

# ANATOMICAL BASIS OF DIFFERENCES IN LOCOMOTOR BEHAVIOR IN *ANOLIS* LIZARDS: A COMPARISON BETWEEN TWO ECOMORPHS

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**ABSTRACT.** *Anolis* lizards have become model organisms for the study of adaptive radiation, as on each of the larger islands in the Caribbean, animals with similar morphologies have independently radiated into similar ecological niches. Central in the study of these animals have been the investigations correlating differences in limb dimensions to substrate characteristics and locomotor performance. However, little is known about differences in the musculoskeletal system that could underlie the observed differences in performance or locomotor style (i.e., gait characteristics). Here, we provide data on the morphology of the appendicular skeleton and musculature in two species of *Anolis* that differ greatly in habitat use and locomotor performance: *A. sagrei* and *A. valencienni*. The first and principal objective was to provide a detailed description of the appendicular morphology that could serve as a basis for further study. Our second objective was to test for quantitative differences in muscle mass and muscle mass distribution between the two species. Finally, we explore how the observed differences in the musculoskeletal system might be correlated with locomotor performance and locomotor style by analyzing data on the spatiotemporal gait characteristics in these two species while they were moving on substrates of different diameters. Our data show distinct differences in the morphology, muscle mass, and muscle mass distribution and illustrate how these may result in greater step and stride lengths in *A. sagrei*, allowing it to achieve higher sprint speeds. *Anolis valencienni* has less robust muscles that might constrain step and stride length, which in turn could provide it with greater stability on narrow substrates.

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## INTRODUCTION

*Anolis* lizards have become model organisms for the study of adaptive radiation, in that on each of the larger islands in the Caribbean, species with similar morphologies have independently adapted to similar ecological niches (Losos, 1990a,b; Losos et al., 1998; Schluter, 2000; Williams, 1983). Central to the study of these animals have been the investigations correlating differences in limb dimensions to substrate characteristics and locomotor performance (Irschick and Losos, 1998, 1999; Losos and Irschick, 1996; Losos and Sinervo, 1989; Losos et al., 1997; Vanhooydonck et al., 2006a,b). These and other studies have demonstrated how the interaction of limb morphology with substrate characteristics is crucial in setting limits on locomotor performance (Irschick and Losos, 1998; Losos and Sinervo, 1989; Vanhooydonck et al., 2005). For example, lizards with long limbs can achieve higher velocities on broad substrates (Irschick and Losos, 1998; Losos and Sinervo, 1989; Sinervo and Losos, 1991) and have greater acceleration capacities on both broad and narrow substrates (Vanhooydonck et al., 2006b) but could face a decrease in stability on narrow substrates, causing them to stumble and fall more often (Losos and Sinervo, 1989). Moreover, the trade-off between sprint speed and surefootedness has been suggested to be an important component of habitat choice in arboreal lizards (Irschick and Losos, 1999).

Despite the importance of limb mor-

phology in shaping locomotor performance and habitat use, little is known about differences in the musculoskeletal system that are responsible for the observed differences in performance and locomotor style among species and ecomorphs (but see Vanhooydonck et al., 2006a). Yet differences in muscle mass, muscle architecture, and muscle position could be crucially important in allowing animals to achieve greater performance in specific ecological settings. For example, Zaaf and co-workers (1999, 2001) demonstrated how differences in the mass and position of the fore and hindlimb muscles might provide a performance advantage to climbing geckos moving on vertical substrates. Consequently, one would expect that *Anolis* lizards that spend more time in arboreal habitats would also show specializations in the forelimb muscles, allowing them to generate greater forces to move against gravity, as has been demonstrated for geckos (Autumn et al., 2006). Specifically, we predict that arboreal species will allocate more of the total forelimb muscle mass to humerus retractors, which are thought to be important in generating pulling forces with the forelimbs (Zaaf et al., 1999). Conversely, fast terrestrial or semi-arboreal species can be expected to have more robust hindlimb extensors that allow them to achieve greater velocities and accelerations (see also Vanhooydonck et al., 2006a). Given the trade-off previously noted between sprint speed and surefootedness (Losos and Sinervo, 1989), we predict that animals adapted to moving on narrow substrates will have shorter step and stride lengths and will move their limbs at lower frequency, which would allow them to maintain stability on narrow substrates (Spezzano and Jayne, 2004).

Here, we explore differences in the morphology of the appendicular system in two species of *Anolis* lizards, *A. sagrei* and *A. valencienni*, that differ markedly in overall body and limb shape (Losos, 1990a,b; Fig. 1), maximal locomotor speed (Losos, 1990b), acceleration capacity (Van-

hooydonck et al., 2006b), and habitat use (Losos, 1990b) but are relatively closely related to each other (both belong to the Norops clade of *Anolis*; see Nicholson et al., 2005). Whereas *A. sagrei* is a typical trunk-ground anole that often occurs on the ground and on broad substrates, *A. valencienni* is a twig anole that spends most of its time moving on narrow substrates. The first and principal goal of this paper is to give a complete and detailed description of the anatomy of the fore- and hindlimb muscles. Our second objective is to test for quantitative differences in muscle mass and muscle mass distribution between species. Our final objective is to explore whether the observed differences in the morphology of the appendicular skeleton can be linked to differences in locomotor style by analyzing the spatiotemporal gait characteristics of both species moving on two substrates of different diameters.

## MATERIALS AND METHODS

### Animals

Between November 2001 and February 2002, we captured 15 male *A. sagrei* Cocteau (snout-vent length [SVL] =  $59.22 \pm 0.36$  mm; mean  $\pm 77$  SD) and 10 male *A. valencienni* Dumeril and Bibron (SVL =  $67.9 \pm 1.4$  mm) by hand or noose. The *A. sagrei* individuals were captured on the mainland United States (Miami, Florida). *Anolis valencienni* individuals were caught around the Discovery Bay Marine Laboratory in Jamaica. All the animals were transported back to the laboratory at Tulane University (New Orleans, Louisiana). Upon arrival in the lab, the lizards were housed in pairs in 40-liter terraria lined with leaf litter and containing a dowel. Terraria were placed in a temperature-controlled room ( $29 \pm 2^\circ$  C) with a 12:12 hour light:dark photoperiod. We fed the animals live crickets dusted with calcium and vitamin supplements three times a week; lizards were sprayed with water daily.

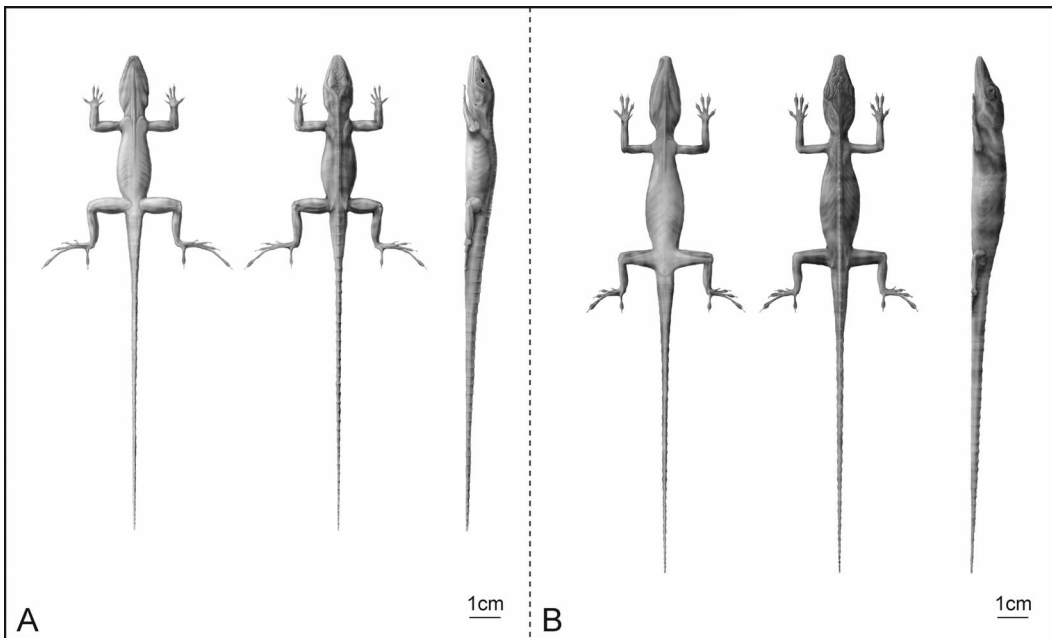


Figure 1. Drawing of (A) *Anolis sagrei* and (B) *Anolis valencienni* in ventral, dorsal, and lateral view illustrating differences in overall body and limb proportions. Note how *A. sagrei* has relatively longer distal hindlimb segments and a longer tail but shorter body and head compared with *A. valencienni*. Differences in distal hindlimb segments (tibia, metatarsus, longest toe) and the length of the longest toe of the forelimb are significantly different between species. Scale bar: 1 cm.

## Morphology

A different set of preserved specimens of both *A. sagrei* ( $N = 6$ ;  $SVL = 55.79 \pm 1.88$  mm) and *A. valencienni* ( $N = 6$ ;  $SVL = 66.26 \pm 2.52$  mm) were dissected, and all muscles were taken out and sorted by function into the following groups: femur protractors, femur retractors, femur adductors, femur abductors, knee flexors, knee extensors, ankle flexors, ankle extensors, a miscellaneous group (containing the lower hindlimb pronators and rotators), humerus protractors, humerus retractors, humerus adductors, humerus abductors, elbow flexors, elbow extensors, wrist flexors, wrist extensors, and a group containing the lower forelimb pronators and rotators. The assignment of muscles to functional groups is based on their position and on manipulation of dissected specimens. Note, however, that the assignment of muscles to functional groups

needs to be confirmed by in vivo studies of muscle function and that our assignment need not correspond to descriptions for other species because of variation in muscle attachment sites. Muscles were stored by group in vials with 70% ethanol, blotted dry, and weighed per functional group on a Mettler MT5 electronic balance ( $\pm 0.1$  mg). Note that, given the small size of these animals, muscle groups often weigh less than 10 mg and thus require the use of a precision balance.

## Running Trials

We induced lizards to run up a plastic dowel covered with metal wire mesh (mesh width 1 mm) by clapping our hands or tapping the lizards slightly on the base of their tail. All lizards were tested on both a broad and a narrow dowel (diameters of 8 and 1 cm, respectively). Both dowels were 2 m long and placed against the wall

at an angle of 45° (see Vanhooydonck et al., 2006a,b). Lizards were filmed in lateral view over a distance of 1 m with a high-speed video camera (Redlake Motionscope PCI camera) set at 250 frames/s. We performed between five and 10 trials per individual on each dowel. Trials were conducted on several nonconsecutive days, with trials on the broad and narrow dowel alternated among days. Before experimentation and between trials, the lizards were placed in an incubator set at 32° C for at least 1 hour to allow the lizards to attain body temperatures similar to their preferred field body temperatures (see also Toro et al., 2003).

After filming, we digitized the tip of the snout at 250 frames/s with the use of Peak Performance MOTUS software from the moment the lizard started running until it ran out of view. Of the same sequences, we obtained footfall patterns by recording the frames at which the right hindfoot touched the substrate (i.e., foot contact) and the frames at which the right hindfoot lost contact with the substrate (i.e., foot release). On the basis of displacement of the snout tip and the footfall patterns, we subsequently calculated stride length (the distance traveled by the center of mass of an animal in a complete cycle of limb movements), stride frequency (the number of cycles per second), step length (the distance the body moves forward during the stance of a particular leg), and mean speed per stride for successive strides during steady state locomotion.

### Statistical Analyses

Morphometric and muscle mass data were log transformed before analysis to conform to assumptions of homoscedascity and normality required for parametric analyses. Analyses of variance were used to test for differences between species in limb dimensions, in total hindlimb and front limb muscle mass, and in the mass of the different functional groups.

Because we were mainly interested in steady state locomotion, we only used

data on gait characteristics of the third, fourth, and fifth stride in a sequence (i.e., after the initial acceleration phase, and when locomotion was largely steady, as indicated by the absence of fluctuations in the velocity profile; see Vanhooydonck et al., 2006b). Before statistical analyses, stride length, step length, and stride frequency were expressed in units of hindlimb length, because hindlimb length differs significantly between *A. valencienni* and *A. sagrei* and because gait characteristics are determined on the basis of hindlimb footfall patterns. Total hindlimb length was determined on the basis of the sum of the individual limb segments. All gait characteristics were log transformed before analyses. A two-way multivariate analysis of covariance, with stride length, stride frequency, and step length as dependent variables; stride speed as covariate; and species and dowel as factors, was performed. Nonsignificant interaction effects were removed from the final model. All analyses were performed using SPSS V.13.0.

## RESULTS

### Anatomy

Here, we first provide a brief qualitative description of the differences in the pectoral and pelvic girdle of the two species. Next, we give a brief description of the ligaments of the pelvic girdle and a description of the fore- and hindlimb muscles. The descriptions are principally based on *A. sagrei* except where important differences between species were observed. We follow the terminology adopted by Zaaf et al. (1999), Moro and Abdala (2004), and Abdala and Moro (2006) in our descriptions of the muscles. In addition, we used papers by Landsmeer (1984, 1990) and Russell (1988) as a basis for our descriptions of the limb muscles.

*Pelvic and Pectoral Girdle* (Figs. 2, 3). Both the pelvic and pectoral girdle show differences in shape between the two species. The most striking difference is the

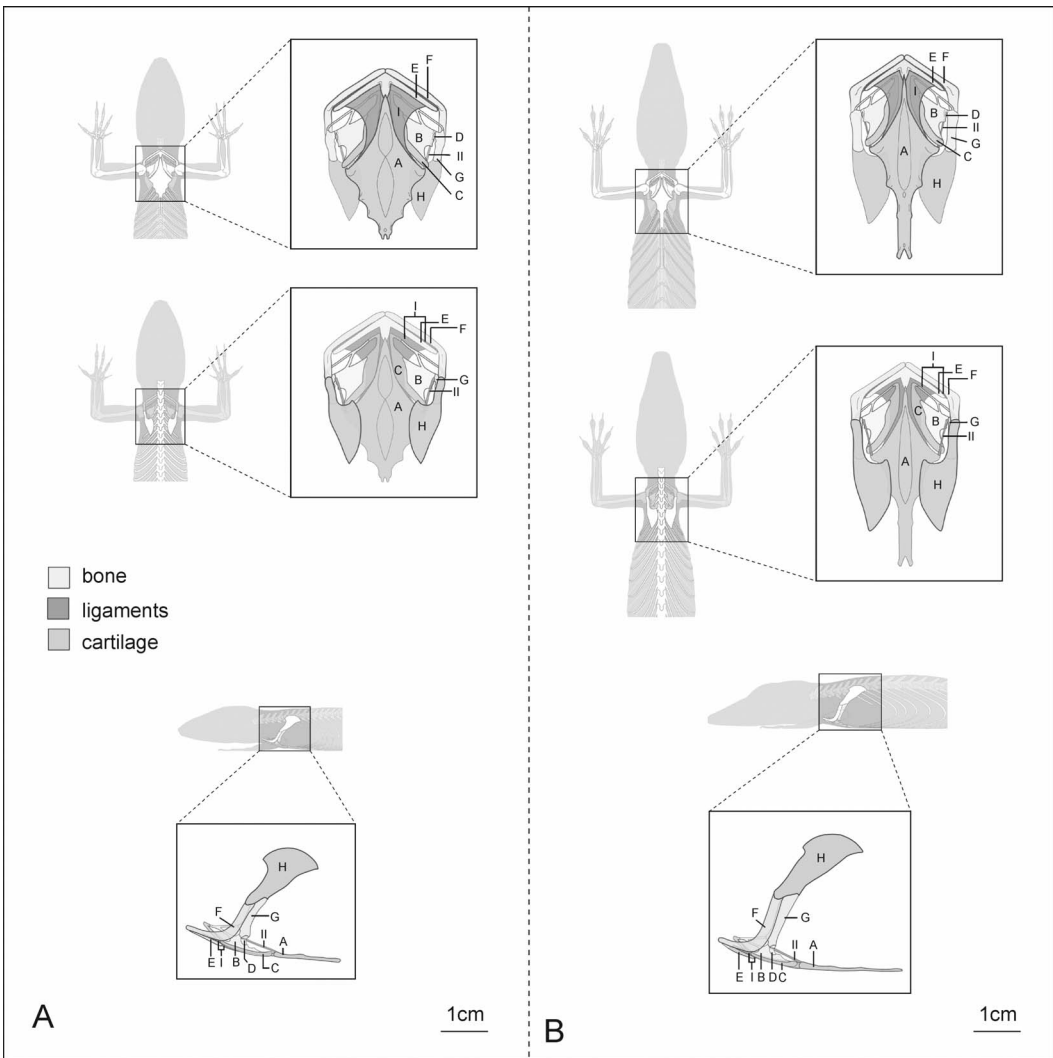


Figure 2. Schematic drawing illustrating the pectoral girdle in (A) *A. sagrei* and (B) *A. valencienni*. Shown are a ventral, a dorsal, and a lateral view (from top to bottom) for each species. The position of the girdle in the body, as well as a blow-up detailing the girdle itself, is shown for each view. Note the more elongated and narrower pectoral girdle with elongated sternum in *A. valencienni*. I, Ligamentum sternoclaviculare; II, Ligamentum sternocoracoideum; A, sternum; B, coracoid; C, epicoracoid; D, glenoid fossa; E, interclavicular; F, clavicular; G, scapular; H, suprascapular.

more elongated and narrower appearance of the girdles in *A. valencienni* compared with *A. sagrei* (see also Beuttell and Losos, 1999). The pectoral girdle in *A. valencienni* is further characterized by an elongated sternum, an expanded suprascapula and a more perpendicularly positioned scapula and clavicular. The pelvic girdle in *A. sagrei*

is generally broader and has an ilium that is directed more dorsally compared with that of *A. valencienni* (Fig. 3). The anterior part of the ischium is, however, more elongated in *A. valencienni*.

**Ligaments** (Figs. 2, 3). The following description of the ligaments applies to both species.

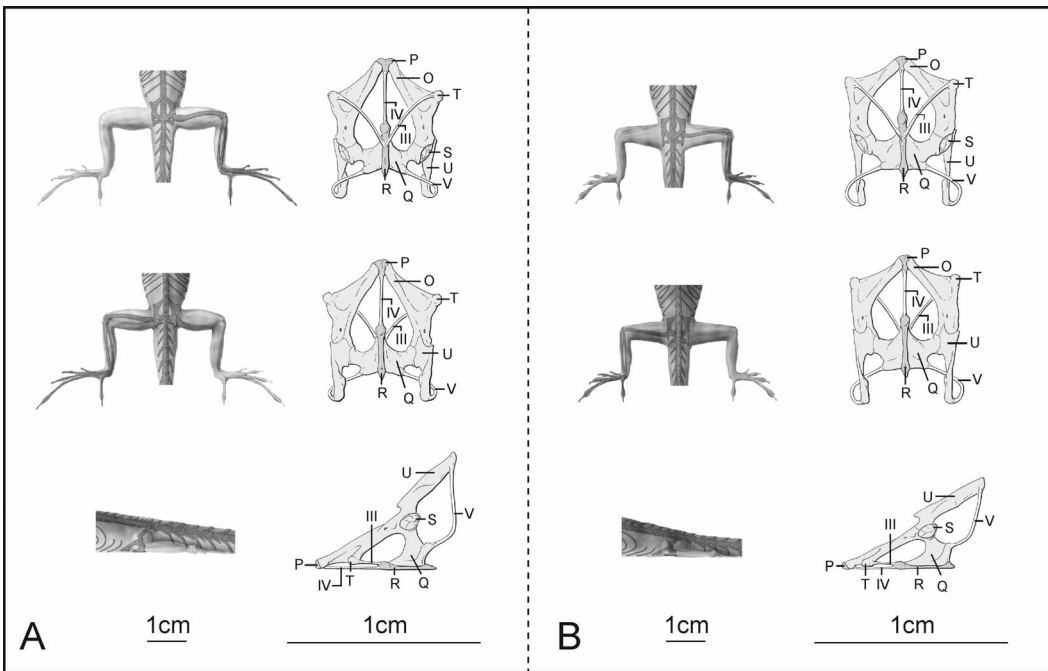


Figure 3. Schematic drawing illustrating the pelvic girdle in (A) *A. sagrei* and (B) *A. valencienni*. Shown are a ventral, a dorsal and, a lateral view (from top to bottom) for each species. The position of the girdle in the body, as well as a blow up detailing the girdle itself, is shown for each view. Note the more elongate and narrower pelvic girdle with relatively shorter ilium in *A. valencienni*. III, ligamentum puboischiadum pars lateralis; IV, ligamentum puboischiadum pars medialis; V, ligamentum ilioischiadum; O, pubis; P, epipubis; Q, ischium; R, hypoischium; S, acetabulum; T, pectineal tubercle; U, ilium.

Ligamentum sternoclaviculare (I): runs from the lateroventral aspect of the sternum to the interclaviculum and claviculum, where it attaches broadly along the posterior ventral aspect.

Ligamentum sternocoracoideum (II): runs from its origin on the dorsal side at the lateralmost aspect of the sternum to the lateral dorsal side of the coracoid near its articulation with the scapula.

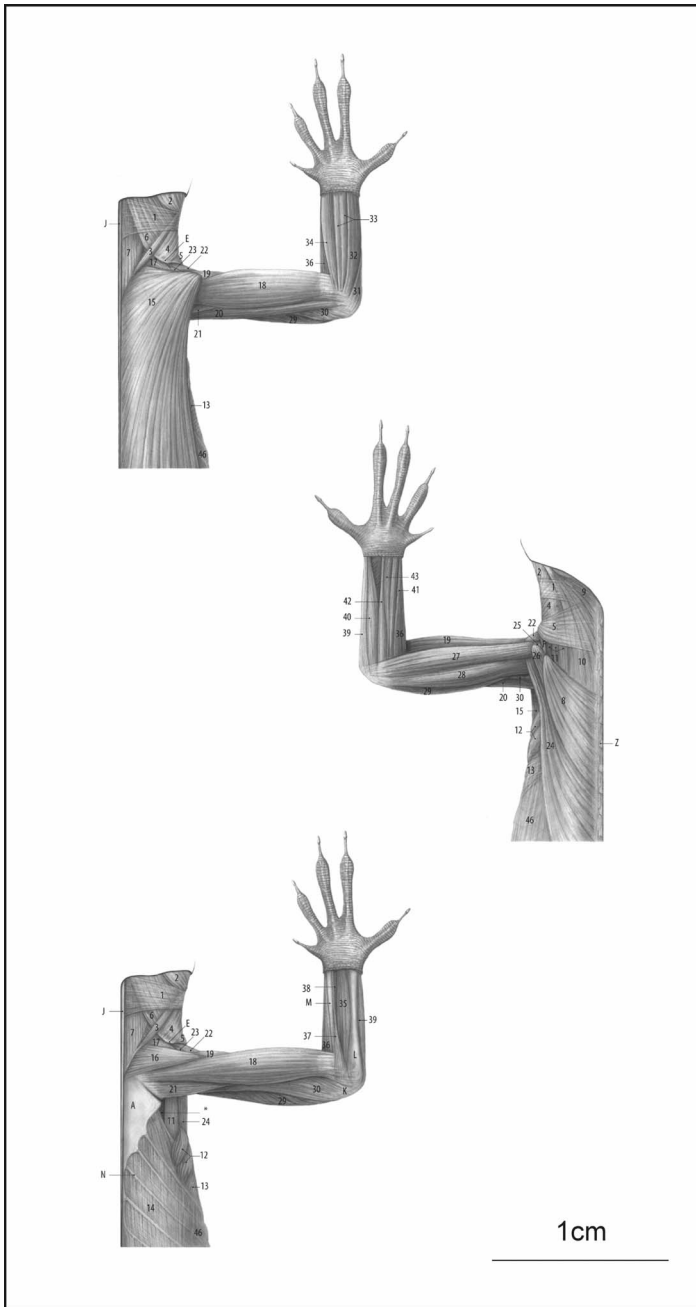
Ligamentum puboischiadum pars later-

alis (III): originates at the ventral aspect of the ischium and runs to the ventrolateral side of the lateralmost protuberance of the pubis (pectineal tubercle).

Ligamentum puboischiadum pars medialis (IV): originates at the cranial end of the pubis (epipubis), runs directly posterior, and inserts on the ventrocranial side of the ischium.

Ligamentum ilioischiadum (V): runs from the caudodorsal and lateral side of

Figure 4. Anatomical drawings illustrating the forelimb musculature in *A. sagrei*. Shown are a superficial ventral view, a superficial dorsal view, and a deep ventral view (from top to bottom). 1. M. constrictor colli. 2. M. pterygoideus. 3. M. episternocleidomastoideus pars anterior. 4. M. episternocleidomastoideus pars posterior. 5. M. levator scapulae. 6. M. omohyoideus. 7. M. sternohyoideus. 8. M. trapezius. 9. M. depressor mandibulae. 10. M. cervicomandibularis. 11. M. transversospinalis complex. 12. M. serratus. 13. Mm. levatores costae. 14. M. intercostalis. 15. M. pectoralis pars superficialis. 16. M. pectoralis pars profundus. 17. M. coracobrachialis. 18. M. biceps brachii pars ventralis. 19. M. biceps brachii pars dorsalis. 20. M. coracobrachialis longus. 21. M. coracobrachialis brevis. 22. M. clavodeltoideus pars superficialis. 23. M. clavodeltoideus pars profundus. 24. M. latissimus dorsi. 25. M. scapulodeltoideus pars anterior. 26. M. scapulodeltoideus pars posterior. 27. M. triceps pars humeralis anterior. 28. M. triceps pars humeralis posterior. 29. M. triceps pars scapulohumeralis. 30. M. triceps pars scapularis. 31. M.



epitrocheloanconus. 32. M. flexor carpi ulnaris. 33. M. flexor digitorum longus pars ulnaris. 34. M. flexor digitorum longus pars radialis. 35. M. flexor digitorum longus pars profundus. 36. M. flexor carpi radialis. 37. M. pronator teres. 38. M. pronatoraccessorius. 39. M. extensor carpi ulnaris. 40. M. abductor pollicis longus. 41. M. extensor carpi radialis. 42. M. extensor digitorum longus pars superficialis. 43. M. extensor digitorum longus pars profundus. 46. M. obliquus abdominis. A, sternum; E, interclav-icula; J, ceratobranchiale 2; K, humerus; L, ulna; M, radius; N, costa sternalis; Z, processus spinosus vertebra. \* Deeper struc-tures, not labeled.

the ischium to the posterolateral side of the ilium.

*Forelimb Musculature* (Figs. 4, 5). *Musculus pectoralis* (15, 16): consists of two distinct parts:

1) *M. pectoralis pars superficialis* (15): This is the largest part of the *M. pectoralis* and originates at the lateral edge of the sternum. In *A. valencienni*, the *M. pectoralis pars superficialis* originates at the anterior aspect of the last sternal rib, as well as the anterior aspects of the abdominal ribs. In both species, the muscle inserts by means of a short, robust tendon at the anterior proximal aspect of the humerus on the humeral tubercle. Proposed function: humeral retraction.

2) *M. pectoralis pars profundus* (16): The *pars profundus* is partly hidden under the *pars superficialis* in superficial view. The fibers originate at the ventromedial aspect of the sternum and the interclavicular. The fibers converge near their insertion and insert proximal to the humeral tubercle. Proposed function: humeral adduction.

*M. coracohumeralis anterior* (17): originates at the cranioventral surface of the coracoid and inserts at the medial side of the humeral tubercle. Proposed function: humeral protraction.

*M. biceps* (18, 19): consists of two parts. The first part (19) originates by means of a long narrow tendon on the medioventral aspect of the coracoid. The second part (18) originates fleshy along the entire cranioventral side of the humerus, anterior to the humeral tubercle. The fibers of both parts merge and insert partly fleshy and partly by means of a short aponeurosis at the proximal aspect of both the ulna and radius. Proposed function: elbow flexion.

*M. coracobrachialis longus* (20): originates by means of a short tendon at the posterior aspect of the coracoid and inserts along the ventral aspect of the humerus, near the elbow joint. Proposed function: humeral adduction.

*M. coracobrachialis brevis* (21): originates along the posterior half of the ventral

aspect of the coracoid and inserts ventrally along the proximal 30% of the humerus. In *A. valencienni* the *M. coracobrachialis* inserts along the proximal 60% of the humerus. Proposed function: humeral adduction. Note that this muscle functions to retract the humerus in *Varanus* (Jenkins and Goslow, 1983). In the *Anolis* species studied here, this muscle could also induce humeral retraction following a full protraction of the arm. This needs, however, to be corroborated by *in vivo* studies.

*M. clavodeltoideus superficialis* (22): originates at the ventral aspect of the interclavicular and the posteroventral aspect of the clavicular. The fibers run obliquely posterolaterad and insert on the cranial aspect of the humerus proximal to the deltopectoral tubercle. Proposed function: humeral protraction.

*M. clavodeltoideus profundus* (23): originates at the ventral side of the interclavicular, runs anteriorad, curves around the interclavicular, runs posteriorad in between the clavicular and scapular, and inserts proximally on the dorsocranial side of the humerus. Proposed function: humeral abduction.

*M. latissimus dorsi* (24): originates at the mid-dorsal cervical connective tissue raphe and the neural spines of the thoracic vertebrae. The fibers run anteroventrad and insert by means of a short and thick tendon along the proximal dorsocaudal aspect of the humerus. Proposed function: humeral retraction.

*M. scapulodeltoideus anterior* (25): originates at the junction of the scapular and suprascapular as well as on the medioventral side of the scapular. The fibers insert by means of a short but clear tendon at the dorsal side of the humerus, anterior to the insertion of the *M. scapulodeltoideus posterior*. Proposed function: humeral abduction.

*M. scapulodeltoideus posterior* (26): originates at the external side of the suprascapular and inserts proximally on the dorsal side of the humerus at the level of

the humeral tubercle. Proposed function: humeral abduction.

*M. triceps brachii* (27–30): consists of three bundles: The medial bundle originates by means of a thin tendon at the lateral side of the base of the scapula (pars scapularis, 30). The caudal bundle originates by means of a long, thin tendon from the scapulocoracoid ligament. Some fibers coming from the caudal side of the humerus join the bundle (pars scapulohumeralis, 29). The cranial bundle originates at the cranial aspect of the humerus (pars humeralis anterior, 27). A second slip originating at the caudal aspect of the humerus (pars humeralis posterior, 28) joins this bundle about midway. Both slips are separated from one another by the insertion of the *M. latissimus dorsi*. All parts merge near the elbow and insert onto a common thick tendon that curves around the elbow and inserts at the proximal side of the ulna. Proposed function: elbow extension.

*M. epitrocleoanconus* (31): originates by means of a short tendon on the ventral side of the distal aspect of the humerus and runs alongside the ulna to insert along the first quarter of the ventral side of the ulna. Proposed function: radio-ulnar rotation.

*M. flexor carpi ulnaris* (32): originates by means of a short tendon at the ventral side of the distalmost aspect of the humerus. The muscle consists of two parts: a lateral part that inserts onto the ulnare by means of a short tendon and a medial part that inserts along the distal aspect of the ulna. Proposed function: the lateral part, wrist flexor; the medial part, elbow flexor.

*M. flexor digitorum longus* (33–35): consists of three parts. The pars radialis (34) lies at the radial side, originates at the distal tubercle of the humerus, and runs between the radius and ulna. It inserts by means of a tendon which splits to insert on the distal phalanges of toes three and four. The *M. flexor digitorum longus pars ulnaris* (33) is composed of two bellies that both originate at the distal aspect of the

humerus by means of a short tendon. The two bellies unite about halfway down and converge into a thick tendon that ultimately splits and inserts on the distal phalanges of toes 2, 3, and 4. A small group of fibers coming from the ulna joins this muscle along its course. The *M. flexor digitorum longus pars profundus* (35) is the deepest of the three parts. It originates on the ventral side of the ulna and inserts by means of a clear tendon that trifurcates at the level of the hand. The first tendon inserts on the distal phalanx of toe 1, the second on the distal phalanx of toe 2, and the third on the distal phalanx of toe 3. Proposed function: wrist and digit flexion.

*M. flexor carpi radialis* (36): originates at the dorsolateral surface of the distal tubercle of the humerus. The muscle runs alongside the radius and inserts on the distal half thereof. Proposed function: elbow flexion.

*M. pronator teres* (37): originates by means of a short tendon at the ventral side of the distal aspect of the humerus and inserts fleshy on the proximal fourth of the radius. In *A. valencienni*, this muscle inserts on the distal fourth of the radius. Proposed function: radio-ulnar rotation.

*M. pronator accesorius* (38): originates along the proximal two thirds of the ulna and inserts on the middle third of the radius. Proposed function: radio-ulnar rotation.

*M. extensor carpi radialis* (39): originates by means of a short tendon at the distal aspect of the humerus. The muscle runs alongside the radius and inserts along its entire dorsal side. Proposed function: elbow extension.

*M. abductor longus pollicis* (40): originates broadly along the distal third of the ulna. The muscle narrows toward its insertion and inserts tendinously at the distal, dorsal aspect of the first metacarpal of digit 1. Proposed function: wrist extension.

*M. extensor carpi ulnaris* (41): originates at the distal head of the humerus by means of a short tendon. The muscle runs alongside the ulna and the fibers insert partly

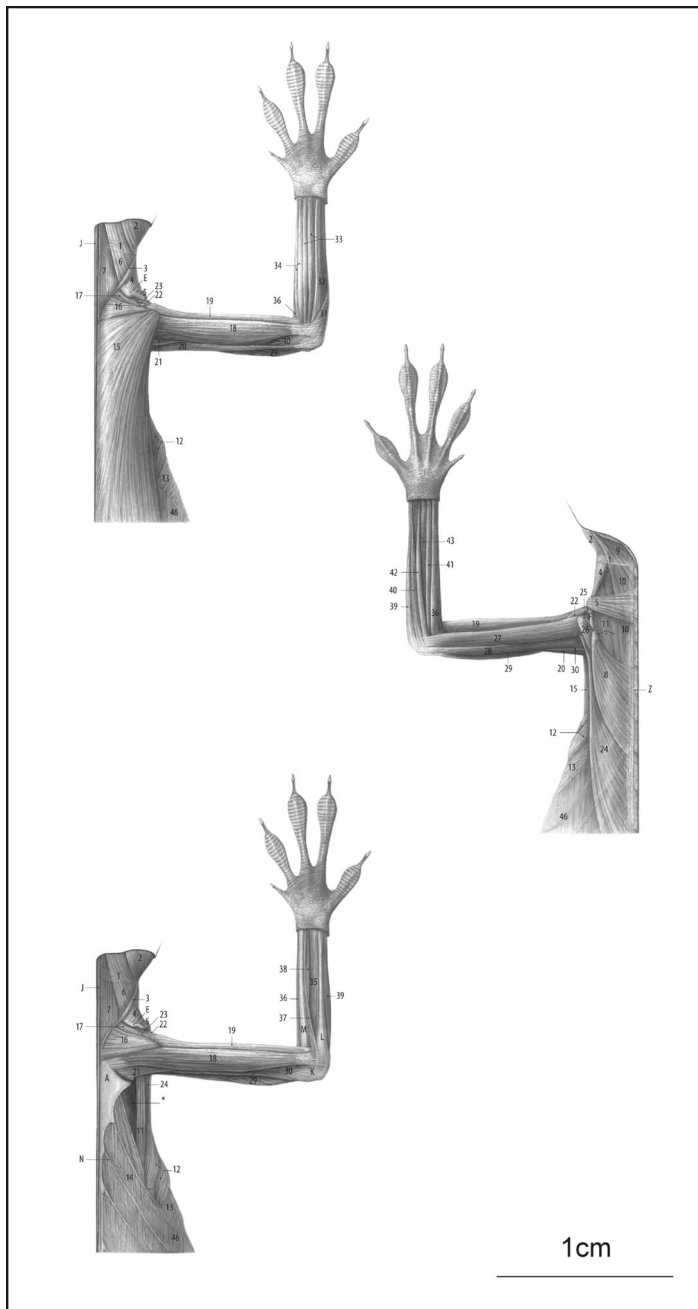


Figure 5. Anatomical drawings illustrating the forelimb musculature in *A. valencienni*. Shown are a superficial ventral view, a superficial dorsal view, and a deep ventral view (from top to bottom). Note the more robust musculature in *A. sagrei* depicted in Figure 4. 1. *M. constrictor colli*. 2. *M. pterygoideus*. 3. *M. episternocleidomastoideus* pars anterior. 4. *M. episternocleidomastoideus* pars posterior. 5. *M. levator scapula*. 6. *M. omohyoideus*. 7. *M. sternohyoideus*. 8. *M. trapezius*. 9. *M. depressor mandibulae*. 10. *M. cervicomandibularis*. 11. *M. transverso spinalis* complex. 12. *M. serratus*. 13. *Mm. levatores costae*. 14. *M. intercostalis*. 15. *M. pectoralis* pars superficialis. 16. *M. pectoralis* pars profundus. 17. *M. coracobrachialis*. 18. *M. biceps brachii* pars ventralis. 19. *M. biceps brachii* pars dorsalis. 20. *M. coracobrachialis* longus. 21. *M. coracobrachialis* brevis. 22. *M. cla-*

fleshy, partly through a joined tendon with the *M. flexor carpi ulnaris* at the distal part of the ulna. A tendon coming from this muscle also runs to the lateral aspect of the fifth metacarpal. Proposed function: elbow and wrist extension.

*M. extensor digitorum longus pars superficialis* (42): originates by means of a short tendon at the distal aspect of the humerus together with the *M. extensor carpi radialis*. Both muscles run adjacent to one another for the first third of their length. The *M. extensor digitorum longus pars superficialis* inserts at the dorsal aspect of the fifth metacarpal. Proposed function: wrist extension.

*M. extensor digitorum longus pars profundus* (43): runs alongside the *M. extensor carpi radialis* and inserts at the dorsal side of metacarpals 2 and 3. Proposed function: wrist extension.

*M. scapulohumeralis superficialis* (not drawn): originates at the cranial aspect of the ventral part of the suprascapula and the dorsal part of the scapula. The muscle inserts proximally on the caudal aspect of the humerus. Proposed function: humeral abduction.

*M. scapulohumeralis profundus* (not drawn): originates at the caudal aspect of the scapula and inserts at the proximal dorsal side of the humerus. Proposed function: humeral abduction.

*M. coracohumeralis posterior* (not drawn): originates at the ventral surface of the coracoid, posterior to the coracoidal fenestra, and inserts proximally at the ventral aspect of the humerus, caudal to the humeral tubercle. Proposed function: humeral adduction.

*M. supracoracoideus* (not drawn): orig-

inates at the anterior dorsal side of the coracoid and inserts at the proximodorsal aspect of the humerus. Proposed function: humeral retraction and shoulder stabilization (see also Jenkins and Goslow, 1983).

*Mm. extensores digitorum breves* (not drawn): is a set of short muscles that originate at the dorsal side of the ulnare and insert on metacarpals 2 to 4. The last one runs to the base of the first phalanx of the fifth toe. Proposed function: wrist extension.

*M. pronator profundus* (not drawn): originates on the distal two thirds of the ulna and inserts on the distal two thirds of the radius. Proposed function: radio-ulnar rotation.

#### *Hindlimb Musculature* (Figs. 6–9).

*M. puboischiotibialis* (50): is the superficialmost muscle in ventral view. It originates at the ventral side of the lateral puboischiodic ligament (the cranialmost fibers), the ventrolateral side of the ischium, and the ilioischiodic ligament. The fibers converge toward their insertion on the cranial, ventromedial side of the tibia. The insertion is partly fleshy, partly by a shared tendon with the *M. flexor tibialis internus*. Proposed function: knee flexion and femoral adduction.

*M. pubofibularis* (51): originates on the aponeurosis communis. The muscle crosses the *M. adductor femoris* and inserts together with the *M. ilioischiofibularis* by means of a short tendon at the cranial aspect of the fibula. Proposed function: femoral adduction.

*M. tensor aponeurosis communis* (52): is a short and small muscle that originates at the aponeurosis communis and inserts at the cranioventral side of the femoral

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vodeltoideus pars superficialis. 23. *M. clavodeltoideus pars profundus*. 24. *M. latissimus dorsi*. 25. *M. scapulodeltoideus pars anterior*. 26. *M. scapuladeltoideus pars posterior*. 27. *M. triceps pars humeralis anterior*. 28. *M. triceps pars humeralis posterior*. 29. *M. triceps pars scapulohumeralis*. 30. *M. triceps pars scapularis*. 31. *M. epitrocheloanconus*. 32. *M. flexor carpi ulnaris*. 33. *M. flexor digitorum longus pars ulnaris*. 34. *M. flexor digitorum longus pars radialis*. 35. *M. flexor digitorum longus pars profundus*. 36. *M. flexor carpi radialis*. 37. *M. pronator teres*. 38. *M. pronator accesorius*. 39. *M. extensor carpi ulnaris*. 40. *M. abductor pollicis longus*. 41. *M. extensor carpi radialis*. 42. *M. extensor digitorum longus pars superficialis*. 43. *M. extensor digitorum longus pars profundus*. 46. *M. obliquus abdominis*. A, sternum; E, interclavicula; J, ceratobranchiale 2; K, humerus; L, ulna; M, radius; N, costa sternalis; Z, processus spinosus vertebra. \* Deeper structures, not labeled.

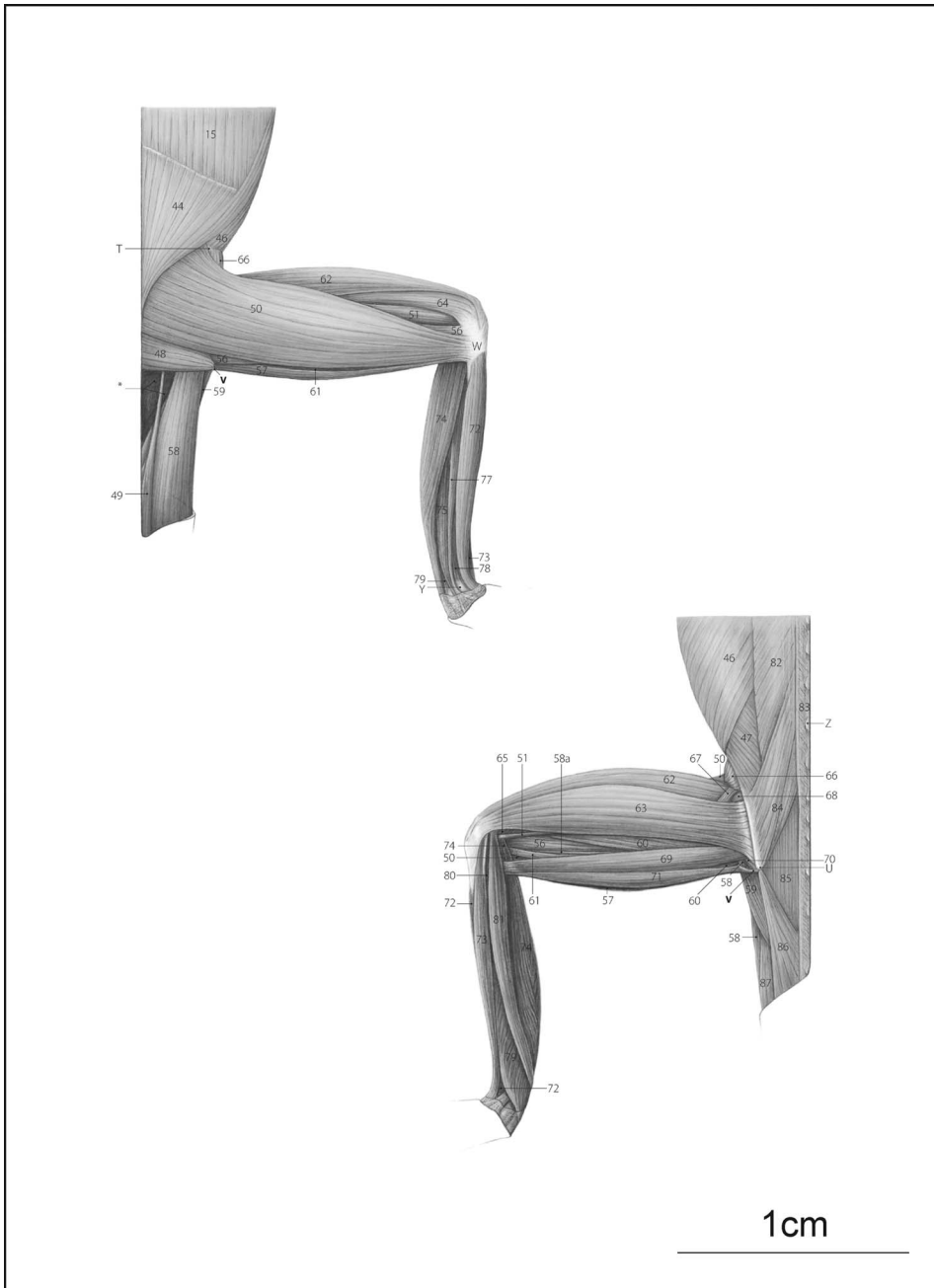


Figure 6. Anatomical drawings illustrating the superficial hindlimb musculature in *A. sagrei*. Shown are a ventral and dorsal view (top and bottom, respectively). 15. *M. pectoralis pars superficialis*. 44. *M. rectus abdominis pars superficialis*. 45. *M. rectus abdominis pars profundus*. 46. *M. obliquus abdominis*. 47. *M. transversus abdominis complex*. 48. *M. transversus perinei*. 49. *M. cocygeus inferior*. 50. *M. puboischiotibialis*. 51. *M. pubofibularis*. 56. *M. flexor tibialis externus*. 57. *M. flexor tibialis internus*. 58. *M. caudofemoralis longus*; 58a. *tendino m. caudofemoralis longus*. 59. *M. caudofemoralis brevis*. 60. *M. adductor femoris*. 61. *M. ilioischiofibularis*. 62. *M. ambiens pars ventralis*. 63. *M. ambiens pars dorsalis*. 64. *M. femorotibialis pars ventralis*. 65. *M. femorotibialis pars dorsalis*. 66. *M. pubofemoralis pars dorsalis externus*. 67. *M. pubofemoralis pars dorsalis internus*. 68. *M.*

head. Proposed function: femoral protraction/moment arm changes.

M. ischiofemoralis posterior (53): originates at the posterolateral ventral side of the ischium. A number of fibers originate at the anterolateral part of the ischium, superficial to the fibers of the M. ischiofemoralis anterior. The muscle inserts at the dorsocaudal part of the femoral head. Proposed function: femoral retraction.

M. pubofemoralis pars ventralis (54): originates at the entire ventral surface of the pubis and partially also from the medial puboischiadic ligament. The muscle inserts ventrally on the proximal aspect of the trochanter. Proposed function: femoral adduction.

M. ischiofemoralis anterior (55): originates at the cartilaginous anterolateral aspect of the ischium, the medial puboischiadic ligament and the medioventral edge of the pubis. The muscle inserts at the ventral aspect of the base of the trochanter. Proposed function: femoral adduction.

M. flexor tibialis externus (56): originates at the ventral side of the ilioischiadic ligament and runs from its origin toward the tibia, where the muscle inserts on the ventral side of the tibial head by means of a short aponeurosis. This is the most superficially positioned muscle originating from the ilioischiadic ligament. Proposed function: femoral adduction. Note that this muscle is typically considered a knee flexor (Higham and Jayne, 2004; Snyder, 1954). However, given its attachment at the knee joint, this muscle does not appear to result in knee flexion in the species studied here.

M. flexor tibialis internus (57): originates at the ilioischiadic ligament, but

deep, dorsal, and caudal to the M. flexor tibialis externus. This is the most caudally positioned of the four muscles originating in this area. The fibers run slightly outward and insert by means of a tendon at the ventral, cranial side of the tibia, distal to the insertion of the M. flexor tibialis externus. Near its origin it runs adjacent to the M. iliotibialis. Proposed function: knee flexion and femoral adduction.

M. caudofemoralis longus (58): originates at the ventral processi, the ventral side of the vertebral body, and the ventral side of the transverse processi of caudal vertebrae 2–8 (2–9 in *A. valencienni*). The muscle runs dorsal to the ilioischiadic ligament and inserts by means of a short and thick tendon on the cranial face of the femur, just distal to the trochanter. An accessory tendon splits off from the main tendon and runs toward the tibia, where it inserts just distal to the knee joint. In *A. valencienni*, the insertion is shifted more distally. Proposed function: femoral retraction.

M. caudofemoralis brevis (59): originates at the ventral side of the vertebral body and at the transverse processi of caudal vertebrae 1–4. The muscle lies external to the M. caudofemoralis longus and inserts on the ilioischiadic ligament. Proposed function: ilioischiadic ligament tension/changing moment arm of the M. caudofemoralis longus.

M. adductor femoris (60): the proximal fibers originate at the caudal aspect of the lateral puboischiadic ligament, the intermediate fibers at the ventral aspect of the ischium, and the more caudal fibers laterally at the caudal side of the ischium. A small group of fibers originating on the ilioischiadic ligament also join the rest of

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ischiofemoralis dorsalis pars anterior. 69. M. iliofibularis. 70. M. iliofemoralis. 71. M. ilioischiotibialis. 72. M. tibialis anterior. 73. M. extensor digitorum longus. 74. M. gastrocnemius pars major. 75. M. gastrocnemius pars minor. 77. M. flexor digitorum communis. 78. M. extensor ossi metatarsi hallucis. 79. M. peroneus brevis. 80. M. popliteus. 81. M. peroneus longus. 82. M. longissimus. 83. M. spinalis. 84. M. iliocostalis. 85. M. longus cauda. 86. M. iliocaudalis. 87. M. ischiocaudalis. V, ligamentum ilioischiadum; T, pectineal tubercle; U, ilium; W, tibia; X, fibula; Y, astragalocalcaneum; Z, processus spinosus vertebra. \* Deeper structures, not labeled.

the muscle. The fibers run outward and insert along the distal three quarters of the femur. Proposed function: femoral adduction.

*M. ilioischiofibularis* (61): originates at the ilioischadic ligament and the ilium, cranial to the *M. iliotibialis*. The muscle runs dorsal to the *M. flexor tibialis externus*. The muscle inserts by means of a clear tendon at the cranialmost aspect of the fibula. Proposed function: femoral adduction.

*M. ambiens* (62, 63): has a bipartite origin; the dorsal group of fibers (*pars dorsalis*) originates by means of a wide aponeurosis along the ascending first half of the ilium (=iliotibialis; in Snyder, 1954). The ventral group of fibers (*pars ventralis*) originates by means of a short aponeurosis at the base of the pubis and the proximalmost aspect of the trochanter. The muscle runs dorsal to the aponeurosis communis and inserts by means of a short, thick aponeurosis that runs across the knee joint and inserts on the proximal aspect of the tibia. Together with the *Mm. femorotibialis* (dorsal and ventral parts), the *M. ambiens* forms the *M. quadriceps femoris*. Proposed function: knee extension.

*M. femorotibialis ventralis* (64): originates along the distal two-thirds of the femur. The muscle inserts by means of a tendon at the cranial side of the tibia. Proposed function: knee extension.

*M. femorotibialis dorsalis* (65): originates at the dorsal side of the femur and inserts by means of a short tendon at the dorsolateral side of the tibia. Proposed function: knee extension.

*M. pubofemoralis pars dorsalis* (66, 67): the externus part originates at the dorso-cranial side of the pubis. The muscle partly inserts on the aponeurosis communis (the externalmost fibers coming from the tip of the pubis) and partly on the femur (*internus* part), just distal to the trochanter. Proposed function: femoral protraction.

*M. ischiofemoralis dorsalis anterior* (68): originates at the dorsal side of the ischium, runs dorsal, curves around the pubis, runs

anterior to the articulation with the femur, and inserts at the cranial aspect of the femur just distal to the trochanter. Proposed function: femoral protraction.

*M. iliofibularis* (69): originates at the base of the ilium just anterior to the posterior ascending process. The muscle inserts at the fibula by means of a thin tendon, deep to the dorsalmost part of the *M. gastrocnemius*. Proposed function: knee flexion.

*M. iliofemoralis* (70): is a narrow muscle that originates at the anterior ventrolateral part of the ilium and inserts proximally on the caudal aspect of the femur at the level of the insertion of the *M. caudofemoralis longus*. Proposed function: femoral abduction.

*M. ilioischiotibialis* (71): originates at the dorsolateral aspect of the ilioischadic ligament. The muscle inserts by means of a clear tendon that splits at the level of the *M. gastrocnemius*. The first part of the tendon inserts proximally on the ventromedial side of the tibia, the other part runs across the tibial part of the *M. gastrocnemius* and inserts proximally on the ventrolateral side of the tibia. Proposed function: knee flexion.

*M. tibialis anterior* (72): has two clear bellies. The first one originates at the anterior aspect of the tibia, whereas the second originates on the ventral aspect of the entire tibia. The insertion of both parts is on the lateral aspect of the first metatarsal. Proposed function: ankle flexion.

*M. extensor digitorum longus* (73): originates by means of a long thin tendon on the fibular side of the femur. It inserts at the dorsal side of the third metatarsal. Proposed function: ankle flexion.

*M. gastrocnemius* (74–76): consists of two parts:

1) *M. gastrocnemius pars profundus* (76): the tibial deep part originates at the distal part of the femur on the tibial side. This is the smallest of the two parts and is reduced in *A. valencienni*. It inserts by means of a tendon that crosses to the other side, runs under the plantar aponeurosis,

and inserts medially at the level of the fifth metatarsal.

2) *M. gastrocnemius pars fibularis*: This is the most prominent part of the *M. gastrocnemius* and is positioned on the fibular side. It originates on the dorsal tubercle of the femur on the fibular side by means of a thick tendon. This muscle belly can be split into two parts. The pars major (74) inserts onto the first phalanx of the fourth and fifth toe; the pars minor (75) inserts on the first phalanx of the fourth toe. Proposed function: ankle extension.

*M. flexor digitorum communis* (77): consists of two parts. The tibial part originates fleshy at the proximal third along the inner aspect of both tibia and fibula. The fibular part originates at the proximal third along the inner part of the fibula. The two bellies converge onto a tendon that wraps around the ankle. The tibial part inserts by means of a long narrow tendon on the distal phalanges of toes 1–4. The fibular part inserts by means of a long thin tendon at the distal phalanx of the fifth toe. Proposed function: ankle extension and toe flexion.

*M. extensor ossi metatarsi hallucis* (78): originates at the ventral side of the distal two thirds of the fibula and inserts by means of a short tendon on the dorsal aspect on the tibial side of the astragalocalcaneum. Proposed function: ankle extension and rotation.

*M. peroneus brevis* (79): originates from the distal two thirds of the cranial edge of the fibula and inserts at the posterodorsal side of the fifth metatarsal. Proposed function: ankle extension.

*M. popliteus* (80): originates at the mesial side of the most proximal part of the fibula. The muscle runs obliquely ventrad to insert on the mesial side of the proximal fifth of the tibia. Proposed function: tibio-fibular rotation.

*M. peroneus longus* (81): originates by means of a long, narrow tendon on the fibular side of the femur. The muscle wraps around the ankle and inserts at the ventral

side of the fifth metatarsal. Proposed function: ankle extension.

*M. iliofemoralis posterior* (not drawn): originates from the posterior part of the ilium (at the level of the attachment of the ilioischadic ligament) and from the ventral aspect of the first caudal vertebra. The muscle inserts onto the femur, proximal to the tendon of the *M. caudofemoralis longus*. Proposed function: femoral abduction.

*M. ischiofemoralis dorsalis posterior* (not drawn): originates at the dorsocaudal side of the ischium and inserts at the dorsocaudal side of the femur. Proposed function: femoral abduction.

*M. pronator profundus* (not drawn): originates fleshy at the distal quarter on the mesial aspect of the fibula. The muscle runs obliquely ventrad and inserts on the mesial side of the distal fifth of the tibia. Proposed function: tibio-fibular rotation.

### Morphometrics

The *A. valencienni* in our sample were significantly larger than the *A. sagrei* (SVL:  $F_{1,16} = 68.35$ ,  $P < 0.001$ ). However, for its body size, *A. sagrei* had significantly longer tibia (analyses of covariance with SVL as covariate; slope:  $F_{1,6} = 1.28$ ,  $P = 0.30$ ; intercept:  $F_{1,7} = 15.32$ ,  $P = 0.006$ ), metatarsi (slope:  $F_{1,6} = 0.23$ ,  $P = 0.65$ ; intercept:  $F_{1,7} = 6.59$ ,  $P = 0.037$ ) and toes on both front limbs (slope:  $F_{1,6} = 1.16$ ,  $P = 0.32$ ; intercept:  $F_{1,7} = 16.89$ ,  $P = 0.005$ ) and hindlimbs (slope:  $F_{1,6} = 0.35$ ,  $P = 0.58$ ; intercept:  $F_{1,7} = 7.48$ ,  $P = 0.029$ ) compared with *A. valencienni*. These results are consistent with previous analyses of limb dimensions in these species (Beuttell and Losos, 1999; Higham et al., 2001).

### Muscle Mass and Muscle Mass distribution (Table 1)

The two species differed significantly in total hindlimb (ANOVA:  $F_{1,5} = 13.79$ ,  $P = 0.004$ ) and total forelimb ( $F_{1,5} = 25.67$ ,  $P = 0.001$ ) muscle mass, with *A. sagrei* having heavier fore- and hindlimb muscles than *A. valencienni* despite its smaller

TABLE 1. SUMMARY TABLE OF THE ANALYSIS OF MUSCLE MASSES AND MUSCLE MASS DISTRIBUTIONS IN *A. SAGREI* AND *A. VALENCIENNI*.

	<i>Anolis sagrei</i>	<i>Anolis valencienni</i>
Snout-vent length (mm)	55.79 ± 1.88	66.26 ± 2.52
Total hindlimb muscle mass (mg)	393.03 ± 74.80	278.60 ± 25.41
Total forelimb muscle mass (mg)	209.07 ± 38.16	125.33 ± 16.36
Femur protractors (mg)	33.00 ± 17.35	17.20 ± 10.37
Femur retractors (mg)	83.84 ± 23.07	78.52 ± 27.39
Femur abductors (mg)	6.31 ± 2.08	5.14 ± 1.01
Femur adductors (mg)	49.44 ± 18.83	28.26 ± 11.96
Knee flexors (mg)	49.93 ± 22.38	38.72 ± 17.62
Knee extensors (mg)	57.98 ± 20.25	32.08 ± 14.00
Ankle flexors (mg)	14.10 ± 6.82	5.43 ± 2.35
Ankle extensors (mg)	49.21 ± 27.05	18.04 ± 9.33
Other hindlimb (mg)	3.42 ± 3.78	3.24 ± 2.07
Humerus retractors (mg)	81.99 ± 44.94	39.60 ± 18.32
Humerus protractors (mg)	10.33 ± 2.15	8.40 ± 5.53
Humerus abductors (mg)	13.52 ± 4.9	7.94 ± 2.88
Humerus adductors (mg)	12.48 ± 6.67	8.46 ± 3.73
Elbow flexors (mg)	20.91 ± 7.33	9.46 ± 3.97
Elbow extensors (mg)	24.82 ± 10.51	13.17 ± 6.92
Wrist flexors (mg)	11.24 ± 4.93	5.86 ± 3.02
Wrist extensors (mg)	7.13 ± 3.41	4.76 ± 4.00
Other forelimb (mg)	2.22 ± 1.25	1.47 ± 0.84

Table entries are means ± standard deviation.

body size. Absolute differences in most functional groups tended to be nonsignificant. However, the ankle extensors ( $F_{1,8} = 8.11$ ,  $P = 0.022$ ), ankle flexors ( $F_{1,8} = 9.94$ ,  $P = 0.014$ ), and elbow flexors ( $F_{1,6} = 7.25$ ,  $P = 0.036$ ) were significantly heavier in *A. sagrei*. Femur adductors ( $F_{1,8} = 4.22$ ,  $P = 0.07$ ) and knee extensors ( $F_{1,8} = 4.87$ ,  $P = 0.058$ ) were generally (but not significantly) larger in *A. sagrei* compared to *A. valencienni*.

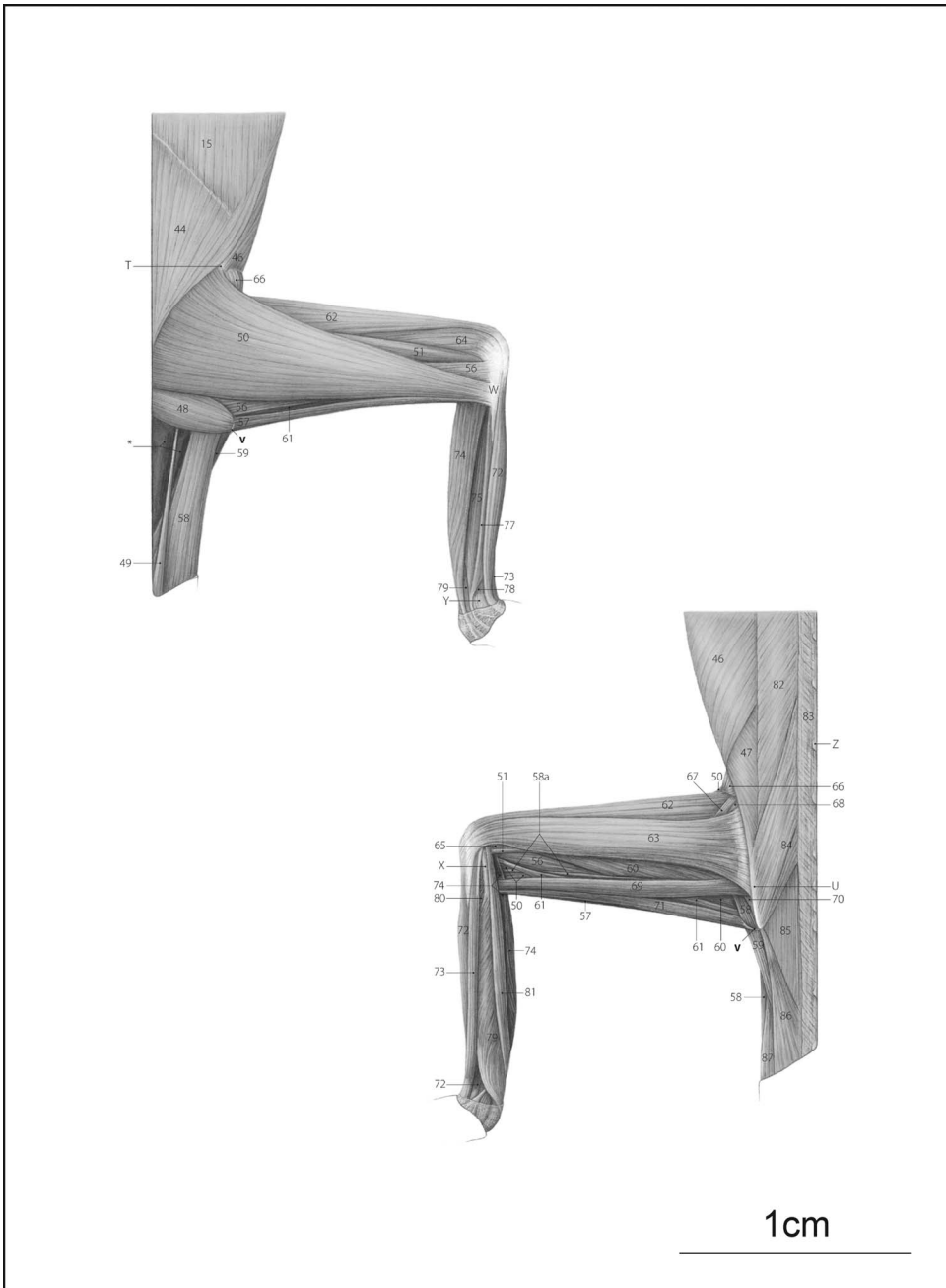
The femur retractors are the largest muscle group in the hindlimb, followed by the knee extensors and flexors (Fig. 10A). Whereas the femur retractors are relatively larger in *A. valencienni* (i.e., relative to total limb muscle mass;  $F_{1,7} = 27.30$ ,  $P = 0.001$ ), the knee extensors ( $F_{1,7} = 9.16$ ,  $P$

$= 0.019$ ) and ankle extensors ( $F_{1,7} = 13.25$ ,  $P = 0.008$ ) are relatively bigger in *A. sagrei*. In the forelimb, the humerus retractors are the biggest muscle group, and these are somewhat, but not significantly, better developed in *A. sagrei* compared with *A. valencienni* (Fig. 10B). In general, species-specific differences in forelimb muscle mass distribution are much smaller than for the hindlimb. The proportions of hindlimb and forelimb muscle mass relative to the total muscle mass were similar for both species (hindlimb, ±70%; forelimb, ±30%).

#### Locomotor Behavior

In the two-way MANCOVA with stride length, stride frequency, and step length as

Figure 7. Anatomical drawings illustrating the superficial hindlimb musculature in *A. valencienni*. Shown are a ventral and dorsal view (top and bottom, respectively). Note the generally more robust musculature in *A. sagrei* as depicted in Figure 6. 15. M. pectoralis pars superficialis. 44. M. rectus abdominis pars superficialis. 45. M. rectus abdominis pars profundus. 46. M. obliquus abdominis. 47. M. transversus abdominis complex. 48. M. transversus perinei. 49. M. coccygeus inferior. 50. M. puboischiotibialis. 51. M. pubofibularis. 56. M. flexor tibialis externus. 57. M. flexor tibialis internus. 58. M. caudofemoralis longus; 58a. tendino m. caudofemoralis longus. 59. M. caudofemoralis brevis. 60. M. adductor femoris. 61. M. ilioischiofibularis. 62. M. ambiens pars



ventralis. 63. M. ambiens pars dorsalis. 64. M. femorotibialis pars ventralis. 65. M. femorotibialis pars dorsalis. 66. M. pubofemoralis pars dorsalis externus. 67. M. pubofemoralis pars dorsalis internus. 68. M. ischiofemorals dorsalis pars anterior. 69. M. iliofibularis. 70. M. iliofemorals. 71. M. ilioischiotibialis. 72. M. tibialis anterior. 73. M. extensor digitorum longus. 74. M. gastrocnemius pars major. 75. M. gastrocnemius pars minor. 77. M. flexor digitorum communis. 78. M. extensor ossi metatarsi hallucis. 79. M. peroneus brevis. 80. M. popliteus. 81. M. peroneus longus. 82. M. longissimus. 83. M. spinalis. 84. M. iliocostalis. 85. M. longus cauda. 86. M. iliocaudalis. 87. M. ischiocaudalis. V, ligamentum ilioischiadum; T, pectineal tubercle. U, ilium. W, tibia. X, fibula. Y, astragalocalcaneum. Z, processus spinosus vertebra. \* Deeper structures, not labeled.

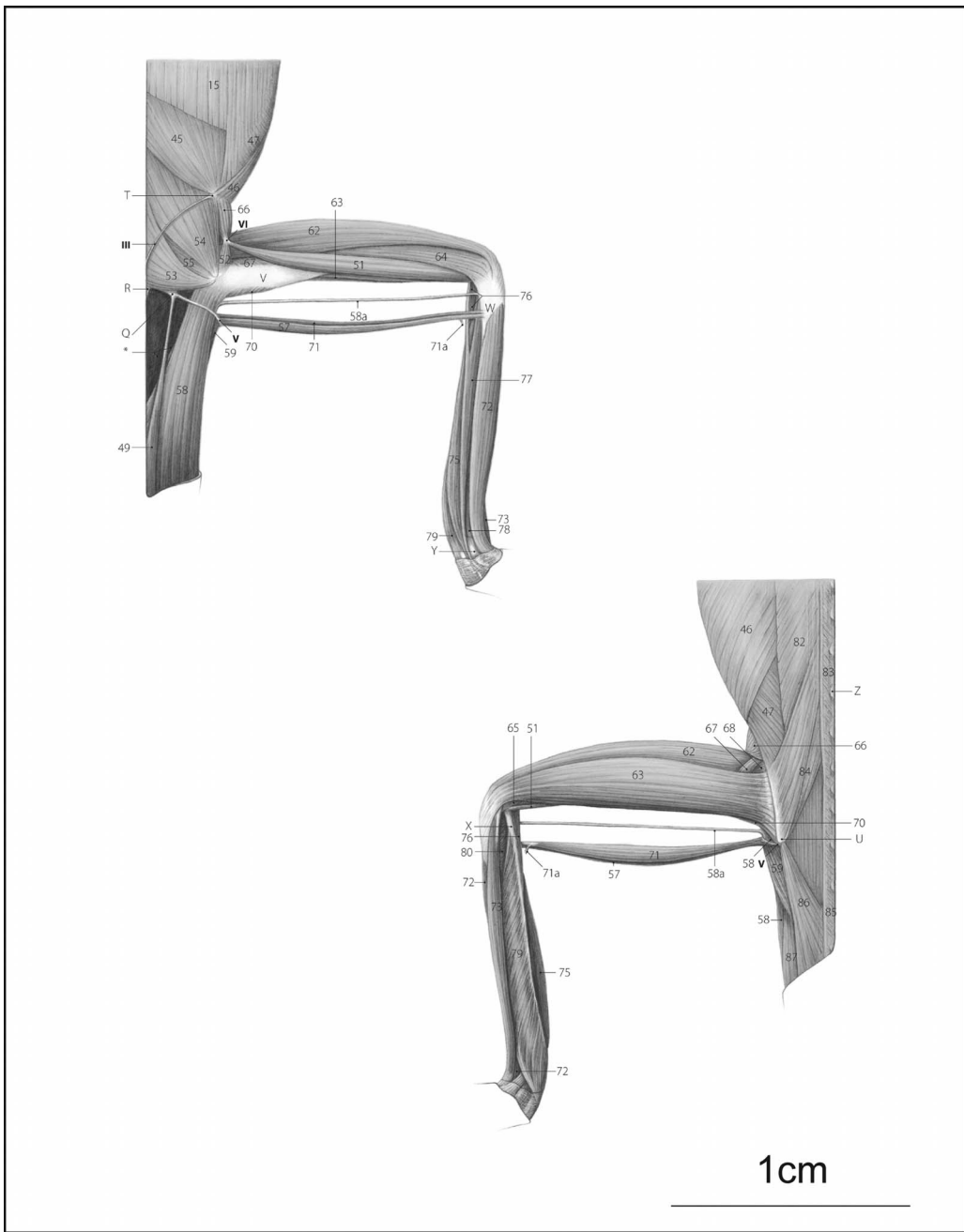


Figure 8. Anatomical drawings illustrating the deep hindlimb musculature in *A. sagrei*. Shown are a ventral and dorsal view (top and bottom, respectively). 15. *M. pectoralis pars superficialis*. 45. *M. rectus abdominis pars profundus*. 46. *M. obliquus abdominis*. 47. *M. transversus abdominis complex*. 49. *M. cocygeus inferior*. 51. *M. pubofibularis*. 52. *M. tensor aponeurosis communis*. 53. *M. ischiofemoralis pars posterior*. 54. *M. pubofemorals pars ventralis*. 55. *M. ischiofemoralis pars anterior*. 57. *M. flexor tibialis internus*. 58. *M. caudofemoralis longus*; 58a. *tendino m. caudofemoralis longus*. 59. *M. caudofemoralis brevis*. 62. *M. ambiens pars ventralis*. 63. *M. ambiens pars dorsalis*. 64. *M. femorotibialis pars ventralis*. 65. *M. femorotibialis pars dorsalis*. 66. *M. pubofemorals pars dorsalis externus*. 67. *M. pubofemorals pars dorsalis internus*. 68. *M. ischiofemorals dorsalis pars anterior*. 70. *M. iliofemorals*. 71. *M. ilioischiotibialis*; 71a. *tendino m. ilioischiotibialis*. 72. *M. tibialis anterior*. 73. *M. extensor digitorum longus*. 75. *M. gastrocnemius pars minor*. 76. *M. gastrocnemius pars profundus*. 77. *M. flexor digitorum communis*.

dependent variables, stride speed as covariate and species and dowel as factor, none of the interaction effects were significant (all  $P > 0.07$ ). Average velocity over a stride had a significant effect on the spatiotemporal gait characteristics (Wilks'  $\lambda = 0.044$ ,  $F_{3,6} = 42.99$ ,  $P < 0.0001$ ). In addition, gait characteristics differed significantly between species (Wilks'  $\lambda = 0.064$ ,  $F_{3,6} = 29.02$ ,  $P = 0.001$ ; Fig. 11). For a given speed, *A. sagrei* takes longer strides and longer steps at lower frequencies compared with *A. valencienni*. Differences between substrates were also significant (Wilks'  $\lambda = 0.086$ ,  $F_{3,6} = 21.36$ ,  $P = 0.001$ ; Fig. 11). Locomotion on broad dowels was associated with higher step and stride lengths, but lower stride frequencies compared with narrow dowels. Univariate  $F$  tests showed that species and substrate effects were highly significant for all parameters tested (Table 2).

## DISCUSSION

A number of distinct and striking differences in the morphology of the pectoral girdle and associated appendicular musculoskeletal system were observed when comparing two distinct *Anolis* species. The pectoral girdle itself, for example, is relatively narrower and longer in *A. valencienni* compared with *A. sagrei* and is reflected in the more gracile overall body shape in the former species (see also Beuttell and Losos, 1999). The difference in body shape itself can be related to selection for increased stability on narrow substrates in *A. valencienni* (Losos and Irschick, 1996; Losos and Sinervo, 1989). Additionally, it allows this species and other twig anoles with a similar body shape to remain cryptic against its preferred substrate of narrow branches and twigs (Huyghe et al., 2007;

Irschick and Losos, 1996; Vanhooydonck et al., 2007).

Our results on muscle mass show that total forelimb muscle mass is considerably greater in *A. sagrei* despite its smaller body size (Table 1). Although not different in absolute size, the relative contribution of the humerus retractors to the total forelimb muscle mass is greater (but not significantly so) in this species as well. This was unexpected given the subordinate role of the forelimbs during locomotion on horizontal substrates, more characteristic of the habitat use of *A. sagrei*, and the importance of humerus retraction during climbing (Zaaf et al., 1999, 2001), which is expected to be associated with the more arboreal lifestyle of *A. valencienni*. However, twig anoles like *A. valencienni*, despite being highly arboreal, do spend a significant proportion of their time on horizontal or inclined substrates (Irschick and Losos, 1996; Mattingly and Jayne, 2004, 2005). Thus, humerus retraction might be less important for these species than initially expected. *Anolis sagrei*, on the other hand, although spending a considerable amount of time on the ground, does run up the vertical bases of tree trunks (i.e., trunk-ground anoles use steeper surfaces than other ecomorphs; Mattingly and Jayne, 2004) which might explain the importance of humerus retraction in this species. The significantly greater absolute mass of the elbow flexors (also important during climbing) in *A. sagrei* corroborates this finding. Additional data on other trunk-ground versus twig anoles are needed, however, to test the generality of these findings.

As predicted a priori, the anatomy of the hindlimb muscles also differs between the two species, with a larger absolute overall

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78. M. extensor ossi metatarsi hallucis. 79. M. peroneus brevis. 80. M. popliteus. 82. M. longissimus. 83. M. spinalis. 84. M. iliocostalis. 85. M. longus cauda. 86. M. iliocaudalis. 87. M. ischiocaudalis. III, ligamentum puboischiadum pars lateralis; V, ligamentum ilioischiadum; VI, aponeurosis communis; Q, ischium; R, hypoischiium; T, pectineal tubercle; U, ilium; V, femur; W, tibia; X, fibula; Y, astragalocalcaneum; Z, processus spinosus vertebra. \* Deeper structures, not labeled.

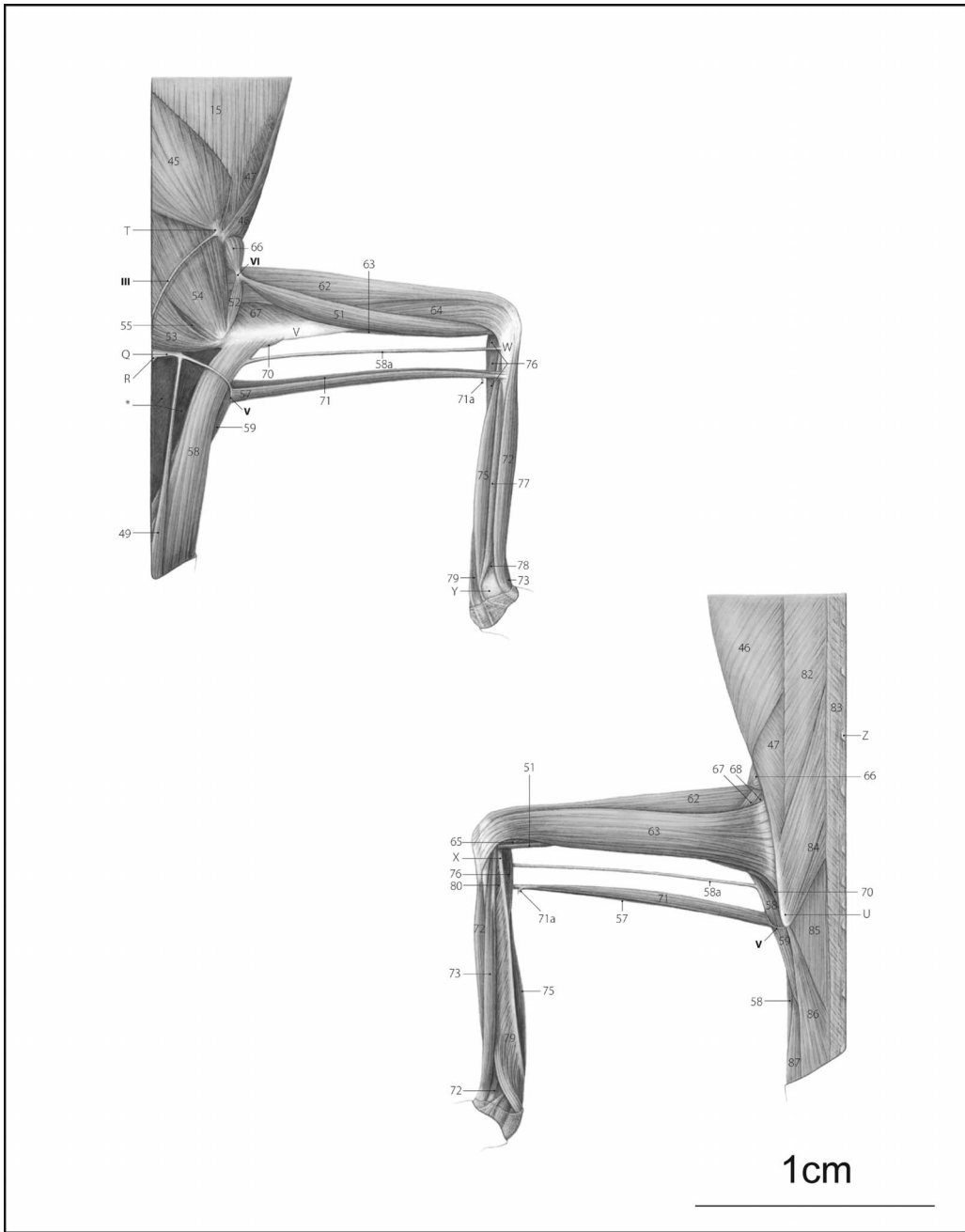


Figure 9. Anatomical drawings illustrating the deep hindlimb musculature in *A. valencienni*. Shown are a ventral and dorsal view (top and bottom, respectively). Note the subtle differences in the insertion of the m. caudofemoralis and its accessory tendon in *A. valencienni* compared with *A. sagrei*, as depicted in Figure 8. 15. M. pectoralis pars superficialis. 45. M. rectus abdominis pars profundus. 46. M. obliquus abdominis. 47. M. transversus abdominis complex. 49. M. coccygeus inferior. 51. M. pubofibularis. 52. M. tensor aponeurosis communis. 53. M. ischiofemoralis pars posterior. 54. M. pubofemoralis pars ventralis. 55. M. ischiofemoralis pars anterior. 57. M. flexor tibialis internus. 58. M. caudofemoralis longus; 58a. tendino m. caudofemoralis

TABLE 2. SUMMARY OF UNIVARIATE ANALYSIS ON SIZE-CORRECTED GAIT CHARACTERISTICS FOR *A. SAGREI* AND *A. VALENCIENNI* MOVING ON TWO DIFFERENT SUBSTRATES.

	<i>df</i>	<i>F</i>	<i>P</i>
Dowel			
Stride length	1, 8	24.41	0.001
Stride frequency	1, 8	40.28	<0.0001
Step length	1, 8	14.02	0.006
Species			
Stride length	1, 8	55.25	<0.0001
Stride frequency	1, 8	11.98	0.009
Step length	1, 8	8.48	0.02
Stride speed			
Stride length	1, 8	0.26	0.62
Stride frequency	1, 8	22.63	0.001
Step length	1, 8	3.68	0.09

Note that all kinematic variables were expressed relative to hindlimb length. *df*, degrees of freedom.

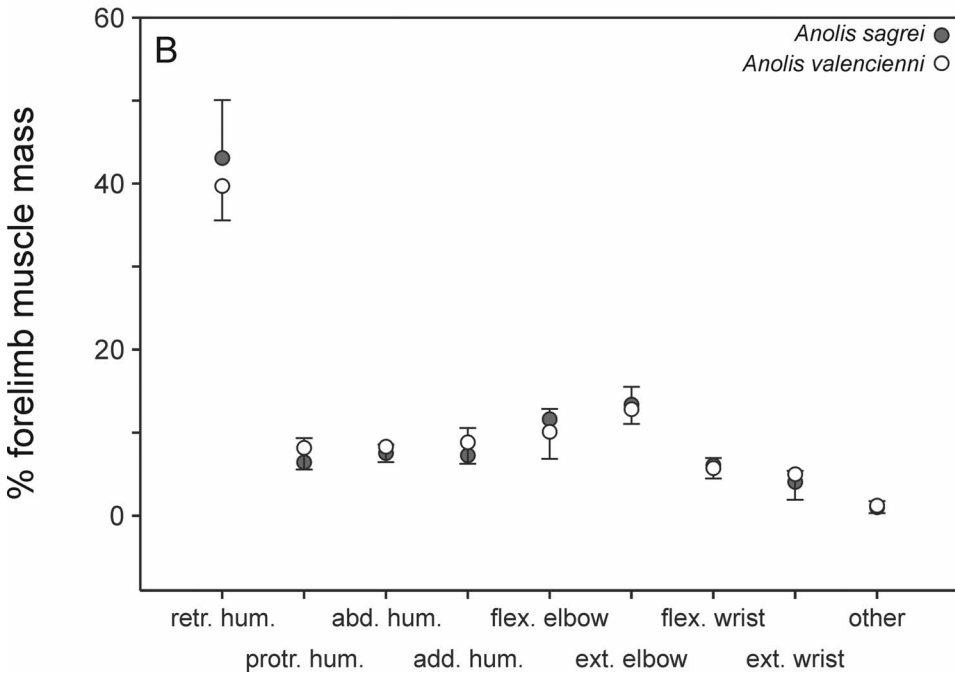
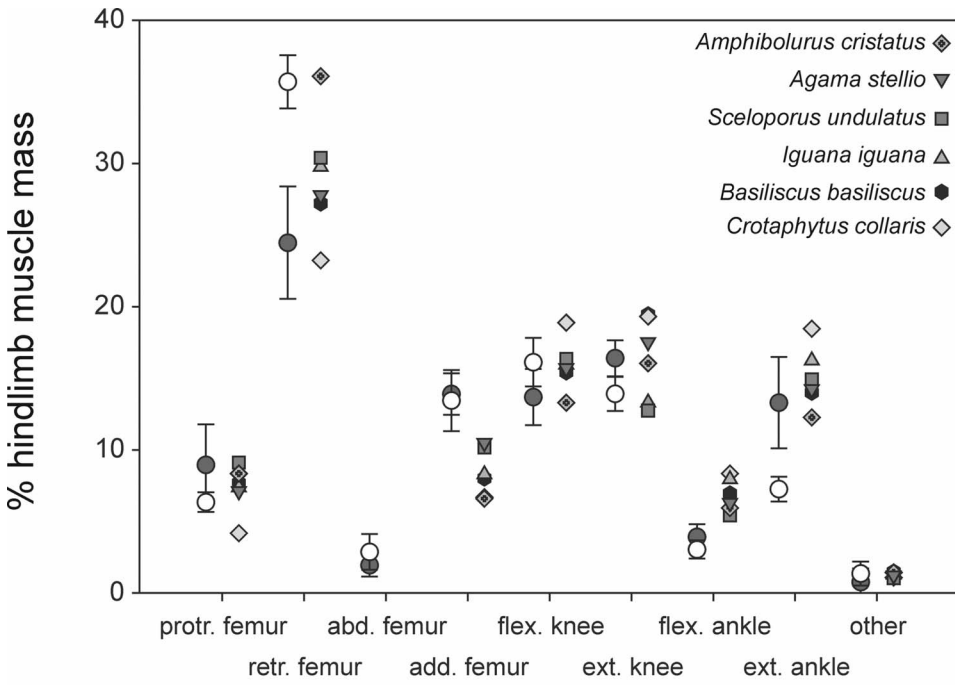
hindlimb muscle mass as well as significantly larger ankle extensors and ankle flexors observed in *A. sagrei* (Table 1). Muscle mass allocation also differed significantly between species, with *A. sagrei* having relatively larger knee and ankle extensors and *A. valencienni* having relatively larger femur retractors. Also, the shape of the pelvic girdle shows remarkable differences in the two species. Whereas the pelvis is longer and narrower in *A. valencienni*, the ilium is elongated and inclined more dorsally in *A. sagrei* (see also Beuttell and Losos, 1999). Whereas the overall shape differences in the pelvis can be related to overall differences in body shape (longer and narrower in *A. valencienni*), the differences in ilial structure can be directly related to differences in locomotor mode. The ilium is the principal area of insertion for the knee extensors, and the knee extensors are the principal determinants of variation in sprint speed, jump,

and acceleration capacity in *Anolis* lizards (James et al., 2007; Vanhooydonck et al., 2006a). The longer the ilium, the more space is available for the knee extensors. Indeed, *A. sagrei* has more massive knee extensors in both absolute and relative terms compared with *A. valencienni*. *Anolis valencienni*, on the other hand, appears to rely more on femoral retraction, as suggested by the relatively greater allocation of muscle mass to femur retractors and the distal shift of the insertion of the *M. caudofemoralis*, thus providing for a greater moment arm and, consequently, moment around the hip joint.

Given the importance of keeping the center of mass close to the middle of the substrate when running on narrow branches, relying on knee extension for propulsion could effectively be less optimal because of the induced lateral displacement away from the center of the branch, at least when the foot is positioned at the lev-

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longus. 59. *M. caudofemoralis brevis*. 62. *M. ambiens pars ventralis*. 63. *M. ambiens pars dorsalis*. 64. *M. femorotibialis pars ventralis*. 65. *M. femorotibialis pars dorsalis*. 66. *M. pubofemoralis pars dorsalis externus*. 67. *M. pubofemoralis pars dorsalis internus*. 68. *M. ischiofemoralis dorsalis pars anterior*. 70. *M. iliofemoralis*. 71. *M. ilioischiotibialis*; 71a. *tendino m. ilioischiotibialis*. 72. *M. tibialis anterior*. 73. *M. extensor digitorum longus*. 75. *M. gastrocnemius pars minor*. 76. *M. gastrocnemius pars profundus*. 77. *M. flexor digitorum communis*. 78. *M. extensor ossi metatarsi hallucis*. 79. *M. peroneus brevis*. 80. *M. popliteus*. 82. *M. longissimus*. 83. *M. spinalis*. 84. *M. iliocostalis*. 85. *M. longus cauda*. 86. *M. iliocaudalis*. 87. *M. ischiocaudalis*. III, ligamentum puboischium pars lateralis; V, ligamentum ilioischium; VI, aponeurosis communis; Q, ischium; R, hypoischium; T, pectineal tubercle; U, ilium; V, femur; W, tibia; X, fibula; Y, astragalocalcaneum; Z, processus spinosus vertebra. \* Deeper structures, not labeled.



el of or in front of the pelvis (Spezzano and Jayne, 2004). This appears to be reflected in the morphology of the hindlimb muscles and locomotor patterns in the two species. Indeed, an additional important difference between the two species in locomotor style is the reduced protraction of the limb during the swing phase in *A. valencienni*, causing it to take smaller steps and strides and resulting in a placement of the foot behind the pelvic girdle. Again, this can be coupled to differences in hindlimb morphology between the two species. The insertion of the accessory tendon of the M. caudofemoralis is displaced more distally from the knee joint in *A. valencienni*, thus effectively preventing knee extension when the femur is protracted. The morphology is however different in *A. sagrei*, with the insertion being at the level of the joint, thus allowing knee extension and femur protraction at the same time. This results in greater step and stride lengths and ultimately also sprint speeds. The cost of the greater protraction and dependence on knee extension is a potential decrease in stability because of the greater lateral displacement of the center of mass away from the center of the branch.

A comparison of our data on muscle mass distribution with previously published data for several species of iguanid (sensu lato) and agamid lizards indicates that the differences between the two species of anole included here are nearly as great as between a dedicated terrestrial lizard (*Crotaphytus collaris*) and an exclusively arboreal species (*Iguana iguana*) (see Fig. 10A). Moreover, differences observed between the two anole ecomorphs tend to mimic those (although being different in absolute terms) observed between the terrestrial and the arboreal spe-

cies, with *A. sagrei* being more similar to *C. collaris* and *A. valencienni* being more similar to *I. iguana*. Among iguanid lizards, *Sceloporus undulatus*, being semi-arboreal, resembles *A. valencienni* and *I. iguana* in its muscle mass distribution. *Basiliscus basiliscus*, being ecologically more similar to *A. sagrei* in that it uses both arboreal and terrestrial substrates, is generally intermediate between the more dedicated ground dweller *C. collaris* and the arboreal *I. iguana*. Among the agamid lizards, *Amphibolurus cristatus* (now placed in the genus *Ctenophorus*) is unusual in that it resembles more arboreal lizards like *I. iguana* and *A. valencienni* in some features of the hindlimb muscle mass distribution, despite being a largely terrestrial lizard. Like *A. valencienni* and *I. iguana*, *A. cristatus* appears to rely predominantly on femur retraction rather than knee and ankle extension for generating propulsion. Clearly, data for additional agamid and iguanid lizards are needed to investigate the generality of these patterns and to quantitatively test for associations between muscle morphology and habitat use in a comparative context.

Our data show how an understanding of the morphology of the locomotor apparatus might help explain the correlated evolution of morphology, performance, locomotor style (i.e., gait characteristics) and habitat use in *Anolis* lizards. In providing this detailed morphological account, we hope to provide a basis for future studies investigating the morphology of the musculoskeletal system and its role in the evolution of locomotor performance and habitat use in *Anolis* lizards and to show that morphological adaptations to habitat use go beyond mere external differences in limb size and shape.

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Figure 10. Graphs illustrating the relative muscle mass distribution expressed as the proportion of the total hindlimb (A) or forelimb (B) muscle mass. Data are represented as means  $\pm$  standard deviation for the two *Anolis* species included in our study. Whereas differences in muscle mass allocation are strikingly different for the hindlimb muscles, differences for the forelimb are less conspicuous. Solid circles, *A. sagrei*; white circles, *A. valencienni*. Also plotted are literature data on hindlimb muscle mass distribution taken from Snyder (1954). Note, however, that Snyder did not consider femur abductors.

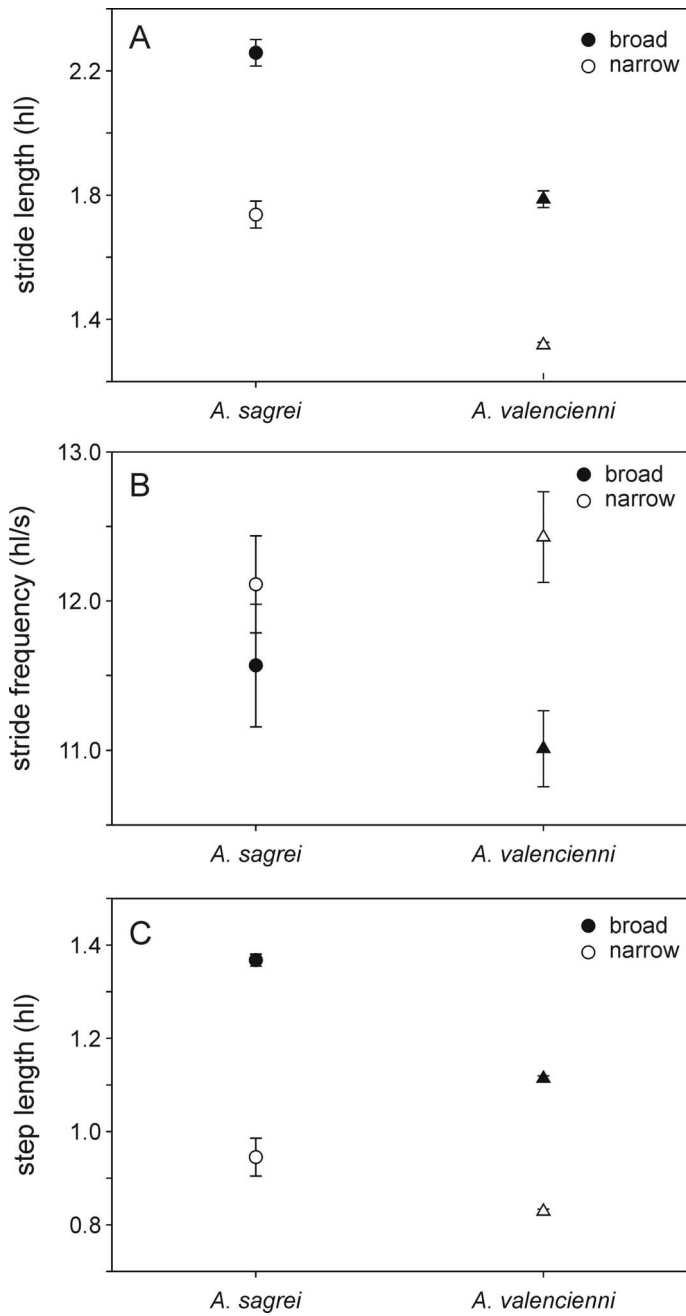


Figure 11. Graphs illustrating the differences in spatiotemporal gait characteristics in *A. sagrei* and *A. valencienni* while moving across two different substrates. Data are represented as means  $\pm$  standard deviation. Illustrated are the stride length (A), stride frequency (B), and step length (C) expressed in hindlimb lengths. Thus, for a given hindlimb length, *A. sagrei* takes larger steps and strides on both substrates. Broad substrates are associated with greater step and stride lengths and lower stride frequencies in both species. hl, hindlimb.

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## LITERATURE CITED

- ABDALA, V., AND S. MORO. 2006. Comparative myology of the forelimb of *Liolaemus* sand lizards (Liolaemidae). *Acta Zoologica*, **87**: 1–12.
- AUTUMN, K., S. T. HSIEH, D. M. DUDEK, J. CHEN, C. CHITAPHAN, AND R. J. FULL. 2006. Dynamics of geckos running vertically. *Journal of Experimental Biology*, **209**: 260–272.
- BEUTTELL, K., AND J. B. LOSOS. 1999. Ecological morphology of Caribbean anoles. *Herpetological Monographs*, **13**: 1–28.
- HIGHAM, T. E., M. S. DAVENPORT, AND B. C. JAYNE. 2001. Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards. *Journal of Experimental Biology*, **204**: 4141–4155.
- , AND B. C. JAYNE. 2004. In vivo muscle activity in the hindlimb of the arboreal lizard, *Chamaeleo calyptratus*: general patterns and the effects of incline. *Journal of Experimental Biology*, **207**: 249–261.
- HUYGHE, K., A. HERREL, B. VANHOODYONCK, J. J. MEYERS, AND D. J. IRSCHICK. 2007. Microhabitat use, diet, and performance data on the Hispaniolan twig anole, *Anolis sheplani*. *Zoology*, **110**: 2–8.
- IRSCHICK, D. J., AND J. B. LOSOS. 1996. Morphology, ecology, and behavior of the twig anole, *Anolis angusticeps*, pp. 291–301. In R. Powell and R. W. Henderson (eds.), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*. Ithaca, New York: Society for the Study of Amphibians and Reptiles.
- , AND ———. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, **52**: 219–226.
- , AND ———. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *American Naturalist*, **154**: 293–305.
- JAMES, R. S., C. A. NAVAS, AND A. HERREL. 2007. How important are skeletal muscle mechanics in setting limits on jumping performance? *Journal of Experimental Biology*, **210**: 923–933.
- JENKINS, F. A., AND G. E. GOSLOW. 1983. The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exanthematicus*). *Journal of Morphology*, **175**: 195–216.
- LANDSMEER, J. M. F. 1984. Morphology of the anterior limb in relation to sprawling gait in *Varanus*. *Symposia Zoological Society London*, **52**: 27–45.
- . 1990. Functional morphology of the hindlimb in some lacertilia. *European Journal of Morphology*, **28**: 3–34.
- LOSOS, J. B. 1990a. The evolution of form and function: morphology and locomotor performance ability in West Indian *Anolis* lizards. *Evolution*, **44**: 1189–1203.
- . 1990b. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs*, **60**: 369–388.
- , AND D. J. IRSCHICK. 1996. The effect of perch diameter on the escape behavior of *Anolis* lizards: laboratory-based predictions and field tests. *Animal Behaviour*, **51**: 593–602.
- , T. R. JACKMAN, A. LARSON, K. DE QUEIROZ, AND L. RODRIGUEZ-SCHETTINO. 1998. Historical contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**: 2115–2118.
- , AND B. SINERVO. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology*, **145**: 23–30.
- , K. I. WARHEIT, AND T. W. SCHOENER. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, **387**: 70–73.
- MATTINGLY, W. B., AND B. C. JAYNE. 2004. Resource use in arboreal habitats: structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology*, **85**: 1111–1124.
- , AND ———. 2005. The choice of arboreal escape paths and its consequences for the locomotor behaviour of 123 species of *Anolis* lizards. *Animal Behaviour*, **70**: 1239–1250.
- MORO, S., AND V. ABDALA. 2004. Análisis descriptivo de la miología flexora y extensora del miembro anterior de *Polychrus acutirostris* (Squamata, Polychrotidae). *Papéis Avulsos de Zoologia*, **44**: 81–90.
- NICHOLSON, K. E., R. E. GLOR, J. J. KOLBE, A. LARSON, S. B. HEDGES, AND J. B. LOSOS. 2005. Mainland colonization by island lizards. *Journal of Biogeography*, **32**: 929–938.
- RUSSELL, A. P. 1988. Limb muscles in relation to lizard systematics: a reappraisal, pp. 119–218. In R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of Lizard Families: Essays Commemorating Charles L. Camp*. Palo Alto, California: Stanford University Press.
- SCHLUTER, D. 2000. *The Ecology of Adaptive Radiation*. Oxford, United Kingdom: Oxford University Press.
- SINERVO, B., AND J. B. LOSOS. 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology*, **72**: 1225–1233.
- SNYDER, R. C. 1954. The anatomy and function of

- the pelvic girdle and hindlimb in lizard locomotion. *American Journal of Anatomy*, **95**: 1–45.
- SPEZZANO, L. C., AND B. C. JAYNE. 2004. The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). *Journal of Experimental Biology*, **207**: 2115–2131.
- TORO, E., A. HERREL, B. VANHOOYDONCK, AND D. J. IRSCHICK. 2003. A biomechanical analysis of intra- and interspecific scaling of jumping biomechanics and morphology in Caribbean *Anolis* lizards. *Journal of Experimental Biology*, **206**: 2641–2652.
- VANHOOYDONCK, B., A. ANDRONESCU, A. HERREL, AND D. J. IRSCHICK. 2005. Effects of substrate structure on speed and acceleration capacity in climbing geckos. *Biological Journal of the Linnean Society London*, **85**: 385–393.
- , A. HERREL, R. VAN DAMME, AND D. J. IRSCHICK. 2006a. The quick and the fast: the evolution of acceleration capacity in *Anolis* lizards. *Evolution*, **60**: 2137–2147.
- , ———, AND D. J. IRSCHICK. 2006b. Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. *Journal of Experimental Biology*, **209**: 4515–4523.
- , ———, AND ———. 2007. Determinants of sexual differences in escape behavior in *Anolis* lizards: a comparative approach. *Integrative and Comparative Biology*, **47**: 200–210.
- WILLIAMS, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*, pp. 326–370. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard Ecology: Studies of a Model Organism*. Cambridge, Massachusetts: Harvard University Press.
- ZAAF, A., A. HERREL, P. AERTS, AND F. DE VREE. 1999. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). *Zoomorphology*, **119**: 9–22.
- , R. VAN DAMME, A. HERREL, AND P. AERTS. 2001. Spatio temporal gait characteristics of level and vertical locomotion in a level-running and a climbing gecko. *Journal of Experimental Biology*, **204**: 1233–1246.