates (Hoffstetter, 1977; Youlatos, 2008). These results clearly suggest an evolutionary convergence of grasping in mammals. Besides being used by the woolly opossum (*Caluromys philander*) and the feathertail glider marsupial (*Acrobates pygmaeus*) (Youlatos, 2008; Youlatos et al., 2018), hallucal grasping is also used by small rodents moving on fine branches: namely, the harvest mouse (*Micromys minutus*), and domestic mice raised in a simulated fine-branch arboreal niche (Byron et al., 2011; Urbani & Youlatos, 2013). Hallucal grasping would ensure balance and safety for arboreal locomotor behaviors such as climbing and walking (Urbani & Youlatos, 2013). In fact, while such pedal grasping is maintained across the whole of mouse lemur development, manual postures become less ulnarly deviated, suggesting different functional roles between limbs and emphasizing the role of anchoring ensured by grasping feet (Boulinguez-Ambroise et al., 2020a). This more substantial role of the feet in primate locomotion is also suggested by other studies. Red ruffed lemurs (*Varecia rubra*) rely more on hind limb than on forelimb grasping during arboreal quadrupedal locomotion, with the toe flexors being activated more forcefully and for longer than the finger flexors (Patel et al., 2015). Alternatively, other species, like sciurid rodents, lack primate grasping adaptations but still move on fine terminal branches. Young and Chadwell (2020) compared the Eastern grey squirrel (*Sciurus carolinensis*) and two platyrrhine primates (*Callithrix jacchus* and *Saimiri boliviensis*); they found the primate grasping morphology to improve the locomotor performance on narrow supports compared to the squirrel limb morphology. So, according to the authors, such findings suggest that “basal primate morphological adaptations may have specifically facilitated improved locomotor performance in a fine-branch niche, rather than merely permitting access to the environment”. Eastern grey squirrels and European red squirrels (*Sciurus vulgaris*), however, also feed and forage on terminal branches (Samaras & Youlatos, 2010; Orkin & Pontzer, 2011). Selection for locomotion on fine branches therefore seems to not be a sufficient condition for primate origins and this hypothesis may oversimplify the evolution of primates. Another specific feature of the primate grasping apparatus that has been related to locomotion on fine branches are their flattened nails (i.e., ungulae). These

are homologous to, but different from, the claws (i.e., *calculae*) of non-primate mammals (for a description and review, see Maiolino et al., 2016). The form of the nail shows a high degree of variation among primates: flattened nails are not present on all digits in some primate species, such as some callitrichine monkeys that instead possess claw-like nails (i.e., *tegulae*) (Sussman & Kinzey, 1984; Ford, 1986). It has been suggested that non-primate mammal claws and primate *tegulae* facilitate the use of large vertical substrates (e.g., tree trunks that are too large to grip) when climbing up and down (Cartmill, 1974; Toussaint et al., 2020). In tree kangaroos and sloths, claws even take the form of large hooks to facilitate the grasping of arboreal substrates (Mendel, 1981; Iwaniuk et al., 1998; Warburton et al., 2011; Patiño et al., 2021). In parallel, it has been suggested that the possession of flattened nails and the lack of claws is related to increased grasping abilities, in that claws potentially hinder the grasping of thin and small items (Napier, 1993). However, in their study comparing primates and non-primate arboreal mammals, Toussaint et al. (2020) did not observe an advantage to possessing nails in moving on small substrates (while the possession of a grasping pollex and hallux was found to be crucial for negotiating small vertical substrates). As highlighted by Maiolino et al. (2016), the extensive diversity of nail morphology among primates suggests different roles for the nails of different species and more research is required to explain its functional significance. Primates possess many morphological features that did not evolve simultaneously, suggesting the operation of a wide range of selective pressures (Dagosto, 2007; Sargis et al., 2007).

12.5.3 *Manual Food Grasping and Manipulation*

The ability to grasp food or prey, or manipulate them, is often considered to be most advanced in mammals (Ivanco et al., 1996; Iwaniuk et al., 1999; Iwaniuk & Whishaw, 1999a, 2000; Endo et al., 2007; Sacrey et al., 2009). However, we still do not know whether the use of the hand for grasping represents convergent evolution, arising independently within each mammal lineage (Lassek, 1954; Bracha et al., 1990), or if this ability is plesiomorphic, having arisen early in mammalian evolution (Whishaw et al., 1992) before being lost or elaborated in different lineages. To answer this question, studies have explored hand grasping behavior in various taxa such as xenarthrans (sloths and anteaters; Taylor, 1985), pholidotes (pangolins; Grzimek, 1990), scandentians (tree shrews; Bishop, 1964), dermopterans (colugos; Macdonald, 1984), rodents (Whishaw, 1996; Whishaw et al., 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 et al., 1998; Christel & Billard, 2002; Pouydebat et al., 2008, 2009, 2011; Pouydebat & Bardo, 2019). Mice and rats detect food using olfaction and typically adopt a 'sitting' posture on their haunches while grasping the food with the mouth and using their digits to manipulate it (Whishaw et al., 1998). Marsupials such as the northern quoll (*Dasyurus hallucatus*), opossums, and gliders, share some common

characteristics with rodents (Schwensen, 1994; Ivanco et al., 1996; Landy, 1997): the food is detected using olfaction, or in some cases by proprioception, and is initially grasped by the mouth. On the contrary, carnivorous marsupial species (dasyurids and didelphids: Schwensen, 1994; Ivanco et al., 1996; phalangerids and petaurids: Landy, 1997) initially grasp some animal matter between digits II and III ('scissor grip') as well as with the entire hand (power grip) and ingest it (Landy, 1997). Most carnivores use olfaction to detect food, but the marsh mongoose (*Atilax paludinosus*), small-clawed otters (*Amblonyx* spp.), and the raccoon (*Procyon lotor*) use both visual and tactile means. Raccoons essentially use their hands to grasp food, often using a bipedal posture (Iwaniuk & Whishaw, 1999b) and the scissor grip, as seen in carnivorous marsupials. They also often roll the food between the palms of both hands, as do otters when manipulating food or other objects such as stones during playing behaviors (personal observation). Other carnivores 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). In contrast to raccoons, which seem to possess fine control of forepaw digits, the kinkajou (*Potos flavus*; Pocock, 1917) and the olingo (*Bassaricyon* spp.; Ewer, 1973) grasp objects with a power grip involving a single-handed converging grip (Rensch & Dückler, 1969; McClearn, 1992). The ringtail (*Bassariscus astutus*) and coatis (*Nasua* spp.) seem also to be less dexterous, having little fine control of digit movements (Ewer, 1973; McClearn, 1992). Interestingly, coatis are excellent diggers and shredders. Their lack of fine control of finger movements and the associated musculoskeletal parameters may not allow them to benefit from a complex grasping ability or to feed on the terminal branches as kinkajous, for example, can do (McClearn, 1992). Indeed, there is certainly a relationship between arboreality and skillful food grasping in carnivores (Fabre et al., 2013).

Manipulation of food items is not always linked to arboreality. For example, forepaw manipulation in semi-aquatic mustelids may result from their tendencies to handle a diversity of food items associated with their omnivorous diet (Hall & Schaller, 1964; Fujii et al., 2015; Zellmer et al., 2021). If we extend the reasoning further, the grasping abilities may not be linked to the hand at all! Indeed, in proboscideans, the trunk not only detects food (i.e., olfaction), but is also used as a prehensile organ to grasp it; the absence of bones in this organ allows for a high degree of freedom for movement in all directions. A study of African elephants (*Loxodonta africana*) revealed a plethora of manipulative strategies and grasping behaviors of the trunk during feeding activities (Lefevre et al., 2020). As food grasping strategies, the authors namely reported the catching of items between the trunk's fingers (i.e., finger-like distal projections), the wrapping of the trunk around bigger items, or the wrapping followed by torsion of the trunk allowing the breaking of the item (Lefevre et al., 2020). In primates, food detection occurs through a mixture of visual, olfactory and auditory stimuli in most strepsirrhines (lemuriforms and loriforms; Siemers et al., 2007; Piep et al., 2008; Perrenoud et al., 2015), and mainly visually in haplorhines (Martin, 1990). Strepsirrhines appear to grasp static

foods first with the mouth and show no digital individualization (Petter, 1962; Bishop, 1964; Toussaint et al., 2013). In contrast, when grasping mobile prey, as well as during manipulation, cheirogaleids (*Microcebus murinus*; Reghem et al., 2011; Toussaint et al., 2015; Boulinguez-Ambroise et al., 2019) and several lorisiforms catch insects with one or both hands (Martin, 1972; Oates, 1984; Lemelin, 1996; Nekaris, 2005). Also, the specialized aye-aye (*Daubentonia madagascariensis*) is known to use the third finger to pry insects from holes in trees (Erickson, 1991; Milliken et al., 1991; Erickson et al., 1998). 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 et al., 2004; Pouydebat et al., 2008). To a lesser extent food grasping in primates can involve social manipulation. It has been reported that orangutan mothers may manipulate their offspring as a social tool-use to retrieve food items, guiding their bodies and arms towards the food, and reorienting their hands so that they grab it (Völter et al., 2015). The various grip types used by great apes, namely chimpanzees (*Pan troglodytes*), when grasping static foods are highly comparable to those used by humans (Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Byrne et al., 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 commonly-used in mammals because it is employed 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 resulting from the ability for independent movement of the digits.

12.5.4 Functional Adaptations and Ecological Consequences

The mammalian hand possesses a morphology that perfectly reflects its adaptations for the prehension of arboreal substrates and the strategies for food acquisition with variable properties (e.g., static, mobile, various sizes and structures, etc.) (Hamrick, 2003). A large number of studies have explored the potential adaptive variation of the mammalian hand skeleton and the integumentary structures in relation to foraging behaviors and locomotion (e.g., Jouffroy & Lessertisseur, 1979; Van Valkenburgh, 1987; Norberg, 1994; Szalay, 1994; Thewissen & Etnier, 1995; Hamrick et al., 1999; Rosenberg & Rose, 1999; Lemelin, 1999, 2000; Hamrick, 2001a, b, c).

Interestingly, climbing mammals such as primates, tree shrews, and burramyid marsupials have developed papillary ridges on their fingers that improve their ability to grasp arboreal substrates (Whipple, 1904; Le Gros Clark, 1936; Cartmill, 1974, 1985; Hamrick, 1998; Rosenberg & Rose, 1999; Lemelin, 2000). When comparing two small-bodied marsupials, one arboreal (*Petaurus breviceps*) and the other

mainly terrestrial (*Monodelphis domestica*), kinematic divergences were highlighted between the two species: in contrast to *Petaurus*, *Monodelphis* has relatively shorter digits that are associated with reduced grasping ability and a greater need for stabilizing mechanisms on narrow substrates (Shapiro et al., 2014). The gliding phalangers (*Petaurus breviceps*), as for other marsupials such as koalas (*Phascolarctos cinereus*), can cling to large-diameter substrata using their sharp and keeled claws, whereas pygmy possums (Burramyidae) are better adapted for climbing on narrow branches with their thin and flat nails (Iwaniuk & Whishaw, 2000). Counter to what was previously thought (Napier, 1993), claws are not incompatible with prehensile hands and do not always obstruct the grasping process. The claws of tree kangaroos (*Dendrolagus* spp.) help facilitate unimanual grasping of food objects (Iwaniuk et al., 1998) and clawed rodents are able to grasp food with one hand (Whishaw et al., 1998), as can arboreal tupaiids (*Ptilocercus lowii* and *Tupaia minor*; Sargis, 2001). Similarly, even though colugos (Dermoptera) lack epidermal ridges on their fingers, they are still able to move on arboreal substrates (Lemelin, 2000). Improving friction with smooth arboreal substrates is probably easier for some bats (e.g., *Thyroptera tricolor*) which have adhesive pads on their hands and feet (Wimsatt & Villa, 1970; Thewissen & Etnier, 1995). Anatomical exploration has revealed that many adaptations exist. In order to maintain flexion forces with no additional muscular effort, bats (e.g., Quinn & Baumel, 1993), dermopterans (Simmons & Quinn, 1994), and some climbing rodents (Haffner, 1996) possess intrinsic digital tendon-locking mechanisms that differ among groups in form and function. Interestingly, adaptations may differ at different taxonomic levels and between taxa. For example, bats, birds and rodents have locking tendons that operate using different mechanisms. Bats and birds have a micro-anatomical ratchet mechanism composed of tendon tubercles and tendon sheath plicae (Quinn & Baumel, 1990, 1993). On the other hand, rodents have ventral tendon thickenings that offer better resistance during digital flexion (Haffner, 1996). It is quite possible that adaptive modifications of the integumentary structures of the hand, at least among mammals, have played a major role in the diversification of foraging strategies. In addition to the study of tendons, comparative studies of hand proportions have been very informative and have shown a link between the evolution of these anatomical data and ecological niche (Hamrick, 2001c). For example, primates and marsupials that feed on fruit and insects by foraging on thin branches have relatively short palms, long fingers and small claws (Jouffroy et al., 1991; Hamrick et al., 1999; Lemelin, 1999).

As has been shown for lizards, mammals possess pedal grasping adaptations that may have contributed to the evolution of manual grasping abilities by using the feet to grasp the substratum for support, thereby liberating the hands for other functions (e.g., Mac Neilage et al., 1987). The arboreal marsupials *Caluromys* spp. have long digits, a widely divergent hallux, and a developed hallucal eminence and pad (Argot, 2002; Lemelin et al., 2003), and are capable of 'powerful' pedal grasping (Sargis et al., 2007). An opposable hallux, allowing the foot to grasp, occurs in the molossid bat *Cheiromeles* spp. (Vaughan et al., 2011) and is a shared derived feature of non-human primates (Cartmill, 1972; Martin, 1990). This morphology and ability

may have preceded the evolution of manual grasping (Byron et al., 2011 and references therein). Lemurid strepsirrhines can grasp the arboreal substrate between the first and second digits by hallucial grasping (Cartmill, 1985; Szalay & Dagosto, 1988; Gebo, 1993; Lemelin, 1999; Boyer et al., 2007) due to relatively large *m. adductor hallucis*, and an active *m. peroneus longus* (Kingston et al., 2010). Finally, pedal phalangeal curvature in great apes may be indicative of increased grasping during suspensory and climbing behaviors, in addition to their well-developed hallux (Nakatsukasa et al., 2002; see Congdon, 2012 for review). Besides the opposable hallux, the opposable thumb—allowing numerous manipulative and grasping behaviors (i.e., for food or locomotor substrate grasping or social interactions)—is present in most primate species and shows morphological variability.

In haplorrhines, the saddle-shaped carpo–metacarpal joint of the thumb allows the thumb to oppose the other digits (Napier & Napier, 1985) and to produce, in some cases, a precision grip involving contact between the distal tips of the thumb and other fingers (Marzke, 1997). It appears that chimpanzees have relatively shorter (average) thumb muscle moment arm lengths than humans, allowing them to apply an amount of force lower than that generated by humans when deploying the precision grip (Marzke et al., 1999). These morphological differences might explain why chimpanzees much more frequently use the lateral grip, involving the tip of their thumb and the lateral side of their index finger (Pouydebat et al., 2011). The forces produced by great apes during grasping tasks remain to be tested as we have so far only quantified pulling strength for some primate species, such as olive baboons and mouse lemurs. The measure of pulling strength allows us to assess how well a subject can grasp and hold onto a substrate with its forelimbs or hind limbs. Whereas a rat can pull only 7% of its body weight (40 g; Clark et al., 2004), adult mouse lemurs can pull over 100 times their own body weight (91g; Thomas et al., 2016), just like other specialized narrow branch walkers such as chameleons (Herrel et al., 2013b), suggesting that there has been strong selection for increased grasping strength in arboreal species. Interestingly, as mentioned above, 1-year old olive baboons demonstrate very high pulling strength (i.e., 200% of the adult performance, relative to body mass), this being consistent with the presence of relatively wider phalanges and digit joints in juveniles (Boulinguez-Ambroise et al., 2021). As baby baboons actively cling onto the mother's fur during their first months of life, the effect of infant-carrying should be considered when discussing the origins of grasping in primates.

Comparing the hands of primates overall it is evident that the human hand possesses many derived musculoskeletal traits (Lewis, 1989; Tocheri et al., 2008). Human hands exhibit long, robust thumbs, relatively larger joint surfaces, and hypertrophic thenar muscles, derived traits that are sometimes associated with the origins of making and using stone tools (Marzke, 1997; Susman, 1998). Longer fingers necessitate that relatively less muscle force is needed to stabilize digital joints, and the joints are subjected to relatively lower joint contact stresses during stone tool use. This is reflected in the increased robusticity of metacarpals and phalanges (i.e., robusticity can be assessed as the ratio of the bone midschaft

circumference to the bone length (Bass, 1971; Cope et al., 2005), or as the head breadth of the bone relative to the bone length (Richmond et al., 2016) in humans relative to chimpanzees (Rolian et al., 2011). However, manual forces and pressures acting on the hand during the supposed first stone tool production (by the nearly two-million-year-old hominin fossil populations from Olduvai, Tanzania) showed that peak normal force, pressure, and impulse, are significantly lower for the thumb than for digits II and/or III (Williams et al., 2012).

Revelations from experimental studies showing that some great apes with small thumbs (e.g., bonobos) are able to make stone tools similar to Oldowan tools (Toth et al., 1993; Schick et al., 1993), suggest that the dependence on a derived thumb in the evolution of stone tool use should be re-evaluated. The assumptions linking modern human thumb robusticity specifically to load resistance during stone tool production should be tested again with new methods and approaches, as has recently been done for Neanderthals (Bardo et al., 2020). Finally, the use of the hand among haplorhines (especially in apes and capuchin monkeys) seems to be the most complex among mammals and subject to great variability, but whether this complexity and variability of the grasping and manipulative behaviors are linked to their arboreal origins remains to be examined in a phylogenetic framework (e.g., Fig. 12.16).

12.5.5 Hand Preference, Social Interaction and Emotion in Primate Grasping Behavior

For humans hand preference has been well assessed for both unimanual and asymmetric bimanual grasping tasks, with a population-level bias towards the right hand approximating 90% (for a meta-analysis, see Papadatou-Pastou et al., 2020). Hand preference at both individual- and population- levels has been demonstrated for several non-human primate species as well (chimpanzees: Hopkins, 1996; New-World primates: Hook-Costigan & Rogers, 1997; Olive baboons: Molesti et al., 2016). Evidently handedness for unimanual grasping in these primates seems to be weaker than for bimanual grasping (Fagard & Marks, 2000; Meguerditchian et al., 2015; Molesti et al., 2016) and less sensitive than bimanual manipulations for detecting population-level bias (McGrew & Marchant, 1992; Vauclair et al., 2005). Several studies reported an effect of the mobility, the position, or the size of the item that was being grasped (Lehman, 1993; Meunier et al., 2011; Toussaint et al., 2013; Pouydebat et al., 2014). Such asymmetric use of the hands for bimanual grasping has been correlated with contralateral brain structural asymmetries in a section of the central sulcus related to the motor hand area, suggesting hemispheric specialization of the motor system for the limbs: in chimpanzees (*Pan troglodytes*; Hopkins & Cantalupo, 2004) and Olive baboons (*Papio anubis*; Margiotoudi et al., 2019), as is the situation for manipulative tasks in humans (Hammond, 2002). Interestingly, at the population level it has been reported for

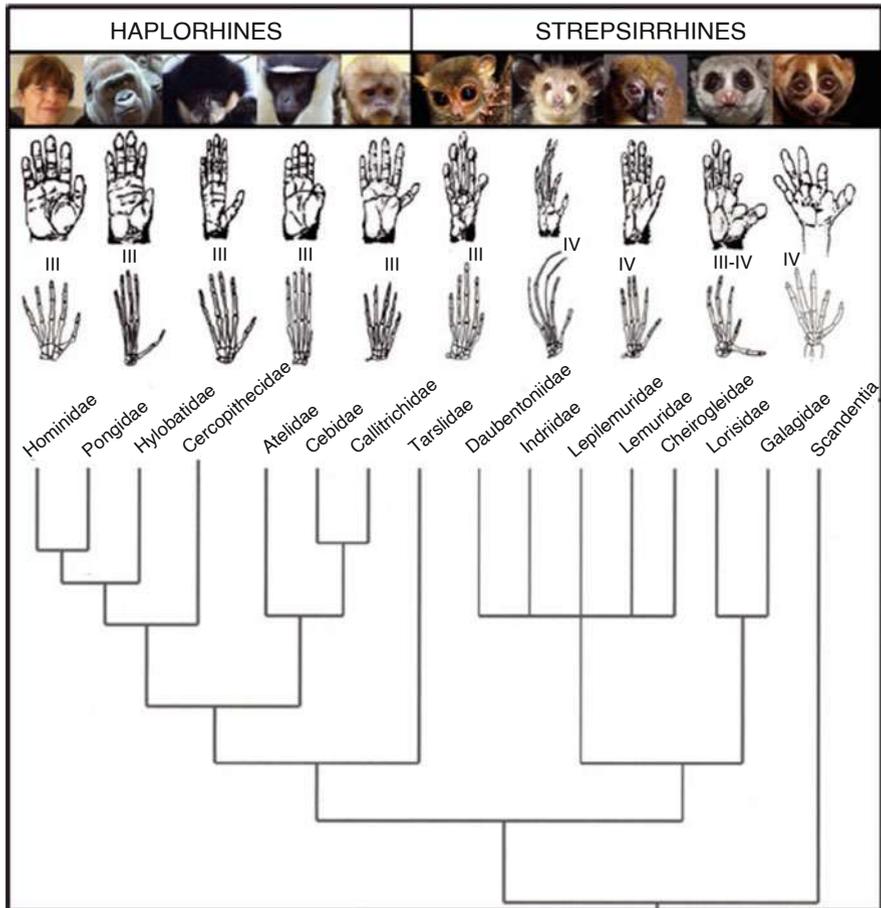


Fig. 12.16 Phylogenetic branching patterns showing morphological and functional differences of the hand of primates. Modified and adapted from Schultz (1972; hand skeleton figures), Hershkovitz (1977; hand skeleton figures), and Chiu and Hamrick (2002; phylogenetic topology). Photos courtesy of A. Bardo (Hylobatidae and Cercopitheciidae), D. Haring (Tarsiidae, Daubentoniidae, Cheirogaleidae, Galagidae); all others by E. Pouydebat

chimpanzees and gorillas (*Gorilla gorilla*) that, while the right hand (i.e., left hemisphere activation) is more involved in unimanual grasping actions directed toward inanimate targets (e.g., objects, food items), no hand preference is reported for animate targets (e.g., conspecifics) (Forrester et al., 2011, 2012). In both humans and great apes, the use of the left hand for self-touching of the face is greater than the use of the right hand (Dimond & Harries, 1984), which may be explained by the fact that grasping actions towards animate targets (i.e., social manipulation) likely imply emotional involvement, and there is a general dominance of the right hemisphere for all kinds of emotions (Gainotti, 2019). In fact, there might be a neural distinction

between targets requiring functional and social manipulation (Baldachini et al. 2021).

The mechanisms that may influence the development of handedness are widely debated on both theoretical and empirical grounds (Boulinguez-Ambroise et al., 2022a, b). Empirical lines of evidence highlight that, besides genetic factors (McManus & Bryden, 1992; Yeo & Gangestad, 1993; Laland et al., 1995), other nongenetic factors associated with the early developmental environment, likely play a role in the development of handedness (Hopkins & Ronnqvist, 1998; Hopkins, 2004; Fagard, 2013). A key factor of the developmental environment is the actions of the mother on the immediate environment of the fetus and then the infant. In humans and non-human primates such as chimpanzees, gorillas and baboons, maternal cradling of newborns is lateralized at the individual level and shows a left-side bias at the population-level, which means the use of left arm is favored over the right arm for cradling the infant in the majority of individuals (Manning et al., 1994; Boulinguez-Ambroise et al., 2020b). For Olive baboons, if the infant is cradled on the left the infant embraces and holds onto the left side of the mother with its right arm, the left hand being free, and vice versa. The hand that is not recruited for clinging to the fur is free to be able to reach and for fine manipulative grasping actions, thereby providing greater motor and neurological stimulation than for the other hand. In fact, in this species (*Papio anubis*), early postnatal individual hand preference for unimanual grasping within the first months of life positively correlates with maternal cradling lateralization (Boulinguez-Ambroise et al., 2021). As maternal left-cradling bias likely reflects brain right hemisphere specialization for emotion (see Manning & Chamberlain, 1991; Malatesta et al., 2019; Forrester et al., 2019), the early emergence of handedness in baboons might be indirectly related to emotional processing. However, very little comparative research on manual lateralization has been conducted for non-primate mammals (Ströckens et al., 2013; Versace & Vallortigara, 2015; Boulinguez-Ambroise et al., 2022b). Interestingly, Giljov et al. (2015) assessed handedness in marsupial species, one of the other large mammalian lineages. The authors reported a population-level manual preference for multiple behaviors (e.g., unimanual feeding, grooming) in red (*Macropus rufus*) and grey (*Macropus giganteus*) kangaroos, which mainly employ a bipedal gait, thereby freeing the hands for performing other tasks. By comparing mainly bipedal and quadrupedal marsupial species Giljov et al. (2015) highlighted the crucial role that postural characteristics (e.g., bipedality), rather than phylogeny, may play in the origin of handedness in mammals. These works on lateralization open many perspectives for comparison within tetrapods: the questions addressed and new ones that arise can be applied to other species outside primates (Karenina et al., 2017).

12.5.6 Concluding Remarks About Grasping in Mammals

To conclude, although many tetrapods grasp substrates for moving and manipulating food, most mammals demonstrate advanced finger mobility. Skilled reaching

movements in rodents and primates are, in part, similar (Bishop, 1964; Jeannerod, 1988; Whishaw, 1996), suggesting an ancestral origin (homology) of skilled forelimb movements (Sacrey et al., 2009). However, grasping ability with the feet and hands can no longer be used to set primates apart from other mammals, or even tetrapods (Le Gros Clark, 1959; Martin, 1990). The great variability of postures and complex in-hand movements and repositioning abilities quantified for several primate species (Craet et al., 2009; Bardo et al., 2016, 2017) suggest that additional data for non-primate species are needed to determine whether grasping behavior is homologous or homoplasious. The high diversity of grasping patterns among primates demonstrates the necessity for developing integrative approaches (e.g., eco-ethology, biomechanics, physiology, morphology) to further our understanding of the complexity and the evolution of this function (Pouydebat & Bardo, 2019).

12.6 Conclusions

Grasping behavior plays an essential role in various contexts including locomotion, feeding, and social interactions in a great diversity of tetrapod vertebrates, but has received relatively little attention beyond 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 highly developed in mammals. Furthermore, although birds are limited to grasping with the hindlimbs, many species demonstrate comparable levels of grasping force and digital dexterity as those evident in mammals. Grasping modalities may differ from group-to-group, but they share common musculoskeletal bases and have been molded by similar selective pressures.

Among lissamphibians, anurans demonstrate the greatest complexity of forelimb movements, and such abilities have evolved several times independently. Features such as relatively long forelimbs, intercalary elements in the skeleton of the hand, 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. Species of *Phyllomedusa* are described as having the most refined examples of manual dexterity among anurans and can generate greater forces and have specific modifications of their hand musculature compared to other tree frogs. These anatomical modifications include highly differentiated forearm muscles that appear to be able to control each finger individually, allowing complete closure of the hand around narrow substrates. Just as in primates, some frog species can adopt various hand positions, allowing them to change the form of their grip to optimize interactions with the features of the substrate they are interacting with (e.g., size, texture, inclination), assuring stability. Beside the various manual gripping configurations, grasping with the feet has also been reported for multiple behaviors and should receive more attention in future research.

Grasping in lizards appears to be driven largely by selection for locomotor attributes associated with navigating in complex three-dimensional habitats, and

plays relatively less of a role in other behaviors, such as feeding. The most commonly observed grip employed by lizards is that corresponding to a power grip. With regard to this, the tendinous pattern of the palm of the hand plays a key role allowing flexion at the metacarpo-phalangeal joints. Complete power grasping abilities are restricted to lizards exhibiting specific tendon structures. Additionally, the configuration of the wrist and hand bones also appears to correlate with grasping ability. Those taxa, such as chameleons (the most specialized arboreal group of lizards), but also other lineages including anoles, geckos, and varanids that exhibit varying degrees of manual grasping abilities, also exhibit pedal grasping. However, the mechanisms behind lizard pedal grasping abilities are still poorly understood and require further investigation. Although phylogeny seems to best explain osteological traits of the lizard foot, it explains little with regard to the variation reported for muscle and tendon anatomy, and it is these that may better predict the ability of the pes to adjust so as to achieve a grip.

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 in generating and maintaining gripping forces. It is to be noted that although most birds able to perform pedal grasping are restricted to the execution of a power grasp, some birds have achieved high levels of digital dexterity, similar to those of other tetrapods whose limbs are far more specialized for grasping. In this regard, further investigation is required to elucidate the functional significance of several features of the avian foot, such as the various toe and digital flexor tendon configurations, proportional phalanx lengths, and claw size and shape. Such features are likely involved in enhancing grasping capability. Although feeding has been a major selective force driving grasping capability, on a broader evolutionary scale the ability to grasp is confounded because of its association with the adoption of an arboreal existence.

In mammals, grasping occurs extensively during food manipulation, namely while moving or standing on arboreal supports, but is also employed in various social interactions. The vast majority of work in this vein pertains to primates. Current hypotheses propose that the use of fine terminal branches (specifically vertical ones) for exploiting fruits, flowers, insects, and nectar as food resources may have constituted an important selective pressure driving the evolution of primate grasping abilities. However, further investigation is required to enable better explanation of variations observed about hand dexterity among species, specifically by examining early grasping experiences in juveniles, such as infants clinging to their mothers. While the power grip may be one of the most commonly employed in mammals (because it is used by animals with opposable, pseudo-opposable, and non-opposable thumbs) many primate species display a great variety of hand and digit postures that permit a fine precision grip. Arboreal mammals, including primates but also marsupials and rodents, show hallucial grasping and seem to rely more on hind limb than on forelimb grasping during quadrupedal locomotion. This is

suggestive of a more substantial role of the feet in locomotion that may have contributed to the evolution of manual dexterity by freeing the hands for other functions (e.g., feeding, social behavior). Adaptive changes in the integumentary structures of the hand in mammals might have been essential in the diversification of foraging strategies. Interestingly, according to the idea of a lateralized “social brain”, there might be a neural distinction in grasping between targets requiring functional and social manipulation and this should be further considered in future research.

Grasping ability and its underlying forearm musculature is 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, although these are not necessarily prerequisites for successful grasping. Digital muscle and tendon complexity may limit, or enhance, digital independence, which, in turn, could have important implications for gripping force production and/or digital dexterity. Neither within nor among the major tetrapod clades is there a one-to-one mapping of grasping form to function, but 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, involving a greater diversity of taxa, are required to allow this hypothesis to be tested in a rigorous phylogenetic framework.

Acknowledgments We warmly thank Vincent Bels for inviting us to participate in this book project. We appreciate the generosity of Hartmut Förstner for providing us with the schematics shown in Fig. 12.7, and of Gilles Berillon for providing the 3D models shown in Fig. 12.14. Part of this work was funded by PICT 2016-2772, 2018-0832 and PIP 0389, and supported by a SU emergence funding “HUMDEXT”. Finally, we would like to warmly thank those experts who helped us to improve this article, in particular Christine Böhmer and Anthony Russell.

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