

# The Tendinous Patterns in the Palmar Surface of the Lizard Manus: Functional Consequences for Grasping Ability

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## ABSTRACT

In lizards, distinct patterns of the tendinous structures associated with the forearm flexors have been described. In most lizards, the m. flexor digitorum longus ends in a tendinous plate with an embedded sesamoid, from which tendons run to the terminal phalanx of each digit. This structure is known as the flexor plate. In many polychrotid lizards, however, the flexor digitorum longus muscle is continuous with individual tendons running to each digit, and no complete flexor plate is present. In most geckos, the flexor plate is reduced to a tendinous plate without sesamoid. To evaluate the consequences of these differences in morphology on locomotion and grasping, we compared the use of the fore-arm and hand in lizards exhibiting three different tendon patterns (*Pogona vitticeps*, an agamid with a well-developed flexor plate; *Gekko gecko*, a gekkonid with a flexor plate, but without an embedded sesamoid; *Anolis equestris*, a polychrotid without flexor plate, but showing independent tendons running to each digit) while moving on different substrates. We found that the presence of a flexor plate with sesamoid bone prevents digital flexion and creates a rather stiff palmar surface in *P. vitticeps*. This configuration makes it impossible for *P. vitticeps* to grasp narrow branches and results in a strongly impaired locomotor performance on narrow substrates. Both *G. gecko* and *A. equestris* can flex the palms of their hands and their fingers more extensively, and do so when moving on narrow substrates. We suggest that the reduction of the flexor plate in both *G. gecko* and *A. equestris* allows these animals to move effectively on narrow substrates. Anat Rec, 292:842–853, 2009. © 2009 Wiley-Liss, Inc.

**Key words: flexor plate; forearm muscles; grasping hand; lizards; palmar sesamoid; tendons**

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All limbed tetrapods have flexor tendons in the palmar surface of the manus that connect the muscles of the forearm with the digits. These tendons emerge from the superficial (m. flexor carpi ulnaris; m. flexor carpi radialis), and deeper (m. flexor digitorum longus) muscles of the forearm. Each layer (superficial and deep) of these skeletal muscles exerts its actions on the bones of the hand by means of an independent set of tendons (Davis, 1964). In lizards, however, only the m. flexor digitorum longus sends flexor tendons to the digits. This muscle flexes the digits via five strong tendons that generally

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originate from a unique tendinous structure, the flexor plate, and insert onto the basal portion of the terminal phalanges. Interestingly, the flexor tendons of the digits are united at the flexor plate in most lizards, and at this point of union, a palmar sesamoid is typically present (Cope, 1892; Krause, 1990). We follow Haines (1950) in naming this structure the flexor plate. In addition to the flexor plate, Haines (1950) distinguished a superficial palmar aponeurosis. The palmar aponeurosis is linked to the palmaris longus muscle, to the flexor retinaculum, or to the *mm. flexores breves superficiales*. However, the absence of the palmar aponeurosis is common in lizards (Haines, 1950). In fact, none of the lizards used in our study showed this structure. The flexor plate is associated with the *m. flexor digitorum longus*, and, as we describe below, constitutes a structure different from the palmar aponeurosis. Consequently, we use the name flexor plate for the entire tendinous structure between the *m. flexor digitorum longus* and the flexor tendons, including the embedded sesamoid.

In a study of the muscular and tendinous structures of the forearm and manus in *Polychrus*, Moro and Abdala (2004) described the patterns of the tendinous connections among the deep layers of the forearm flexor muscles and the digits. In doing so, they recognized two distinct patterns: in the L-pattern (*Liolaemus*-pattern, since it was first described in *Liolaemus*; Moro and Abdala, 2004) there is a tendinous extension between the *m. flexor digitorum longus* and the tendons that insert onto the digits, with one or two palmar sesamoids embedded (flexor plate sensu Haines, 1950; see Figs. 1 and 2B). In the P-pattern (*Polychrus*-pattern, Moro and Abdala, 2004), the flexor plate is highly reduced or absent, and the tendons pass directly to the terminal phalanges (Figs. 1 and 2A). The L-pattern is the most common one and is observed in many lizard groups. The P-pattern is observed predominantly among polychrotid lizards (*Anolis* lizards and their relatives) and chameleons.

Despite this striking variation in the tendinous structures of the lizard manus, little is known about the functional consequences thereof in relation to the use of the hand during locomotion. We hypothesize that those species of lizards with a reduced flexor plate, having more individualized tendons and no sesamoid, can flex the palm of the hand and their digits to a greater degree. This may then improve the capacity of species with these patterns to grasp narrow substrates, as has been suggested for arboreal mammals. Indeed, many arboreal mammals use a grasping motion to maintain balance when walking on narrow substrates or when climbing vertical structures (Sargis, 2001; Bloch and Boyer, 2002; Lammers and Biknevicius, 2004; Schmitt and Lemelin, 2004; Isler, 2005). The presence of a flexor plate with embedded sesamoid, in contrast, might restrict the flexion capacity of the palm and digits, but could act to transfer the forces of the flexor digitorum longus to all digits simultaneously. Such a configuration is likely beneficial for terrestrial animals as a relatively immobile and stiff hand may allow an increase in effective limb length.

In this study, we investigate the functional consequences of differences in the tendinous structures of the hand in lizards by examining the morphology and function of the distal forelimb in representative lizard species dis-

playing the main tendinous patterns observed insofar: *Pogona vitticeps* representing the L-pattern and *Anolis equestris* as a representative of the P-pattern. Additionally, we include a gekkonid species, *Gekko gecko*, in our analysis as our observations indicated that representatives of this lineage showed features of the palmar tendinous pattern that are different from those observed in *Pogona*. We first use external high-speed and X-ray video recordings to describe the position and use of the hand during locomotion on different substrates. Next, we present the results of stimulation experiments that were used to quantify movement potential of the digits in these species. Finally, we measured grasping strength both *in vivo* and based on stimulations of the flexor muscles of the forearm and hand to understand the performance consequences of the observed differences in morphology and function.

## MATERIAL AND METHODS

### Animals

Basic details of the aponeurotic complex of the lizard manus were obtained by means of dissection of 71 specimens belonging to 14 lizard families (see Appendix). However, for the sake of brevity, descriptions and discussions presented are based on the same species as used in the experimental analysis (*P. vitticeps*, *A. equestris*, and *G. gecko*). We adopt Haines' (1950) terminology for the tendinous and muscular structures throughout.

Three adult male *Pogona vitticeps*, three adult male *Gekko gecko* and three adult male *Anolis equestris* were obtained through the pet trade and used in the experiments (Table 1). These animals were selected because of their size, easy of maintenance, and availability for experimental studies. Other species such as *Polychrus* would have been interesting to include in our study but were impossible to obtain through the pet trade. Animals were fed *ad libitum* and were maintained in a climate-controlled room at 25°C, with a basking spot at higher temperature. Before the experiments, all specimens were weighed, and the dimensions of the body (snout-vent length), head (length, width, and height), forelimbs (humerus, radius, metacarpus, and length of longest digit not including the claw), and hind-limbs (femur, tibia, metacarpus, and length of longest toe not including the claw) were determined using digital calipers (Mitutoyo CD-30C and CD-15B;  $\pm 0.01$  mm). In addition, dissections were performed on two additional, preserved adult specimens of each species. All muscles of the fore-arm and hand were dissected under a dissecting microscope and stored in 70% ethanol. Muscles were blotted dry and weighed using an electronic microbalance (Mettler Toledo MT5;  $\pm 0.001$  mg).

### High-Speed Video Recordings

Animals were filmed in lateral view using a Redlake MotionPro 500 camera set at 250 frames  $s^{-1}$  while running on two dowels of different diameters (17 and 58 mm), and across a flat substrate. Animals were stimulated to run as fast as possible without having them jump off the dowel. At least five sequences on each substrate were recorded and analyzed for each individual. Videos were reviewed using Midas player (version 2.1.5; Xcitex) and the timing of forefoot contact events

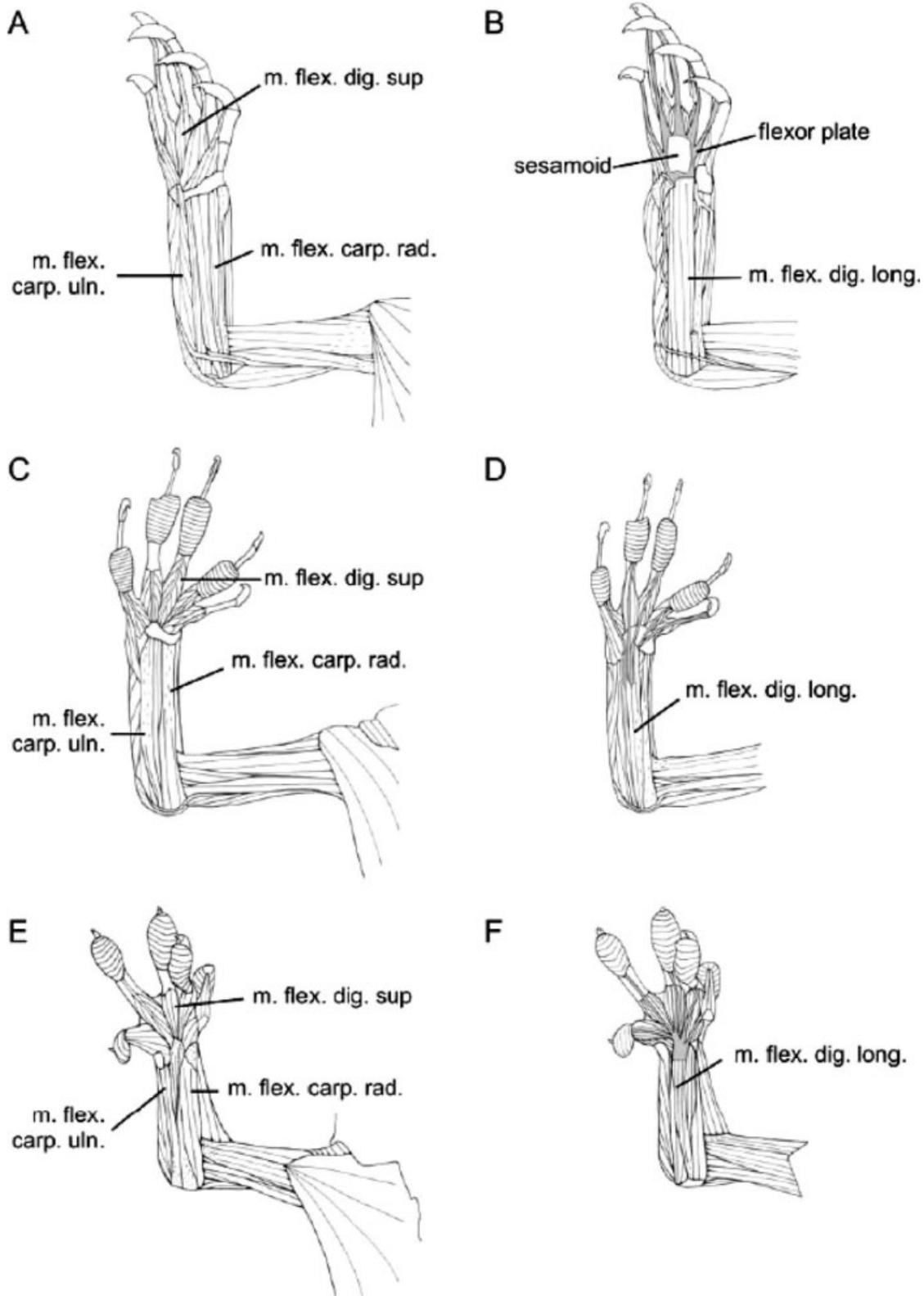


Fig. 1. Superficial (A, C, E) and deep (B, D, F) view of the flexor muscles of the forearm of *Pogona vitticeps* (A, B), *Anolis equestris* (C, D), and *Gekko gecko* (E, F). Note the presence of a well-developed flexor plate with an embedded sesamoid bone in *P. vitticeps*. In *Anolis equestris*, the flexor plate is divided, and individual tendons run to the

respective digits. *Gekko gecko* has a reduced flexor plate: tendinous plate, showing no sesamoid bone. m. flex. dig. long., m. flexor digitorum longus; m. flex. carp. uln., m. flexor carpi ulnaris; m. flex. carp. rad., m. flexor carpi radialis; m. flex. dig. sup., m. flexores digiti brevis superficialis.

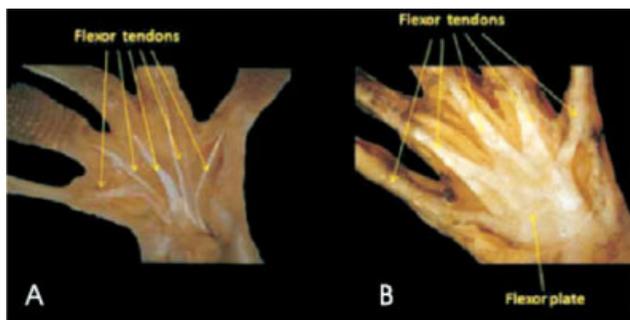


Fig. 2. Photographs illustrating the differences in tendinous structure of the manus in (A) *Anolis equestris* and (B) *P. vitticeps*.

**TABLE 1. Summary of morphometric data for the individuals used in this study**

Species	SVL (mm)	Body mass (g)	fdl mass (mg)
<i>Anolis equestris</i>	144.65 ± 6.66	68.28 ± 11.63	38.55 ± 4.19
<i>Gekko gekko</i>	132.13 ± 11.13	39.33 ± 11.45	19.95 ± 5.04
<i>Pogona vitticeps</i>	179.40 ± 10.45	215.16 ± 29.65	117.43 ± 28.33

Table entries are means ± standard deviations. fdl, flexor digitorum longus.

was recorded. Based on these data, contact (when the hand is in contact with the substrate) and swing phase (when the hand is off the substrate) durations were calculated and qualitative descriptions of the placement of the hand onto the substrate were made. Additionally, we recorded the number of times an animal lost its balance while moving on dowels of different size. Differences between species in their stability were tested using a Chi<sup>2</sup> test.

### X-Ray Recordings

Small metal markers were inserted subcutaneously into the musculature that is close to the bone using hypodermic needles. Markers were positioned on the dorsum of the animal at the level of the pectoral girdle, at the proximal and distal ends of the humerus, at the proximal end of the radius and at the distal ends of the radius and ulna, at the base of the carpals, at the base of the phalanges, and at the penultimate phalanx of the longest toe. During the implantation of the radio-opaque markers, animals were anaesthetized using an intramuscular injection of Ketamine (150–200 mg/kg).

Animals were filmed in lateral view while moving on a broad and narrow dowel (58 and 17 mm, respectively) or a flat substrate in the case of *P. vitticeps*. Again, animals were stimulated to run as fast as possible without having them jump off the dowel. A Philips Optimus M200 X-ray generator was used to emit X-rays and images were recorded using a Philips image intensifier with a Redlake MotionPro2000 camera attached. At least five trials were recorded for each animal moving on both substrates. The following points were digitized using Didge (version 2.2.0; A. Cullum) for the frame in which the hand first contacted the substrate and the frame just prior to release of the sub-

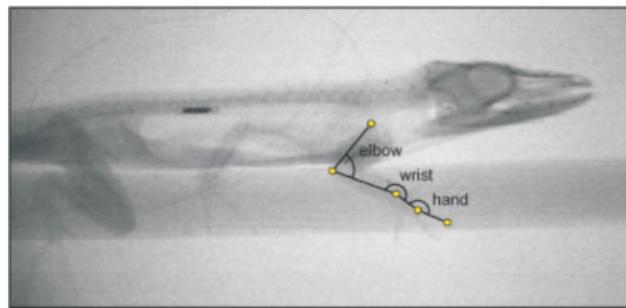


Fig. 3. Frame from an X-ray movie (250 fps) of *Anolis equestris* walking across a narrow (17 mm) dowel. Illustrated are the markers used for digitization and the angles calculated during the stance phase.

strate for all steps recorded in each sequence: the shoulder, the elbow, the wrist, the base of the toes, the toe marker, and the tip of the snout. Based on these points, the elbow, wrist, and hand angles (see Fig. 3) were calculated, as well as the average velocity of movement throughout the sequence.

All kinematic variables (i.e., forelimb segment angles) were Log<sub>10</sub> transformed before analyses, and normality and homoscedasticity were tested using Shapiro-Wilks and Levenes tests, respectively (Sokal and Rohlf, 1995). Nested analyses of variance (with individual assigned as random factor and nested within species) were used to test for differences in kinematics between species, contact phase, and substrate. Nonsignificant interaction effects were removed from the analysis.

### Grasping Force

Grasping forces were measured using a Kistler Squirrel force platform. A glass dowel was mounted on the force plate and animals were allowed to grasp the dowel with both hands. Next, animals were pulled off the dowel at constant speed at an angle of 45° to the horizontal. Three trials, including at least three pull-offs each, were recorded for every animal. Trials were analyzed using the Kistler Bioware software and peak forces in X, Y and Z direction as well as the resultant forces were extracted. The peak grip (resultant force, including friction generated by the adhesive pads) and grasp (vertical component only) forces were recorded for each individual and species means were calculated. Differences among species were tested using analysis of covariance, with the mass of the m. flexor digitorum as covariate.

### Stimulation Experiment

Bipolar teflon-coated NiCr twisted electrodes were inserted in the following muscles in two individuals of each species: the m. flexor digitorum longus, the m. flexor carpi radialis, and the m. flexor carpi ulnaris. Animals were brought under deep anesthesia using Ketamine (225 mg/kg body mass) and the muscles of the right fore-limb were exposed. Electrodes were inserted in the middle of the respective muscle bellies and connected to a stimulator (Grass S48). The stimulation circuit was charge balanced by a coupling capacitor and

bleed resistor (Loeb and Gans, 1986) to avoid muscle damage and undue fatigue. Muscles were stimulated at 12 V with a pulse train of 500 ms at 70 Hz, and 3 ms pulse duration. Animals were positioned on their back on a custom-made platform, and the lower arm was immobilized to allow visualization of movements at the wrist and hand. Stimulation voltage was gradually increased from 3 V, in 1 V steps, until no further wrist flexion was observed.

Animals were filmed during the stimulation experiments in combined ventral and lateral view using a mirror positioned at an angle of 45° to the horizontal at the level of the arm. Muscles were stimulated one by one and movements were recorded. Next, combined stimulations were performed to explore the consequences of coactivation of the different muscles. Finally, the hand of each animal was positioned around two custom-made semi-cylindrical plates attached to a Kistler force transducer (type 9207,  $\pm 5$  N) and portable charge amplifier (type 5995). All muscles were stimulated at once, and both the stimulus and the corresponding grasping forces were recorded digitally on tape using a TEAC DAT recorder. Three to five trials were performed for each individual, and a species average was calculated from the maximal grasp forces of each individual. Forces were multiplied by two to allow a comparison to the forces exerted by both hands *in vivo* using the force plate. At the end of the experiments, animals were sacrificed using an overdose of Ketamine (400 mg/kg body mass) and placed in the private collection of A.H.

All experiments were approved by the animal ethics committee at the University of Antwerp.

## RESULTS

### Morphology

As the arrangement of the m. flexor digitorum longus and associated tendinous structures observed in this study match those described previously in Moro and Abdala (2004) and Abdala and Moro (2006), only a short overview of the L- and P-patterns is given here. *Gekko gekko* exhibited a different pattern from those previously reported, and is described in more detail below.

The L-pattern was observed in most of the dissected specimens, including *Pogona vitticeps* (Figs. 1A,B). In species displaying this pattern, the m. flexor digitorum longus muscle arises tendinously from the distal head of the humerus. The muscle is divided into three branches: a radial belly close to the radius; a medial ulnar belly, and a belly coming from the distal extremity of the ulna (condylo-radialis, centralis, and condylo-ulnaris of Windle, 1889; in Haines, 1950). The bellies join distally and merge into a broad flat tendinous surface, which has a flat palmar sesamoid embedded. Distal to the zone where the sesamoid is embedded, the flexor plate (Haines, 1950) extends further and is composed of several tendinous sheets. Specifically, four triangular surfaces can be recognized, each ending in a thick tendon that runs within the flexor tunnels and inserts onto the terminal phalanx of its respective digit. The belly coming from the distal end of the ulna also converges onto the flexor plate but is slightly separated from the other two parts and persists as a bulky, divided tendon. One branch continuing to the fifth finger, runs within the fibrous flexor tunnel and inserts onto the terminal pha-

lanx. The other branch converges onto the ulnar side of the triangular surface associated with digit IV. The flexor plate is connected to the underlying carpals through the palmar head of the flexor digitorum longus (Russell and Bauer, 2008).

The P-pattern was observed in *Furcifer oustaleti*, *Polychrus acutirostris*, and *Anolis equestris* (Fig. 1C,D). In this pattern, the m. flexor digitorum longus is composed of the three branches described above (note, however, that the usual branch number in *Anolis* is four, Russell, Personal Communication). The tendons of the m. flexor digitorum longus pass across the palmar surface straight to the terminal phalanges. There are three layers arranged on different levels. Tendons coming from the medial branch of the mm. flexores digitorum longus lie deep. They form a bulky layer which occasionally includes a highly reduced sesamoid, and supports the other more superficial levels. From this deep level, the tendons of digits I to IV arise. Superficial to this layer lies a tendon coming from the more radial branch of the m. flexor digitorum longus. The tendon divides, and its two branches reinforce the digital tendons of digits III and IV. The branch on the ulnar side forms a bulky tendon that runs to digit V. It is noteworthy that the radial carpal and the head of the radius, on the one hand, and the pisiform along with the ulnar head on the other hand, are well developed and jointly form a deep carpal tunnel. It is through this tunnel that the tendons run toward the digits.

In *G. gekko* and the other geckos examined (see Appendix), we observed a pattern that was notably different from the L- and P-patterns previously described, and thus we decided to name it the G-pattern (note, however, that other patterns are present in other gecko species; Russell and Bauer, 2008). In the G pattern (Figs. 1E,F) the m. flexor digitorum longus arises tendinously from the distal head of the humerus (see also Zaaf et al., 1999). It is divided into three heads of origin with one closer to the radius, one middle branch and one closer to the ulna. The muscle presents a long tendon attached to an expanded tendinous sheet located under the layer of the mm. flexores breves superficiales, with no sesamoid embedded. Distally, the unique tendinous structure distributes single tendons to each digit. The tendon of digit V is, however, slightly independent of the main plate. Note, however, that variation may exist and a slight departure of the pattern observed here for *Gekko* is described in Russell and Bauer (2008).

### Movement Patterns

Our data on the locomotion of each species on different substrates showed some striking contrasts between species (Figs. 4 and 5). *Pogona vitticeps* was unable to run or even walk on the narrowest substrate included in our trials (17 mm). Of the two other species, *Anolis equestris* showed a loss of balance in about 20% of the trials recorded, and *Gekko gekko* in about 36% of the trials when moving across the narrow dowel. This difference in stability between *A. equestris* and *G. gekko* is significant ( $\chi^2 = 8$ ; d.f. = 2;  $P = 0.0018$ ). A detailed review of the videos revealed that both *A. equestris* and *G. gekko* first planted their hand with the palmar surface on the substrate. Subsequently, the fingers are flexed around the dowel (Figs. 4 and 5).

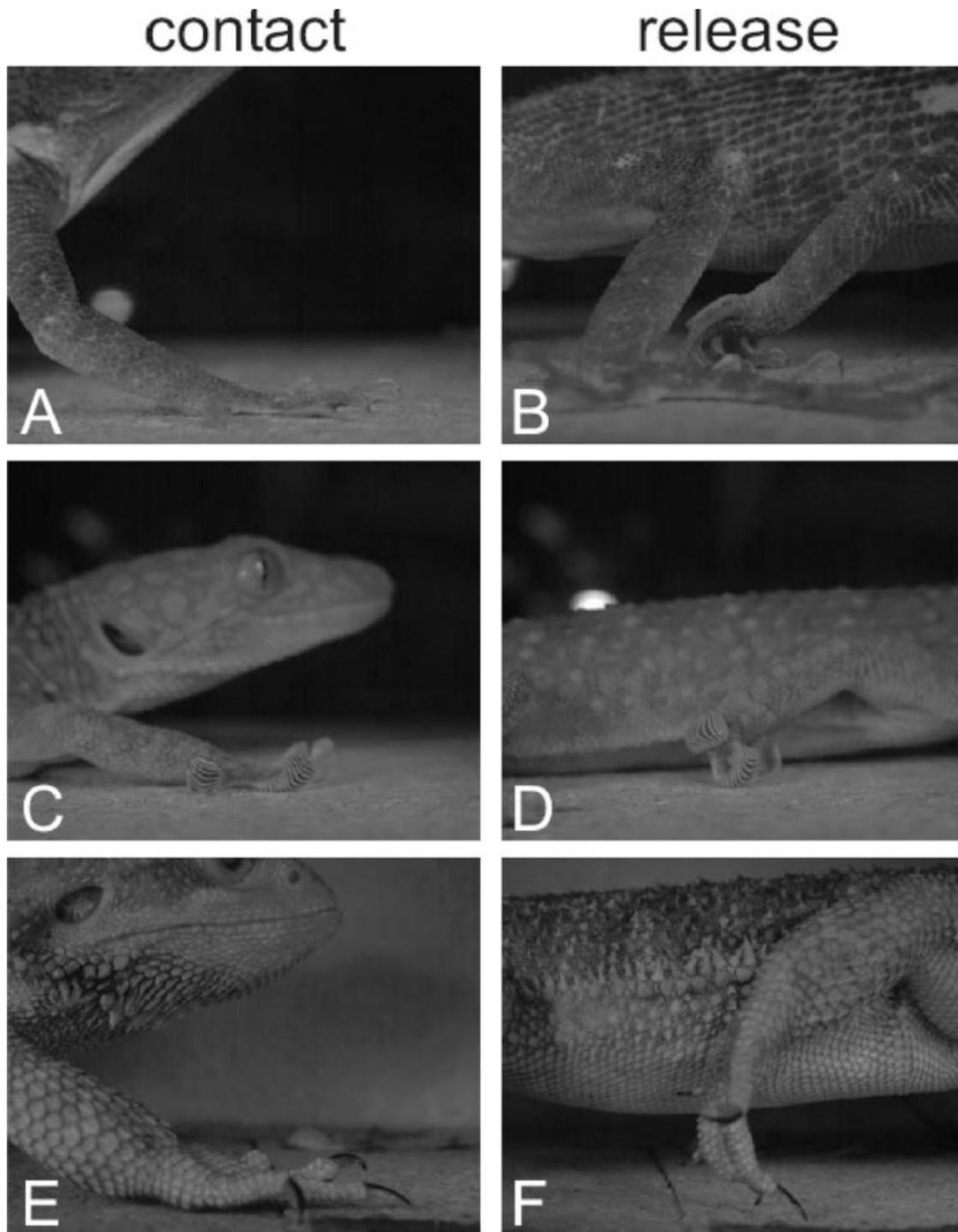


Fig. 4. Selected images from high-speed video recordings (250 fps) of *Anolis equestris* (A, B) *Gekko gecko* (C, D) and *Pogona vitticeps* (E, F) at initial substrate contact, and the frame before the release of the hand from the substrate when running on a flat cork substrate. Note

Interestingly, although *Anolis equestris* did not change its step-time parameters on different substrates, the effect of substrate diameter was generally strong in both *Gekko gecko* and *Pogona vitticeps* (Table 2). In *G. gecko*, for example, stance time (the time that the hand is in

contact with the substrate) increased by 34% and swing time (the time that the hand is off the substrate) by 24% when moving on a narrow versus a broad dowel. Similarly, *P. vitticeps* showed an increase in contact time (20% increase) and swing time (15% increase) when

how all species contact the substrate with the palmar surface of the hand. Although the hand in *Pogona* functions as a rigid pivot, the fingers are actively hyper extended in the gecko, and bend under the weight of the animal in *Anolis*.

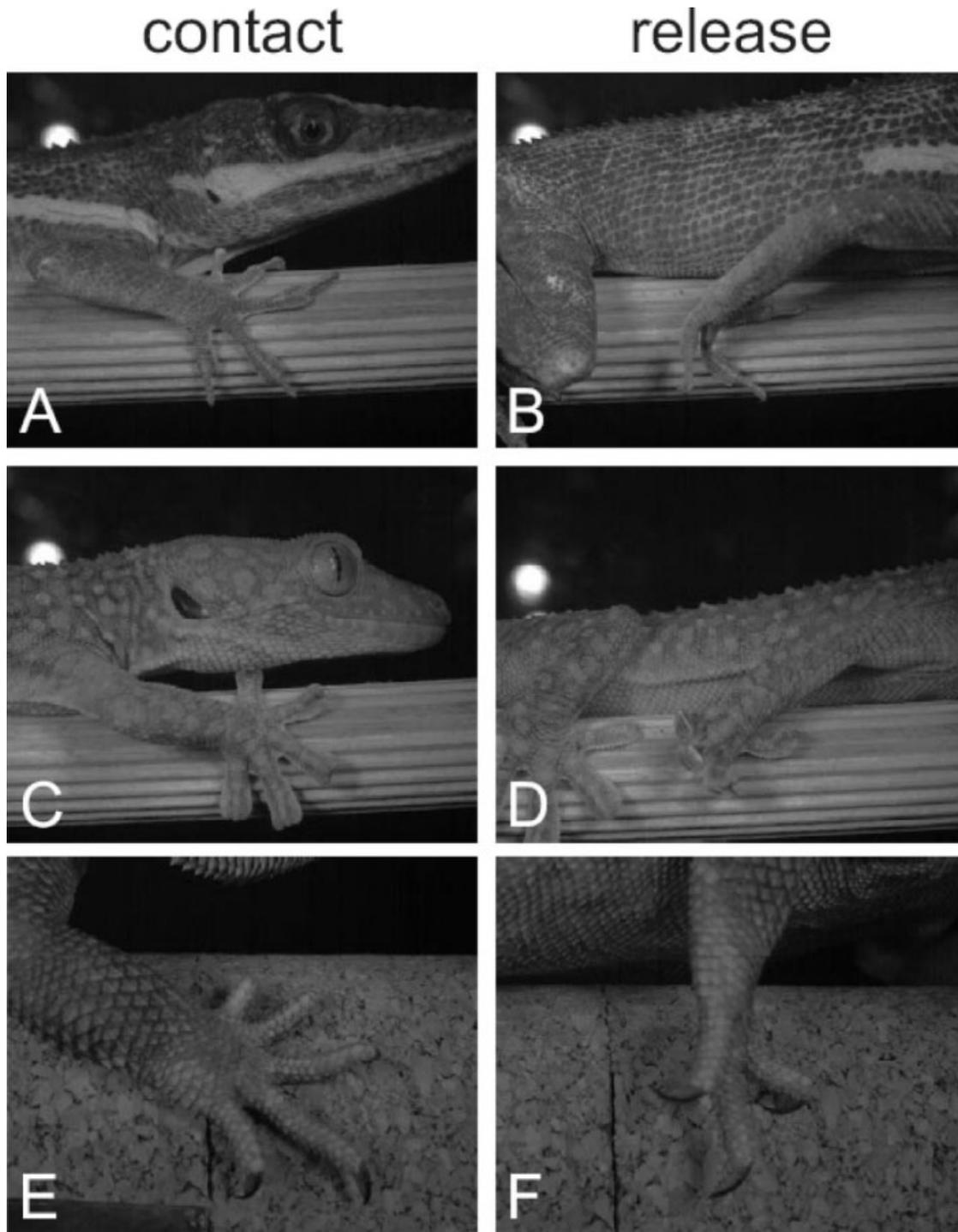


Fig. 5. Selected images from high-speed video recordings (250 fps) of *Anolis equestris* (A, B) *Gekko gecko* (C, D) and *Pogona vitticeps* (E, F) at initial substrate contact and the frame before the release of the hand from the substrate when running on a narrow (A. *equestris* and

*G. gecko*) or broad (*P. vitticeps*) dowel. Note how all species contact the substrate with the palmar surface of the hand after which the fingers are flexed around the support in *A. equestris* and *G. gecko*. The hand remains rigid, however in *P. vitticeps*.

moving on a broad dowel compared to a flat substrate (Table 2). Both species thus appear to switch to slower, more deliberate locomotion on narrower substrates.

An analysis of the elbow angle during locomotion showed significant substrate ( $F_{1,133} = 4.35$ ;  $P < 0.039$ )

and substrate by species interaction effects ( $F_{1,133} = 6.11$ ;  $P = 0.003$ ) indicating that the elbow angle changes in relation to the substrate differently for different species. Whereas the elbow angle did not change on the two substrates for *A. equestris* and *Pogona vitticeps*, it

**TABLE 2. Summary of step-time parameters recorded for the different species examined while running on different substrates**

Species	Substrate	Stance time (s)	Swing time (s)
<i>Anolis equestris</i>	Broad dowel	0.61 ± 0.34	0.24 ± 0.14
	Narrow dowel	0.60 ± 0.25	0.21 ± 0.08
<i>Gekko gekko</i>	Broad dowel	0.43 ± 0.24	0.11 ± 0.04
	Narrow dowel	0.77 ± 0.29	0.15 ± 0.07
<i>Pogona vitticeps</i>	Flat	0.49 ± 0.13	0.14 ± 0.04
	Broad dowel	0.57 ± 0.33	0.20 ± 0.08

Table entries are means ± standard deviations based on 10 trials for two individuals on each substrate.

**TABLE 3. Summary table illustrating differences in limb segment angles during substrate contact and release on two different substrates for each species**

Species	Substrate	Phase (N)	N	Elbow		Wrist		Hand	
				Mean	SD	Mean	SD	Mean	SD
<i>Anolis equestris</i>	Broad dowel	Contact	17	61.83	36.30	158.59	27.78	167.83	27.21
		Release	14	59.35	19.60	143.76	36.37	171.42	46.23
	Narrow dowel	Contact	18	62.13	31.12	167.77	20.85	162.93	22.91
		Release	12	75.86	25.99	133.21	26.03	134.87	21.80
<i>Gekko gekko</i>	Broad dowel	Contact	17	70.86	41.04	168.62	33.16	144.25	36.04
		Release	10	67.82	13.59	140.53	51.90	166.30	27.24
	Narrow dowel	Contact	9	100.66	47.01	177.26	55.72	150.93	54.09
		Release	4	105.82	42.16	124.96	56.94	166.52	18.03
<i>Pogona vitticeps</i>	Broad dowel	Contact	10	62.36	14.67	154.06	17.51	181.27	14.22
		Release	5	63.03	26.20	137.61	12.69	177.41	20.55
	Flat surface	Contact	14	67.43	40.68	136.97	23.21	168.54	14.31
		Release	13	64.03	24.07	128.14	27.10	157.47	19.77

increased significantly for *Gekko gekko*, with the elbow being more extended on the narrower substrate (Table 3). Differences in wrist angle between species, substrates and interaction effects were all non significant (all  $P > 0.05$ ). The wrist angle only showed significant differences between contact phases ( $F_{1,135} = 14.51$ ;  $P < 0.01$ ) with the angle being smaller at toe-off than during contact for all species (Table 3). The hand angle, showed significant species by contact phase ( $F_{2,133} = 3.11$ ;  $P = 0.048$ ) interaction effects indicating that the effect of contact phase on hand angle is different for the different species. Whereas the hand angle was variable in *A. equestris*, it increased at toe-off in *G. gekko* but decreased in *P. vitticeps* (Table 3).

### Stimulation Experiment

Stimulation of the m. flexor digitorum longus in *P. vitticeps* with the lower arm immobilized resulted in a distinct flexion at the wrist which, however, never exceeded 70 degrees in either of the two individuals tested. Stimulation of the same muscle with the lower arm free resulted in a flexion at the elbow of about 90 degrees combined with a flexion at the wrist. Flexion of the digits or the palm of the hand was never observed upon stimulation of the m. flexor digitorum longus in *P. vitticeps*. Stimulation of the same muscle in *P. vitticeps* after surgical removal of the sesamoid bone resulted in a buckling of the flexor plate, adduction of digits 1 and 5, and a decreased amount of flexion at the wrist. In *G. gekko*, stimulation of the m. flexor digitorum longus with the lower arm immobilized resulted in a strong flexion of the wrist of up to 120–140 degrees. Distinct flexion of the digits at the metacarpo-phalangeal joints, and a

strong adduction of all fingers in the plane of the hand were also observed. Stimulation with the lower arm freed resulted in a combined elbow and wrist flexion. In *A. equestris*, stimulation of the m. flexor digitorum longus with the lower arm immobilized resulted in flexion at the wrist of up to 120 degrees and flexion at the metacarpo-phalangeal and basal phalangeal joints. Stimulation of the same muscle with the lower arm free did not result in flexion at the elbow, in contrast to what was observed for the other two species.

Stimulation of the m. flexor carpi radialis with the lower arm immobilized resulted in a flexion at the wrist in all three species. In *G. gekko* and *A. equestris*, stimulation of the m. flexor carpi radialis also resulted in a flexion of digits 1–3 and a slight supination. Freeing the lower arm upon stimulation resulted in pronounced flexion at the elbow in all species. Stimulation of the m. flexor carpi ulnaris was performed in *G. gekko* only and resulted in minimal flexion at the wrist when the lower arm was immobilized. Freeing of the lower arm resulted in flexion at the elbow and a slight pronation. A combined stimulation of the m. flexor carpi radialis and the m. flexor carpi ulnaris with the elbow flexed resulted in a pronounced flexion of over 120 degrees at the wrist in *G. gekko*.

Stimulation of the m. flexor digiti superficialis of digit 3 resulted in flexion at the metacarpo-phalangeal joint and the basal inter-phalangeal joint of that digit in both *G. gekko* and *A. equestris*. In *P. vitticeps*, a marginal flexion of the digit of no more than 5 degrees was observed.

### Grasping Forces

An analysis of *in vivo* grasp forces with flexor digitorum muscle mass as covariate indicated a tendency for grasping

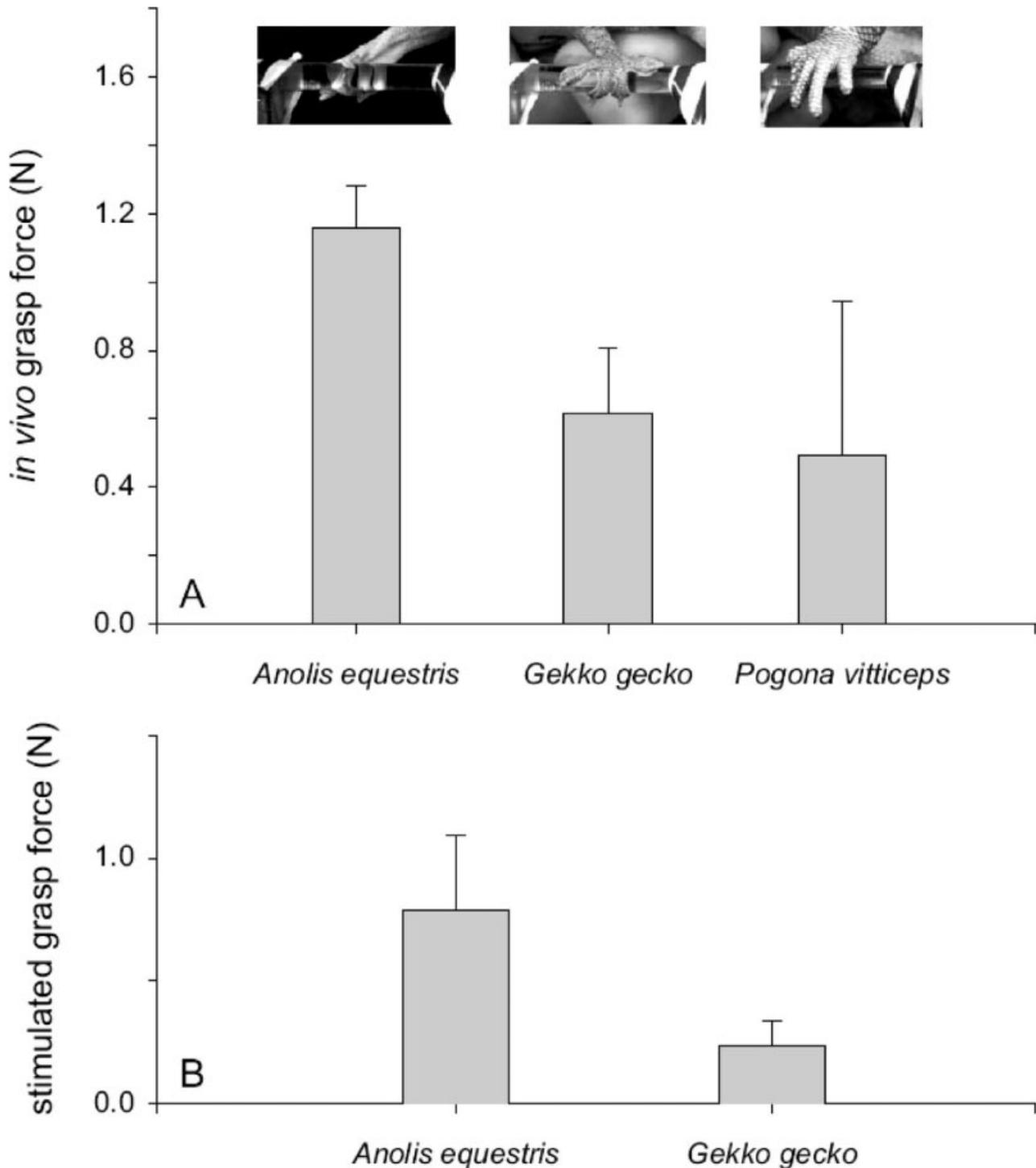


Fig. 6. Bar graphs illustrating differences in grasping forces measured *in vivo* (A) or based on stimulation of the forearm flexor muscles. The pictures illustrate the position of the hand around the glass rod mounted on the force plate. Note how *P. vitticeps* does not flex the palm of its hand nor its fingers around the rod in contrast to the other

force to be significant between species ( $F_{2,4} = 10.84$ ;  $P = 0.075$ ) with *P. vitticeps* having the lowest grasp forces on average (Fig. 6A). However, when excluding *Pogona vitticeps* from the analysis, differences between the other two species

two species. (B). Note that *in vivo* grasp forces measured for *P. vitticeps* are the result of the animal hooking its claws on the glass rod, rather than the animal producing grasping force. Stimulation of the flexor muscles in *P. vitticeps* demonstrated that this animal cannot produce any medially directed force by closing its hand.

are nonsignificant ( $F_{1,2} = 0.23$ ;  $P = 0.68$ ) (Fig. 6B). Thus, although grasp force means were higher in *Anolis equestris* compared to *Gekko gecko* ( $1.16 \pm 0.12$  vs.  $0.62 \pm 0.19$  N), this is largely due to a greater flexor muscle mass in *A. equestris*.

The results of our stimulation analysis, however, unambiguously showed that *P. vitticeps* was unable to generate any medially directed grasping force on the transducer upon stimulation of the m. flexor digitorum longus. Grasping forces in *Anolis equestris* ( $0.35 \pm 0.03$  N) and *Gekko gecko* ( $0.23 \pm 0.10$  N) measured during the stimulation experiment were markedly lower than during the *in vivo* experiment and again forces were higher on average in *A. equestris* compared to *G. gecko*.

## DISCUSSION

Our morphological data suggest that at least three, and potentially more, patterns in the tendinous structures associated with the m. flexor digitorum longus exist among lizards. Whereas the L-pattern associated with the presence of a thick flexor plate with embedded sesamoid is common (Moro and Abdala, 2004; Abdala and Moro, 2006; this work), according to our dissections both the P- and G- pattern seem to have a more restricted distribution among lizard taxa. Whether these derived patterns have originated in a single clade only, or are intimately related to the functional demands of specific ecological contexts, remains currently unclear. Further broad comparative analyses of the morphology of the distal forelimb and manus are needed to address this. Although we examined the morphology of a range of lizard species belonging to different families, we do not claim that no other patterns may exist in lizards.

Our data do, however, suggest clear functional consequences of the observed differences in morphology. For example, our stimulation experiments demonstrate that *Pogona vitticeps*, displaying the typical L-pattern, has a greatly limited flexibility of the hand, and decreased flexion capacity at the wrist and digits. Consequently, these lizards cannot grasp (*sensu* Napier, 1956) or even move effectively on narrow substrates. The role of the m. flexor digitorum longus remains somewhat unclear in *P. vitticeps*, but preliminary electromyographic data suggest that the m. flexor digitorum longus is active only during the swing phase in this species, and thus its main function may be to flex the wrist during the swing phase to prevent an interaction of the toes with the substrate. Our data also indicate that the manus in *P. vitticeps* moves as a single functional unit. The presence of a sesamoid bone in the flexor plate may prevent buckling of this tendon, and thus prevent adduction of the fingers when the wrist is flexed under the weight of the animal during stance. Additionally, our stimulation experiments suggest that the presence of the sesamoid may help ensure a greater movement transmission. Although the hind limb is typically dominant in lizard locomotion (Snyder, 1954; Reilly and Delancy, 1997a,b; Irschick and Jayne, 1999; Spezzano and Jayne, 2004), the rigid unit of the manus in these animals may be beneficial during terrestrial over-ground locomotion as it allows the animal to effectively use its entire hand as a pivot (rather than rolling off over the digits only; see Figs. 3 and 4), thus increasing its effective limb length and minimizing friction of the body with the substrate. The rigid manus may also be beneficial during climbing of broad, rough substrates such as tree trunks. The rigid manus combined with the presence of claws (Zani, 2000) may then provide an effective anchor aligned with the vertical substrate that can be used to actively pull the body upward

against gravity with minimal displacement of the center of mass of the animal away from the substrate.

The tendinous pattern of the hand observed in geckos is distinctly different from that observed in *P. vitticeps* and that observed in *A. equestris* and other polychrotids (Moro and Abdala, 2004). The geckos examined in this study possess no sesamoid and have a markedly reduced flexor plate. Compared to species displaying the L-pattern as observed in *Pogona*, geckos appear to have increased flexibility of the manus and digits. Our experiments show that the effect of the activation of the m. flexor digitorum longus on wrist and digit flexion is much greater in *G. gecko* than in *P. vitticeps*, although digital flexion during stimulation never included flexion of the terminal-most phalanges in geckos. Correlated with the increased flexibility of their manus, *G. gecko* was able to hold on to and effectively move across substrates narrower than the diameter of its body (see Figs. 3–5). However, our kinematic data show that *G. gecko* slows down by one third when moving across these narrow substrates, suggesting that it is experiencing difficulty. Indeed, in about 36% of the trials the individuals lost their balance and stumbled or had to stop to regain their balance. To improve their grip, both individuals of *G. gecko* were observed to pull on the hands after gripping the substrate, which may ensure improved attachment of the toe pads to the substrate (Autumn and Peattie, 2002). The absence of a sesamoid in the tendinous sheet of *G. gecko* not only allows for an increased mobility of the manus, but is likely also crucial for animals needing to maintain close substrate contact to invoke the adhesive capacity of toe-pads (Autumn et al., 2000, 2002; Autumn and Peattie, 2002). Having a rigid tendinous plate would likely also interfere with the digital hyperextension needed to release the toe pads from the substrate (Russell, 1975). The advantage of maintaining a unique tendinous plate (in contrast to those *Anolis* lizards showing the P-pattern with a completely divided aponeurosis) is currently unknown and needs to be investigated further.

The tendinous pattern observed in *Anolis equestris* forefeet was the most highly specialized, showing a complete division of the flexor plate and the presence of individual muscle-tendon complexes controlling the fingers. Despite the high degree of complexity and individuality, our stimulation experiments of the m. flexor digitorum longus and measurements of grasp forces suggested only a marginally improved flexion capacity of the digits in *A. equestris*. The major difference was that the action of the different bundles resulted in a somewhat more individualized action on the different digits. As observed in *G. gecko*, our preliminary electromyographic data suggest that the m. flexor digitorum longus is active during substrate contact, indicating that it could indeed be contributing to generating a grasping force. Interestingly, and in contrast to the other two species, *A. equestris* did not modulate its forelimb kinematics when moving from a broad to a narrow substrate, but rather maintained very similar angular excursions and contact times. Although *A. equestris* is not a fast runner (Vanhooydonck et al., 2006a), it moves effectively on relatively narrow branches. In this respect, it thus appears to be more like a twig anole in having a relatively low sprint capacity but secure mode of locomotion (Losos and Sinervo, 1989; Losos and Irschick, 1996; Vanhooydonck

et al., 2006b). Indeed, our data show that this species stumbled only in 20% of the trials on the narrowest substrate.

Among the lizard species we examined, the absence of a sesamoid and increased individuality of the flexor tendons appear to convey an increased capacity for manual flexion. The species having this improved flexion capacity can move effectively on narrow substrates by using a combined grasping and pull on the substrate. These observations provide an interesting parallel to studies of primate grasping, in which the ecological advantages of being able to move on a narrow substrate have been evoked. Interestingly, the lizards most dedicated to locomotion on very narrow substrates (Chameleons; see Peterson, 1984; Higham and Jayne, 2004a,b) possess uniquely modified hands and feet, which allow them to grasp very narrow branches (Gasc, 1964; Peterson, 1984). Associated with this highly specialized morphology is a dramatically superior grasping performance. Indeed, preliminary data for one species (*Bradypodion pumilum*) show forces in the order of 2 N (Tolley and Measey, 2007), substantially higher than those measured for the lizards included in this study, despite the larger body size of the species examined here. Future studies studying the functional consequences of the uniquely derived morphology of the manus in chameleons could shed further light on the evolution of the grasping hand in these lizards.

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## APPENDIX

Acronyms: AH, personal collection of Anthony Herrel; FML, herpetological collection of Fundación Miguel Lillo, Argentina; MACN, Museo Argentino de Ciencias Naturales; MZUSP, Museu de Zoologia Universidad San Pablo, Brasil; NMW, Naturhistorisches Museum, Wien, Austria; SDSU, San Diego State University, USA.

**Anguidae:** *Elgaria kingii*: N = 1 AH; **Chamaleonidae:** *Furcifer oustaleti*: N = 1 AH; **Gekkonidae:** *Hemidactylus mabouia*: N = 1 FML 02142; *Hemidactylus garnoti*: N = 1 AH; *Homonota underwoodi*: N = 1 FML 1310; *Gekko vittatus*: N = 1 AH; *Phelsuma madagascariensis*: N = 1 AH; *Tarentola mauritanica*: N = 1 AH; **Gymnophthalmidae:** *Cercosaura schreibersii*: N = 1 FML without data; *Vanzosaura rubricauda* (= *Gymnophthalmus multiscutatus*): N = 3 FML 08786-08787-08788; **Helodermatidae:** *Heloderma suspectum*: N = 1 AH; **Leiosauridae:** *Pristidactylus achalensis*: N = 2 FML 6181-6182; *Pristidactylus scapulatus*: N = 1 MACN 35379; *L. belli*: N = 1 NMW 12976, *Leiosaurus paronae*: N = 1 MACN 4386; **Liolaemidae:** *Phymaturus*

*punae*: N = 1 FML 02942; *Phymaturus palluma*: N = 1 FML 00630; *L. cuyanus*: N = 7 FML 02021; N = 1 FML 02971; N = 1 FML 02986; *L. robermertensis*: N = 1 FML 01488, *L. wiegmanni*: N = 2 FML 01856; *L. scapularis*: N = 3 FML 02865; **Opluridae:** *Oplurus sp.*: N = 1 AH; **Polychrotidae:** *Polychrus acutirostris*: N = 2 MZUSP 48151-48156, N = 2 MZUSP 08605-08611; N = 4 MZUSP 08605-08606-08610-08611; *Anolis lineatopus*: N = 1 SDSU 2157; *Anolis cristatellus*: N = 1 SDSU 2145; *Anolis coelestinus*: N = 1 SDSU 2148; *Anolis allogus*: N = 1 SDSU 2136; **Scincidae** *Mabuya frenata*: N = 1 FML 00277, N = 1 FML 01713; *Corucia zebrata*: N = 1 AH; **Teiidae:** *Cnemidophorus ocellifer*: N = 2 FML 03389; *Cnemidophorus longicaudus*: N = 2 FML 00078; *Teius oculatus*: N = 1 FML 03625; *Teius teyou*: N = 2 FML 00290; *Tupinambis rufescens*: N = 1 FML 07429, N = 1 FML 07431; *Ameiva ameiva*: N = 2 FML 03637; **Tropiduridae:** *T. plica*: N = 1 SDSU 2102, *T. etheridgei*: N = 2 FML 03562; *T. oreadicus*: N = 1 FML 08771; *Tropidurus hygomi*: N = 3 FML 08796-08797-08800; **Varanidae:** *Varanus niloticus*: N = 1 AH; **Xantusiidae:** *Xantusia vigilis*: N = 1 AH.