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Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria)

Accepted: 30 November 1998

Abstract In this study a ground-dwelling (*Eublepharis macularius*) and a highly specialised climbing (*Gekko gecko*) lizard were chosen as study objects. The fore- and hindlimbs of two individuals of each species were dissected, and muscle masses, mean fibre lengths, cross-sectional areas and moment arms were determined. Special attention was paid to general muscle architecture (origin, insertion, fibre orientation, etc.) and pennation angles. Using these variables (cross sectional areas and moment arms), maximal moments exertable across the shoulder/hip, elbow/knee and wrist/ankle were calculated for both species. In accordance with the biomechanical predictions related to the preferred locomotor substrate of each species (i.e. level running for *E. macularius* and climbing for *G. gecko*), the results of this study indicate that climbers such as *G. gecko* generally possess powerful retractor muscles crossing the shoulder and hip joints. Additionally, the specialised climber is able to exert higher flexion moments across the elbow, which prevents the animals from falling backwards. However, *G. gecko* appears to be constrained in its ankle extension capabilities by the presence of the adhesive toe pads. The level-running species, on the other hand, shows a relatively stronger development of the extensor muscles in the lower limbs, allowing these lizards to run in an erect posture. In general, both species show large similarities on a gross morphological level as expected when considering their phylogenetic relatedness. Adaptations to their preferred locomotor substrate only become apparent when considering the functional properties (i.e. joint moments) of the appendicular musculature.

A. Introduction

Among extant lepidosaurians, lizards have the widest geographical distribution encompassing a wide range of locomotor habitats. This is reflected in an large morphological diversity of the general body form and of the locomotory apparatus among these animals (Peterson 1984; Miles et al. 1995; Russell et al. 1997). As the use of a terrestrial habitat is considered to be a plesiomorphic characteristic in lizards (Russell 1979), any shift to a fundamentally new habitat will be accompanied by different adaptive character suites (Moermond 1979; Jaksic et al. 1980; Losos 1990a, b; Malhotra and Thorpe 1991; Losos et al. 1997). Lizards are thus an interesting group in which to study the effects of radical changes in locomotor habitat (e.g. climbing, swimming or digging vs running) on the locomotory apparatus.

Species, for which either climbing or level running dominate, can be expected to differ not only in their general appearance (e.g. body shape), but especially in morphology and morphometry of the locomotory apparatus (Pounds 1988; Losos 1990a; Bauer et al. 1996; Losos et al. 1997). Based on general biomechanical principles it can be predicted that level runners should have longer limbs, moving more sagittally to increase the stride length, and should elevate the body from the ground to reduce friction (Rewcastle 1981; Miles et al. 1995; Bauer et al. 1996). Climbers on the other hand, should benefit from shorter limbs and a more sprawling gait to keep the centre of mass as close to the substrate as possible (Peterson 1984; Cartmill 1985; Losos et al. 1993; Miles 1994; Van Damme et al. 1997).

The present paper compares functional morphological aspects of the locomotor apparatus of two closely related lizard species (the same superfamily: Gekkota; see Grismer 1988) with radically different locomotor habitats. *Eublepharis macularius* (Blyth, 1854) is a generalised ground-dwelling gecko (see Grismer 1988). *Gekko gecko* (Linné, 1758), on the other hand, is a highly specialised climber on vertical substrates (see Russell 1975). Both lizards show clear preferences for either horizontal (*E.*

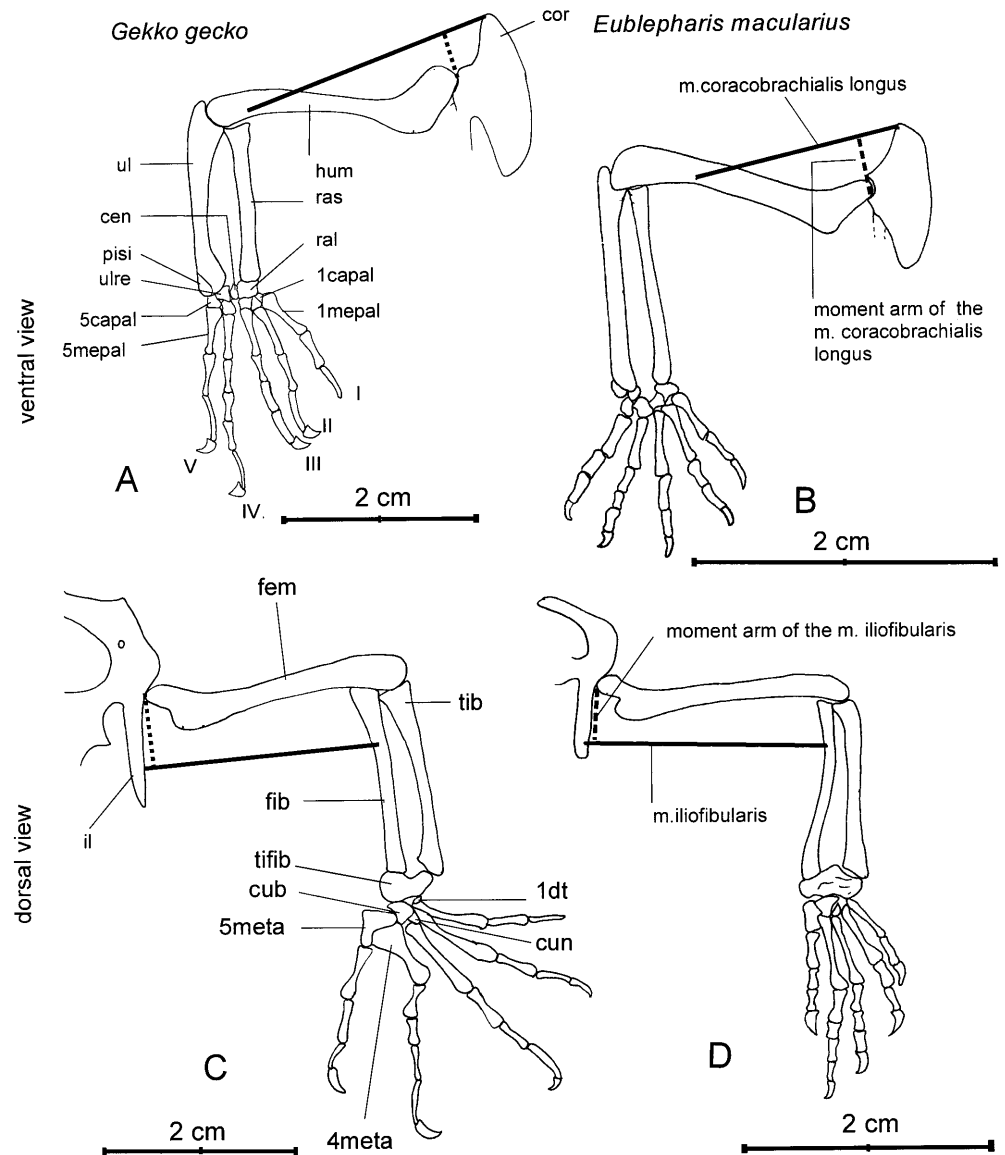
P. Aerts is a research director of the Fund for Scientific Research Flanders. A. Herrel is a postdoctoral research associate of the Fund for Scientific Research Flanders. This study is supported by the FWO-grant G. 0221.96 and GOA-BOF UA 1999.

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Table 1 Morphometric characterisation of the specimens used in this study. (E1 *Eublepharis macularius* 1, E2 *E. macularius* 2, G1 *Gekko gecko* 1, G2 *Gekko gecko* 2

Morphometrics	E1	E2	G1	G2
Mass (g)	57.00	51.70	97.07	102.65
Snout-vent length (cm)	13.54	12.15	15.88	16.80
Body length (cm)	24.01	20.90	30.13	31.20
Humerus length (cm)	1.75	1.74	2.35	2.37
Radius length (cm)	1.32	1.33	1.69	1.71
Ulna length (cm)	1.51	1.49	1.96	1.98
Femur length (cm)	2.02	2.04	2.78	2.79
Tibia length (cm)	1.53	1.52	1.93	1.94
Fibula length (cm)	1.61	1.59	1.89	1.91
Manus length (cm)	1.32	1.36	1.77	1.75
Pes length (cm)	1.84	1.94	2.99	3.01

Fig. 1 Drawing of the skeletal parts exemplifying the determination of the moment arm length (dashed line) in *Gekko gecko* (A,C) and *Eublepharis macularius* (B,D). Skeletal segments were drawn in the same configuration. Muscles are represented as a line of action from the centre of origin to the centre of insertion. The moment arm lengths of the muscles situated at the dorsal side of the pectoral and pelvic girdles and of those at the extensor side of the legs were determined in a dorsal view, those of the ventral side of the girdles and of the flexor side of the legs in frontal view. A,B Representative example (m. coracobrachialis longus) of the determination of the muscle moment arm on a drawing of the front limb in a frontal view. C,D Representative example (m. iliofibularis) of the determination of the muscle moment arm on a drawing of the hind limb in a dorsal view. 1capal First carpal, 5capal fifth carpal, 1dt most distal first tarsal, 1mepal first metacarpal, 5mepal fifth metacarpal, 4meta fourth metatarsal, 5meta fifth metatarsal, I–V digits, cen centrale, cor coracoid, cub cuboid (fourth distal tarsal), cun cuneiform, fem femur, fib fibula, hum humerus, ral radiale, ras radius, tib tibia, tiffib tibiofibulare, pisi pisiform, ul ulna, ulre ulnare



macularius) or vertical (*G. gecko*) substrates and are rarely observed on the other substrate.

In addition to the general considerations just mentioned, such fundamental differences in locomotion habit are hypothesised to go along with further specialisations

of the limb musculature. The vertical climber should possess more forcefully built (i.e. large cross-sectional area (CSA), favourable lever arms) limb retractors, crossing the shoulder and hip joints, as these have to provide propulsive forces, not only to surmount inertia, but

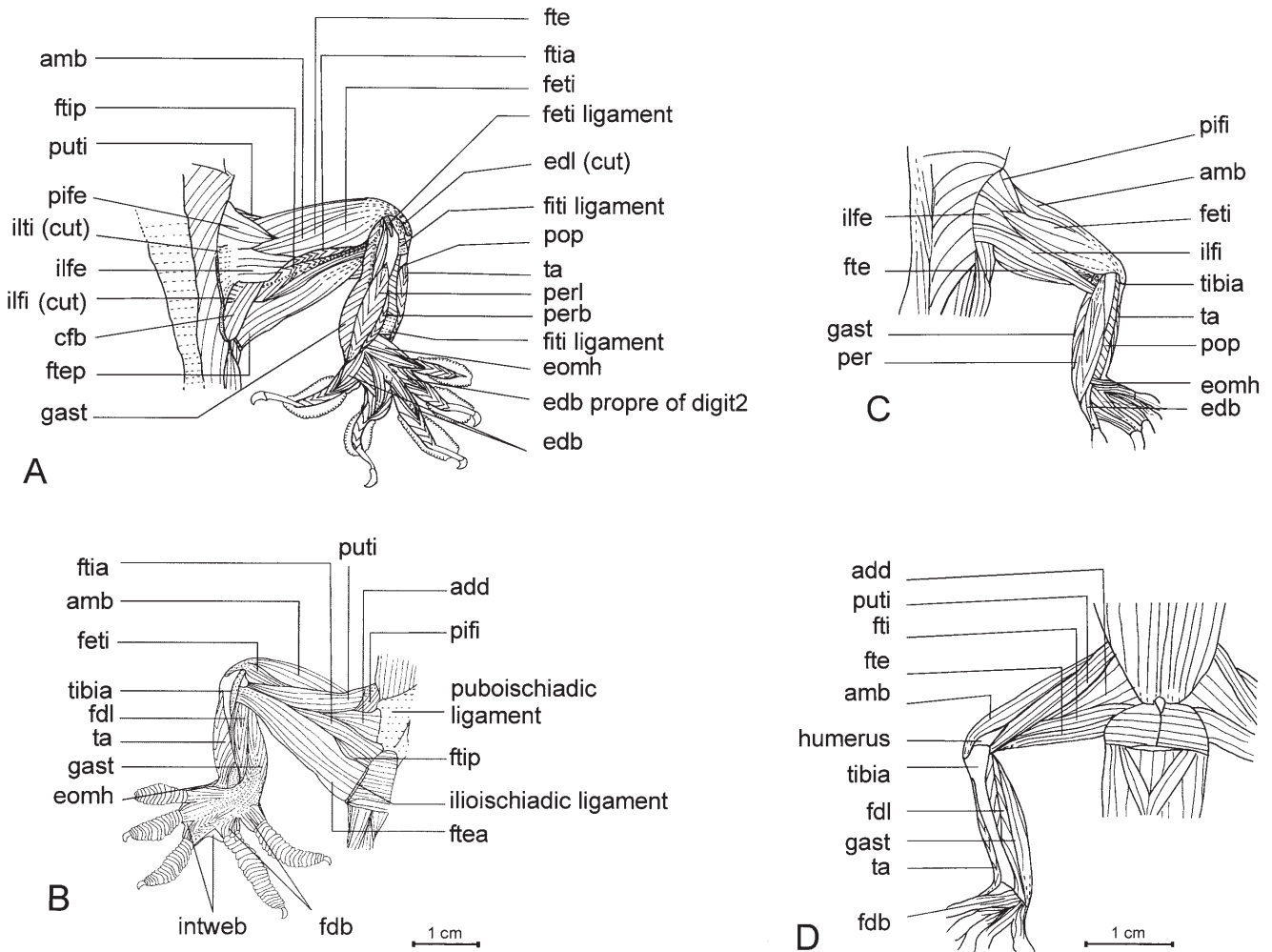


Fig. 2 Hindlimb musculature of *G. gecko* (**A, B**) and *E. macularius* (**C, D**). **A, C** Extensor side, the superficial muscles have been cut. **B, D** Deeper view showing the flexor muscles after removal of the m. flexor tarsi and the m. puboischiotibialis. *add* m. adductor femoris, *amb* m. ambiens, *cfb* m. caudofemoralis brevis, *edb* m. extensor digitorum brevis, *edl* m. extensor digitorum longus, *eomh* m. extensor ossis metatarsi hallucis, *fdb* m. flexor digitorum brevis, *fdl* m. flexor digitorum longus, *feti* m. femorotibialis, *fiti* fibulotibialis ligament, *fte* m. flexor tibialis externus, *ftea* m. flexor tibialis externus anterior, *ftip* m. flexor tibialis internus posterior, *gast* m. gastrocnemius, *ilfe* m. iliofemoralis, *ilfi* m. iliofibularis, *intweb* interdigital tendinous web, *per* m. peroneus, *perb* m. peroneus brevis, *perl* m. peroneus longus, *pife* m. puboischiofemoralis externus, *pifi* m. puboischiofemoralis internus, *pop* m. popliteus, *puti* m. pubotibialis, *ta* m. tibialis anterior

also to counteract gravity. Furthermore, since vertical climbing requires tension by the front legs to avoid backwards tumbling when the hind legs push for propulsion (see for instance Alexander 1992), stronger elbow flexors should be present in *G. gecko*. In contrast, the level-running species with the more parasagittal, erect gait should possess the better-developed elbow and knee extensor muscles, as these have to sustain the body weight throughout locomotion (body elevated from the substrate), in addition to their role in propulsion.

Finally, it can be expected that the presence of the adhesive toe pads in *G. gecko* also induces differences at the level of the wrist and ankle extensors. In level-running lizards, propulsion is partly powered by extension of these joints when foot posture changes from plantigrade to digitigrade at the end of the stance phase (see for instance Fieker and Jayne 1998; own observations for several lizard species, including *E. macularius*). This does not occur in *G. gecko* because this species first lifts the phalanges (hyperextension) in order to detach the adhesive pads from the substrate (Russell 1975). Therefore, it is hypothesised that, even if ankle or wrist extension has a role in propulsion, the involved joint moments in *G. gecko* are small with respect to the total propulsive moment because of the short moment arms (i.e. length of the tarsus and carpus).

To test the hypotheses formulated above, the morphology and morphometrics of the leg musculature of both species are investigated and compared. The premises about differential muscle development are assessed by determination of normalised moments (see Materials and methods) exerted by muscles about the hip/shoulder, knee/elbow and wrist/ankle joints. The aim of this study is thus to test the predictions on morphological adaptations of two geckoes to their preferred orientation in the field of gravi-

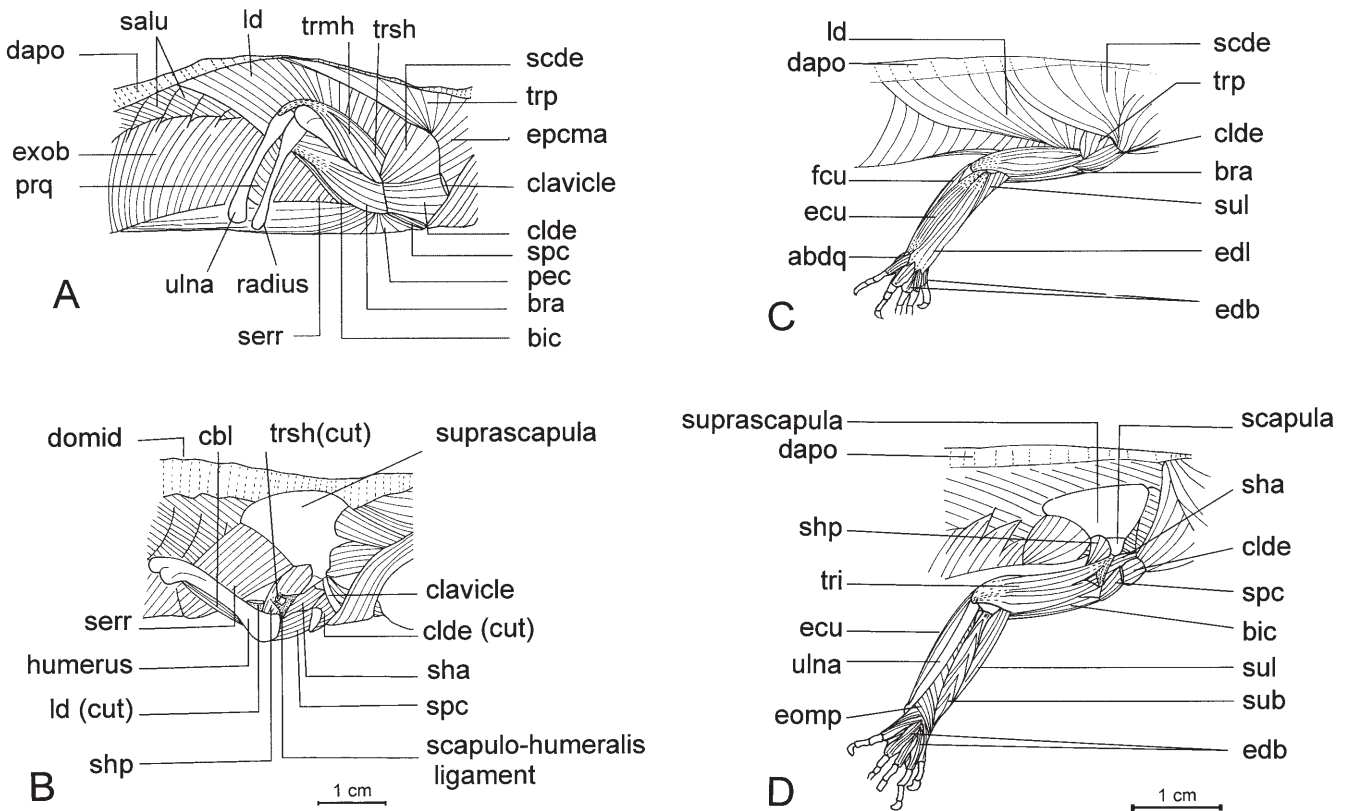


Fig. 3 Front limb morphology of *G. gecko* (A, B) and *E. macularius* (C, D). A, C Superficial musculatures of the shoulder joint and upper arm. A Muscles associated with forearm have been removed. B, D Deep dorsal view of the shoulder muscles. *abdq* M. abductor digiti quinti, *bic* m. biceps, *bra* m. brachialis, *clde* m. clavodeltoideus, *dapo* dorsal aponeurosis, *domid* dorsal midline, *ecu* m. extensor carpi ulnaris, *edb* m. extensor digitorum brevis, *eomp* m. extensor ossis metacarpi pollicis, *epcma* m. episternocleidomastoideus, *exob* m. obliquus externus, *fcu* m. flexor carpi ulnaris, *ld* m. latissimus dorsi, *pec* m. pectoralis, *prq* m. pronator quadratus, *salu* m. sacrolumbalis, *scde* m. scapulodeltoideus, *serr* m. serratus, *sha* m. scapulo-humeralis anterior, *shp* m. scapulo-humeralis posterior, *spc* m. supracoracoideus, *sub* m. supinator brevis, *sul* m. supinator longus, *tri* m. triceps, *trp* m. trapezius, *trmh* m. triceps medial humeral head, *trsh* m. triceps scapular head

ty. Absence of the expected adaptations should then point at behavioural (neuromotoric) compensations.

B. Materials and methods

Two specimens of the species *G. gecko* (G1, G2) and of *E. macularius* (E1, E2) were used in this study (Table 1). Animals were killed by intramuscular administration of an overdose of Ketalar (50 mg/ml), fixed in a 30% aqueous formalin solution and stored in 70% ethanol. The animals used were healthy and showed normal running or climbing abilities. The fore- and hindlimbs of the specimens were dissected and drawings were made using a Wild M3Z stereomicroscope equipped with camera lucida. During the excision of muscles, special attention was paid to the origin and insertion sites and the pennation angles.

From a functional point of view, the moments about specific joints rather than the forces which can be generated by individual muscles are of importance. Muscle moments not only depend up-

on the contraction forces [related to the CSA of the muscle bellies], but also on the muscle architecture (pennation), the general orientation of the muscle-tendon systems (line of action) and on the instantaneous limb geometry. In this study, an effort is made to assess the capabilities of the limb musculature of the climbing and level-running species (in addition to the morphological characterisations) by estimating muscle moments for a standardised limb configuration as described further.

Each isolated muscle was preserved in 70% ethanol. Muscles were blotted dry and weighed (± 0.0001 g) using a Mettler (College) balance. To dissolve the connective tissue and segregate muscle fibres, muscles were placed in 30% nitric acid for 24 h. A minimum of 20 fibres per muscle was selected at random and drawn using a stereomicroscope and camera lucida. The selected fibres were then digitised (Hipad digitiser; Houston Instruments) and the average length per muscle bundle was calculated. The CSA (cm^2) of the muscles was estimated as the mass (g) divided by the mean fibre length (cm), assuming a muscle density of 1 g/cm^3 . In this way, CSA is measured perpendicular to the muscle fibres, irrespective the fibre orientation. Pennation angles were estimated by dissecting away the external layer of fibres and drawing the direction of the internal fibres. The angle of pennation (α) was then measured relative to the muscle tendon or aponeurosis.

To estimate the moment arms of the muscles in a standardised leg configuration one of two procedures was used, depending upon the position of the muscle with respect to the joint. When the muscle-tendon system crosses the joint externally as acting along a pulley (i.e. sliding over the condylar surface), a circle is fitted to a lateral view drawing of the condylar profile and its radius is treated as the moment arm of the muscle involved. This procedure is used for the elbow, wrist, knee and ankle extensors. In all other cases, limb configurations were made identical for both species by positioning all limb segments in a single plane; the upper legs (respectively humerus and femur) perpendicular to the midsagittal plane and the lower legs perpendicular to the upper parts of the limbs (i.e. representing a sprawling configuration). Schematic drawings of the appendicular skeleton G2 and E1 were made (Fig. 1) and the lengths of the moment arms (MAL) were determined as the perpendicular distance from the joint centre to

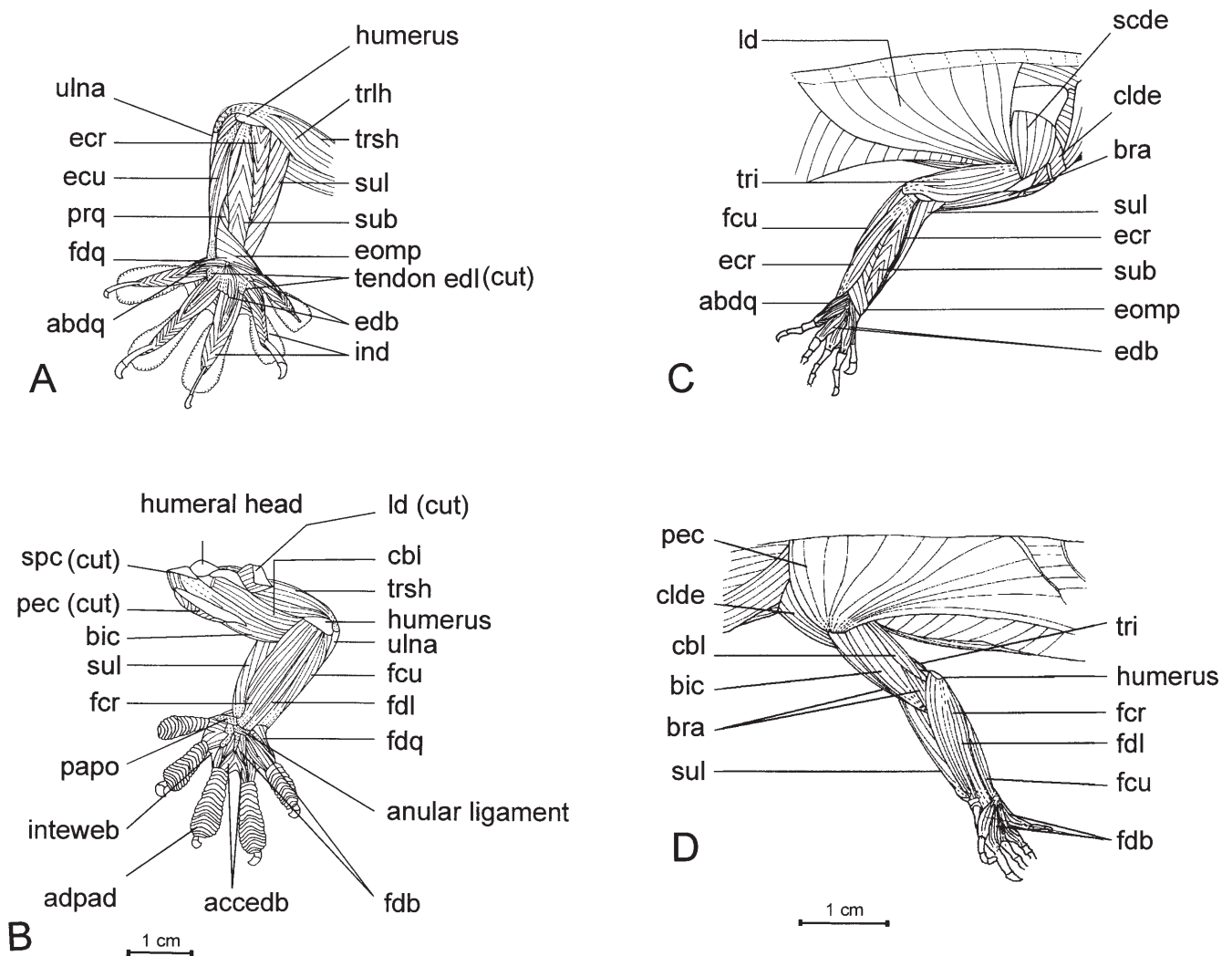


Fig. 4 Forearm musculature in *G. gecko* (**A**, **B**) and *E. macularius* (**C**, **D**). **A**, **C** Extensor side with the m. extensor digitorum longus removed. **B**, **D** Superficial view of the flexor side. *accedb* Accessory heads of m. extensor digitorum brevis, *adpad* adhesive pad, *cbl* m. coracobrachialis longus, *ecr* m. extensor carpi radialis, *fcr* m. flexor carpi radialis, *fdq* m. flexor digiti quinti, *ind* mm. interossei dorsales, *inteweb* interdigital tendinous web, *papo* palmar aponeurosis, *trlh* m. triceps lateral humeral head; for others abbreviations see table 5 and Fig. 3

the line of action of the considered muscle (for some examples see Fig. 1). Certainly, the moment arms thus obtained are only rough estimates, but by treating both species in a strictly identical way, these estimates are considered to be useful for the purpose of comparing muscular capabilities through muscle moments.

Making use of a generalised maximal muscle stress of 25 N/cm² (Herzog 1994), maximal moments exerted by the muscles were calculated as:

$$\text{muscle moment} = \text{MAL} \times \text{CSA} \times 25 \times \cos \alpha.$$

Given the high similarity in linear dimensions of the leg segments of both specimens of *G. gecko* and *E. macularius*, respectively (deviation amounts maximally to about 1%; see Table 1), the same specific moment arms were used to estimate the individual muscle moments. To allow comparison of the moments in both species, they were normalised to the overall general limb dimensions through division by the total muscular weight (i.e. mass \times g) of the considered limb and by the summed lengths of femur and tibia,

and humerus and radius, respectively. Muscle masses and CSA (averaged for the two specimens) were expressed as the percentage of the total mass and the total CSA per limb, respectively (see Table 6). Averaged fibre lengths were normalised to the length of the skeletal elements with which they are associated (see Table 6).

High-speed video recordings (NAC-1000; frame rate: 500 Hz) of climbing *G. gecko* and running *E. macularius* specimens were examined to get a qualitative impression of the leg movements involved in their preferred locomotion mode. Attention is paid to the flexion/extension movements of the major leg joints (hip/shoulder, knee/elbow and ankle/wrist).

C. Results

I. Morphology

The description of the appendicular musculature is summarised in Tables 2 and 3. In general, the nomenclature of Romer (1956) is used, unless indicated otherwise. The descriptions are based on *E. macularius*, as it shows the largest number of plesiomorphic characteristics of both groups of geckoes (Grismer 1991). Where present, differences with the more derived *bauplan* of *G. gecko* are pointed out.

Table 2 Myology of the hindlimb

Muscles	Origin	Insertion	Differences with <i>G. gecko</i> when they occur
<i>Inserting on the femur:</i>			
<i>M. caudofemoralis longus</i>	Muscularly from the first four caudal vertebrae	Tendon winds the trochanter and inserts, after bifurcating, proximoventrally on the shaft of the femur	Origin: first five caudal vertebrae
<i>M. caudofemoralis brevis</i>	Transverse processes of the last two sacral vertebrae	Proximoventrally on the shaft of the femur	Origin: posterior margin of the ilium
<i>M. adductor femoris</i>	Puboischiadic ligament	Posterolateral surface of the femur	
<i>M. iliofemoralis</i>	Muscularly from the antero-lateral margin of the ilium	Proximally on the dorsal side of the femur	
<i>M. ischiotrochantericus</i>	Ischial tuberosity	Proximal edge of the trochanter	Insertion: distal edge of the trochanter
<i>Inserting on the tibia and fibula:</i>			
<i>M. iliotibialis</i>	Lateral surface of the ilium; by a broad aponeurosis	Tendinously on the lateral surface of the tibial condyle	
<i>M. ambiens</i>	Aponeurotically from both the pubis and the proximoventral surface of the femur	Tendinously on the lateral surface of the tibial condyle	
<i>M. femorotibialis</i>	Femoral shaft; by four bellies which surround it	Tendinously on the lateral surface of the tibial condyle	
<i>M. iliofibularis</i>	Posteroventral iliac blade	By means of a wide tendon at the outer side of the fibular shaft	
<i>M. puboischiotibialis</i>	Pubic tubercle, the puboischiadic ligament and the ilioischiadic ligament	Tendinously and proximally on the tibial shaft	
<i>M. pubotibialis</i>	Pubic tubercle by means of an aponeurosis	Lateral tibial condyle	
<i>M. Flexor tibialis externus</i>	Ilioischiadic ligament	Tendinously on the proximal part of the tibia	Additional part arising from the ilioischiadic ligament and inserting onto the proximal olateral part of the tibia
<i>M. flexor tibialis internus</i>	Muscularly from the ilioischiadic ligament and the ischial tuberosity	Tendinously, laterally on the proximal head of the tibia	Additional part arising from ilioischiadic ligament. The tendons of both parts attach at the interarticular of the area knee joint
<i>Of the lower hindleg:</i>			
<i>M. extensor digitorum communis</i>	Anterior aspect of the peroneal condyle of the femur by means of a flat tendon	Ulnar side of metatarsals two and three	
<i>M. peroneus</i>	Partly tendinously (proximal) and partly muscularly from almost the fibula	Fifth metatarsal	Two slips
<i>M. tibialis anterior</i>	Entire anterior surface of the tibia	Tendinously on digit I	Contribution of the tendon to the lateral digital tendon
<i>M. flexor tarsi</i>	Nearly the entire tibia	Tendinously on the ventral side of the base of the fifth metatarsal	Origin only from the proximal part of the tibia
<i>M. flexor digitorum longus</i>	Peroneal condyle of the femur, the interarticular area of the knee joint and proximal portion of the fibula	Distalmost phalanx of digit V	
<i>M. pronator profundus</i>	Muscularly from the base of the fibula	Ventral side of the tibiofibular bone	

Table 2 (continued)

Muscles	Origin	Insertion	Differences with <i>G. gecko</i> when they occur
M. popliteus	Muscularly on the proximal part of the fibula	Partly muscularly and partly tendinously on the antero-lateral shaft of the tibia	
M. extensor digitorum brevis	Tibiofibular bone	Distalmost phalanx of digits I, IV and V	Origin from the cuboid
M. extensor ossis metatarsi hallucis (Sanders 1870)	Base of fibula	Dorsally on the metatarsal bone of digit I	
Mm. interossei dorsales			Well developed (see Russel 1975)
M. flexor metatarsi quinti	Tendinously from the distal extremity of the ventral surface of the tibiofibular	Ventral surface of the fifth metatarsal	
M. flexor digitorum brevis	Proximal extremity of the fifth metatarsal	Terminal phalanx	Insertion at the distal end of metatarsal one digit I, at the distal end of the second phalanx of digits III and IV and at the distal end of the first phalanx of digits II and V
Mm. interossei plantares	Proximally and medially on metatarsals one to four	Distally on the lateral side of the next metatarsal (two to five)	

Table 3 Myology of the forelimb

Muscles	Origin	Insertion	Differences with <i>G. gecko</i> when they occur
<i>Inserting on the humerus:</i>			
M. pectoralis	Interclavicular bone, ventral midline of the sternum and the xiphisternum	Lateral tuberosity of the humerus	
M. supracoracoideus	Anterior cartilaginous part of the coracoid bone	Tendinously on the proximal margin of the lateral tuberosity of the humerus	
M. coracobrachialis	Dorsal, central, and posterior regions of the coracoid bone	Musculously at the first half of the ventral side of the humerus	Origin: restricted to the central region of the coracoid
M. coracobrachialis longus	Posterior side of the coracoid	Ventral and above the inner condyle of the humerus	Insertion: distal most part of the humerus
M. latissimus dorsi	From an aponeurosis adjacent to the dorsal midline of the body	Tendinously and proximally on the dorsal surface of the humerus	Insertion is shifted to the lateral side of the humerus
M. scapulodeltoideus	Musculously from the antero-lateral surface of the suprascapula and the scapula, a second part arises musculously from the ventral and inner border of the clavicle	Tendinously on the deltopectoral crest of the humerus	
M. clavodeltoideus	Internal side of the interconnection between the clavicle and the interclavicle	Tendinously on the deltopectoral crest	
M. scapulohumeralis anterior	Muscularly from the anterior surface of the scapula and from the scapulocoracoid fenestra	Humeral shaft just distal to the medial tuberosity	
M. scapulohumeralis posterior	Posterior surface of the suprascapula and the scapula	Close to the medial tuberosity of the humerus	Insertion is just distal to the lateral tuberosity

Table 3 (continued)

Muscles	Origin	Insertion	Differences with <i>G. gecko</i> when they occur
M. coracohumeralis	Muscularly from the internal surface of the coracoid bone	Medial tuberosity of the humerus	
<i>Inserting on the radius and ulna:</i>			
M. biceps	Muscularly from the ventral surface of the coracoid	Tendinously part of the ulna and on the radius	
M. brachialis	Muscularly from the lateral and ventral sides of the humeral shaft	Partly muscularly and partly tendinously on the proximal sides of both radius and ulna	Origin is confined to the lateral side of the humeral shaft
M. triceps	Scapular part arises by a stout tendon from the lateral surface of the scapula and from the scapulohumeralis ligament. Medial part originates by means of two heads from the medial side of the humeral shaft	Olecranon process of the ulna	Scapular part is connected by a tendon to the posterior margin of the coracoid bone. An additional muscle belly arises from the lateral shaft of the humerus
M. supinator longus	Outer edge of the humerus	Lower two-thirds of the radius	
M. supinator brevis	Outer condyle of the humerus	Along the whole length of the radius	Origin is more proximal on the humerus
<i>Of the lower forelimb:</i>			
M. extensor digitorum longus	By a tendon from the ulnar condyle of the humerus	Proximal ulnar side of metacarpals two, three and four, respectively	Four distal tendinous branches inserting on both side of metacarpals two to four
M. extensor carpi radialis	Muscular from the ulnar condyle of the humerus	Wraps around the ventral and dorsal sides of the radial bone	Distal tendon passes between the radius and the radial to insert onto the latter element
M. extensor carpi ulnaris	Ulnar condyle of the humerus and the proximal part of the ulna	Mainly on the ulnare. A small expansion inserts on the first metacarpal	Insertion is restricted to the pisiform
M. flexor digitorum longus	Medial part of the ulnar condyle of the humerus and from the distal two-thirds of the ulna	On the terminal phalanges of digits I and II	
M. flexor carpi ulnaris	Ulnar condyle of the humerus and the entire laterodorsal border of the ulna	Pisiform	
M. flexor carpi radialis	Inner condyle of the humerus	Tendinously on the radial and muscularly on the distal part of the radius	
M. extensor digitorum brevis	Ulnare	Distalmost phalanx of digits I–V	Insertion at the distal end of the antepenultimate phalanx, except for digit I where it inserts of the first phalanx
M. extensor ossis metacarpi pollicis	Distal border of the ventral surface of the ulna	Radial border of metacarpal bone of the first digit	Some fibres of this muscle partly provide the origin of the radial branch of the M. interossei dorsales
M. abductor digiti quinti	Ulnare	Along the whole length of the ulnar edge of metacarpal five	
Mm. interossei dorsales			Well developed (see Russell 1975)
M. flexor digitorum brevis	Ulnare	Terminal phalanx	Insertion distally on the antepenultimate phalanx

Table 4 Summary of morphometric measurements of the major hindlimb muscles of the two *G. gecko* (G1 and G2) and the two *E. macularius* (E1 and E2) specimens. [*M* Mass (g), *Fl* mean fibre length (cm), *Pcs* physiological cross-section (cm²), *Pi* pennation angle (degrees), *asterisk* parallel-fibred, empty cells=muscle not present]

Abbreviations	Muscle names	G1				G2			
		M	Fl	Pcs	Pi	M	Fl	Pcs	Pi
Ilfe	Iliofemoralis	0.0585	0.4398	0.1330	*	0.0623	0.7955	0.0783	*
Pife	Puboischiofemoralis externus	0.1803	0.6250	0.2885	*	0.2728	0.9190	0.2969	*
Pifi	Puboischiofemoralis internus	0.1924	0.5024	0.3830	*	0.2879	0.9262	0.3108	*
Cfl	Caudofemoralis longus	0.5234	0.8981	0.5828	*	0.6471	0.9984	0.6481	*
Cfb	Caudofemoralis brevis	0.1185	0.4982	0.2379	*	0.1405	0.6594	0.2131	*
Add	Adductor	0.0446	0.8512	0.0524	*	0.0688	1.1398	0.0604	*
Ilti	Iliotibialis	0.2050	0.8579	0.2390	*	0.3025	1.2060	0.2508	*
Amb	Ambiens	0.0966	0.8255	0.1170	*	0.1838	0.9846	0.1867	*
Feti	Femorotibialis	0.1501	0.7468	0.2010	*	0.1829	1.0070	0.1816	*
Ilfi	Iliofibularis	0.1440	1.6850	0.0855	*	0.1582	1.3012	0.1215	*
Ftia	Flexor tibialis internus anterior	0.0449	0.9710	0.0462	15	0.0788	1.0949	0.0720	13
Ftip	Flexor tibialis internus posterior	0.0491	0.9399	0.0522	21	0.0854	0.8593	0.0994	22
Ftea	Flexor tibialis externus anterior	0.0840	0.6357	0.1321	12	0.1368	0.9122	0.1500	20
Ftep	Flexor tibialis externus posterior	0.2413	1.2132	0.1989	*	0.4081	2.0200	0.2020	*
Pit	Puboischiotibialis	0.4238	1.0056	0.4214	29	0.6446	1.6175	0.3985	31
Puti	Pubotibialis	0.0998	1.3129	0.0760	*	0.1324	1.7278	0.0766	*
Edl	Extensor digitorum longus	0.0695	1.0474	0.0664	*	0.0651	1.0900	0.0597	*
Tian	Tibialis anterior	0.0488	0.5743	0.0850	30	0.0782	0.6085	0.1285	25
Perl	Peroneus longus	0.0353	0.4792	0.0737	17	0.0716	0.6835	0.1047	10
Perb	Peroneus brevis	0.0251	0.3708	0.0672	22	0.0422	0.6226	0.0678	16
Gast	Gastrocnemius	0.0837	0.3913	0.2139	26	0.1502	0.5803	0.2588	21
Flta	Flexor tarsi	0.0204	0.6870	0.0297	*	0.0278	0.8053	0.0345	*
Fdl	Flexor digitorum longus	0.0852	0.7466	0.1141	18	0.1000	0.7412	0.1349	13

Abbreviations	Muscle names	E1				E2			
		M	Fl	Pcs	Pi	M	Fl	Pcs	Pi
Ilfe	Iliofemoralis	0.0232	0.6093	0.0381	*	0.0217	0.4350	0.0499	*
Pife	Puboischiofemoralis externus	0.0552	0.4387	0.1258	*	0.0680	0.5686	0.1196	*
Pifi	Puboischiofemoralis internus	0.0552	0.9714	0.0691	*	0.0511	0.8419	0.0607	*
Cfl	Caudofemoralis longus	0.0997	0.6838	0.1458	*	0.0899	0.8080	0.1113	*
Cfb	Caudofemoralis brevis	0.0189	0.3915	0.0483	*	0.0163	0.4571	0.0357	*
Add	Adductor	0.0216	0.7537	0.0287	*	0.0180	0.6559	0.0274	*
Ilti	Iliotibialis	0.621	0.5354	0.1160	*	0.0620	0.5229	0.1186	*
Amb	Ambiens	0.0482	0.6143	0.0584	*	0.0465	0.5032	0.0924	*
Feti	Femorotibialis	0.0910	0.5749	0.1583	*	0.0899	0.5521	0.1628	*
Ilfi	Iliofibularis	0.0290	0.9299	0.0314	*	0.0297	1.0507	0.0283	*
Ftia	Flexor tibialis internus anterior	0.0682	0.7782	0.0876	15	0.0619	0.7871	0.0786	9
Ftip	Flexor tibialis internus posterior								
Ftea	Flexor tibialis externus anterior								
Ftep	Flexor tibialis externus posterior	0.0652	1.0705	0.0609	*	0.0570	1.0749	0.0530	*
Pit	Puboischiotibialis	0.1117	0.9708	0.1151	25	0.1217	0.8978	0.1356	20
Puti	Pubotibialis	0.0288	1.1345	0.0254	*	0.0183	1.0958	0.0167	*
Edl	Extensor digitorum longus	0.0107	0.6037	0.0177	*	0.0157	0.6400	0.0245	*
Tian	Tibialis anterior	0.0143	0.7571	0.0120	16	0.0115	0.6717	0.0171	12
Perl	Peroneus longus	0.0309	0.3667	0.0843	16	0.0257	0.4588	0.0560	8
Perb	Peroneus brevis								
Gast	Gastrocnemius	0.0372	0.4979	0.0747	15	0.0301	0.3493	0.0862	14
Flta	Flexor tarsi	0.0158	0.5889	0.0268	*	0.0115	0.5686	0.0202	*
Fdl	Flexor digitorum longus	0.0440	0.4664	0.1398	*	0.0405	0.4743	0.0854	*

II. Morphometry

Tables 4 and 5 give the mass, fibre length, physiological cross-section and pennation angle for all muscles (except the intrinsic hand and foot muscles) for the four studied specimens. To allow comparison of the two species, Table 6 presents normalised values (averaged per species)

for mass, fibre length and physiological cross-section (see Materials and methods).

III. Moments

The normalised, standardised muscle moments (calculated as mentioned in Materials and Methods) are presented in

Table 5 Summary of morphometric measurements of the major front limb muscles of the two *G. gecko* (G1 and G2) and the two *E. macularius* (E1 and E2) specimens. [*M* Mass (g), *Ft* mean fibre length (cm), *Pcs* physiological cross-section (cm²), *Pi* pennation angle (degrees), *asterisk* parallel-fibred, empty cells=muscle not present]

Abbreviations	Muscle names	G1				G2			
		M	Ft	Pcs	Pi	M	Ft	Pcs	Pi
Ld	Latissimus dorsi	0.4899	1.4490	0.3381	*	0.6007	2.0553	0.2923	*
Scde	Scapulodeltoideus	0.1045	0.5562	0.1879	*	0.1633	0.8646	0.1889	*
Clde	Clavodeltoideus	0.1013	0.7932	0.1277	*	0.1985	1.0741	0.1848	*
Sha	Scapulohumeralis anterior	0.0131	0.7320	0.0179	*	0.0167	0.5763	0.0290	*
Shp	Scapulohumeralis posterior	0.0445	0.2384	0.1867	*	0.0261	0.4034	0.0647	*
Pec	Pectoralis	0.4982	1.3661	0.3647	*	0.6536	1.8617	0.3511	*
Spc	Supracoracoideus	0.0675	0.7128	0.0947	*	0.1633	1.1681	0.1398	*
Cbl	Coracobrachialis longus	0.0378	0.9720	0.0389	*	0.0551	0.9608	0.0573	*
Cbb	Coracobrachialis brevis	0.1085	0.4764	0.2278	*	0.1151	0.4352	0.2645	*
Bic	Biceps	0.0948	0.8626	0.1099	9	0.1324	0.7828	0.1691	13
Bra	Brachialis	0.0835	0.5076	0.1645	*	0.1227	0.5250	0.2337	*
Trsh	Triceps scapular head	0.0772	0.4144	0.1863	11	0.0854	0.4894	0.1745	10
Trlh	Triceps lateral humeral head	0.0618	0.6235	0.0991	25	0.0698	0.7255	0.0962	18
Trmh	Triceps medial humeral head	0.0752	0.4950	0.1682	16	0.0798	0.6220	0.1225	14
Edl	Extensor digitorum longus	0.0561	0.6545	0.0857	*	0.0929	0.8458	0.1098	*
Ecu	Extensor carpi ulnaris	0.0237	0.4079	0.0581	12	0.0337	0.4506	0.0748	11
Ecr	Extensor carpi radialis	0.0083	0.4925	0.0169	12	0.0068	0.4893	0.0139	15
Sul	Supinator longus	0.2000	0.6530	0.3063	17	0.2574	0.8297	0.3102	12
Sub	Supinator brevis	0.0356	0.4777	0.0745	13	0.0476	0.4425	0.1076	13
Fcu	Flexor carpi ulnaris	0.0401	0.2968	0.1351	20	0.0708	0.3195	0.2216	14
Fcr	Flexor carpi radialis	0.1045	0.6733	0.1552	9	0.1254	0.6558	0.1912	9
Fdl	Flexor digitorum longus	0.0618	0.5951	0.1038	18	0.0771	0.6755	0.1141	16

Abbreviations	Muscle names	E1				E2			
		M	Ft	Pcs	Pi	M	Ft	Pcs	Pi
Ld	Latissimus dorsi	0.0973	1.3753	0.0707	*	0.0739	1.1279	0.0655	*
Scde	Scapulodeltoideus	0.0315	0.5158	0.0611	*	0.0315	0.5368	0.0587	*
Clde	Clavodeltoideus	0.0408	0.9353	0.0436	*	0.0395	1.0041	0.0393	*
Sha	Scapulohumeralis anterior	0.0106	0.5152	0.0206	*	0.0081	0.4210	0.0192	*
Shp	Scapulohumeralis posterior	0.0115	0.2639	0.0436	*	0.0063	0.1950	0.0323	*
Pec	Pectoralis	0.1630	1.2452	0.1309	*	0.1584	0.8562	0.1850	*
Spc	Supracoracoideus	0.0367	0.5136	0.0715	*	0.0247	0.5224	0.0473	*
Cbl	Coracobrachialis longus	0.0192	0.8977	0.0214	*	0.0168	0.7383	0.0228	*
Cbb	Coracobrachialis brevis	0.0370	0.4922	0.0752	*	0.0318	0.3999	0.0795	*
Bic	Biceps	0.0300	0.5658	0.0530	*	0.0261	0.6381	0.0409	*
Bra	Brachialis	0.0337	0.8148	0.0414	*	0.0215	0.6897	0.0312	*
Trsh	Triceps scapular head	0.0331	0.2614	0.1266	12	0.0259	0.2836	0.0913	14
Trlh	Triceps lateral humeral head	0.0611	0.5138	0.1189	4	0.0456	0.5327	0.0856	7
Trmh	Triceps medial humeral head								
Edl	Extensor digitorum longus	0.0108	0.5238	0.0206	*	0.0107	0.5701	0.0188	*
Ecu	Extensor carpi ulnaris	0.0116	0.2150	0.0539	11	0.0145	0.2444	0.0593	15
Ecr	Extensor carpi radialis	0.0016	0.2995	0.0053	15	0.0016	0.2995	0.0053	11
Sul	Supinator longus	0.0270	0.7738	0.0349	9	0.0273	0.7297	0.0374	10
Sub	Supinator brevis	0.0154	0.3111	0.0495	17	0.0164	0.2745	0.0597	16
Fcu	Flexor carpi ulnaris	0.0187	0.2942	0.0636	10	0.0182	0.2672	0.0681	13
Fcr	Flexor carpi radialis	0.0153	0.5154	0.0297	7	0.0159	0.3534	0.0450	10
Fdl	Flexor digitorum longus	0.0310	0.4233	0.0732	*	0.0215	0.4744	0.0453	*

Figs. 5 and 6. They are calculated for the hip/shoulder, the knee/elbow and the ankle/wrist and grouped according to their flexion/extension function about the according joint. Biarticular muscles may show up twice in these figures. The small intrinsic foot/hand muscles are not considered.

D. Discussion

A consideration of the results at a gross morphological level (i.e. presence, position and orientations of muscles) indicates little support for the a priori biomechanical predictions. Moreover, origins, insertions and general shapes of the front and hind limb muscles are highly similar. Such similarities indicate the close phylogenetic relationship between the two species. Although all mus-

Table 6 Mean relative morphometric results in two *Gekko* and two *Eublepharis* specimens. Mass (*M. fract*) and physiological cross-section (*Pcsfract*) are expressed as a fraction of the total mass and the total physiological cross-section, respectively, in each limb. Fibre length (*Fibrelen*) is scaled to the femur and humerus for the muscles associated with the upper leg and upper arm, respectively, and the tibia and ulna for the muscles of the lower leg and lower arm, respectively. Empty cells (0.00) indicate that the muscle is absent. (*tri* Triceps)

Muscles	<i>Gekko</i>			<i>Eublepharis</i>		
	<i>M. fract</i>	<i>Pcsfract</i>	<i>Fibrelen</i>	<i>M. fract</i>	<i>Pcsfract</i>	<i>Fibrelen</i>
Upper leg:						
Life	1.69	2.65	22.14	2.47	3.11	25.72
Pife	6.13	7.29	27.67	6.80	8.63	24.81
Pifi	6.51	8.67	25.60	5.85	4.56	44.66
Cfl	16.13	15.31	33.99	10.42	9.01	36.75
Cfb	3.58	5.63	20.75	1.93	2.94	20.90
Add	1.53	1.40	35.68	2.17	1.97	34.72
Ilti	6.88	6.10	36.99	6.83	8.26	26.07
Amb	3.72	3.76	32.44	5.21	5.34	27.52
Feti	4.59	4.77	31.43	9.96	11.31	27.76
Ilfi	4.21	2.57	53.52	3.23	2.10	48.61
Ftia	1.65	1.46	37.02	7.15	5.84	38.55
Ftip	1.80	1.87	32.24	0.00	0.00	0.00
Ftea	2.97	3.51	27.74	0.00	0.00	0.00
Ftep	8.70	4.99	57.94	6.72	4.00	52.84
Pit	14.45	10.23	47.01	12.86	8.84	46.02
Puti	3.18	1.90	54.49	2.58	1.47	54.93
Lower leg:						
Edl	1.90	1.57	55.37	1.46	1.49	40.65
Tian	1.71	2.64	30.64	1.42	1.03	46.69
Perl	1.41	2.21	30.12	3.11	4.91	26.97
Perb	0.90	1.68	25.73	0.00	0.00	0.00
Gast	3.12	5.87	25.17	3.69	5.67	27.69
Flta	0.66	0.80	38.66	1.50	1.65	37.83
Fdl	2.56	3.10	38.54	4.65	7.87	30.74
Upper arm:						
Ld	19.66	9.57	74.24	12.41	5.80	71.52
Scde	4.74	5.71	30.10	4.61	5.10	30.07
Clde	5.23	4.72	39.56	5.87	3.53	55.41
Sha	0.54	0.71	27.72	1.36	1.70	26.75
Shp	1.34	3.84	13.60	1.28	3.22	13.11
Pec	20.66	10.85	68.39	23.51	13.54	60.04
Spc	3.97	3.54	39.85	4.43	5.03	29.60
Cbl	1.65	1.45	40.95	2.62	1.88	46.74
Cbb	4.07	7.45	19.31	5.01	6.60	25.49
Bic	4.06	4.22	34.86	4.09	3.99	34.40
Bra	3.67	6.02	21.88	3.98	3.08	42.99
Tri	8.16	12.85	23.67	12.01	17.93	22.74
Lower arm:						
Edl	2.63	2.96	38.08	1.57	1.68	36.46
Ecu	1.02	2.01	21.79	1.93	4.84	15.31
Ecr	0.28	0.47	24.92	0.23	0.46	19.97
Sul	8.22	9.34	37.63	3.98	3.09	50.12
Sub	1.49	2.75	23.35	2.33	4.67	19.52
Fcu	1.95	5.39	15.64	2.70	5.62	18.71
Fcr	4.15	5.24	33.73	2.29	3.20	28.96
Fdl	2.50	3.30	32.25	3.79	5.02	29.92

cles present in *E. macularius* are also present in *G. gekko*, some may be better developed in one of the species and possess accessory heads (e.g. the m. triceps in *E. macularius*). Still, for most of the appendicular musculature no major differences are observed. Exceptions are clearly the mm. interossei dorsales which are only observed in *G. gekko*, but are clearly related to the presence of adhesive pads in this species. The main function of these muscles is to realise a hyperextension of the digits and thus achieve the break of the scensors with the substrate (Gennaro 1969; Russell 1975).

However, by the introduction of functional components (e.g. CSA and pennation angles) into the morphological analysis, our biomechanical predictions are supported. Still, only when examining compound functional features, such as the joint moments, can the subtle adaptations of the locomotor morphology to substrate use in these species be fully appreciated. Despite the many abstractions and oversimplifications in our model and the fact that our calculations of joint moments are based on standardised leg configurations, the results nicely reflect the proposed hypotheses. Not only do the hip and shoul-

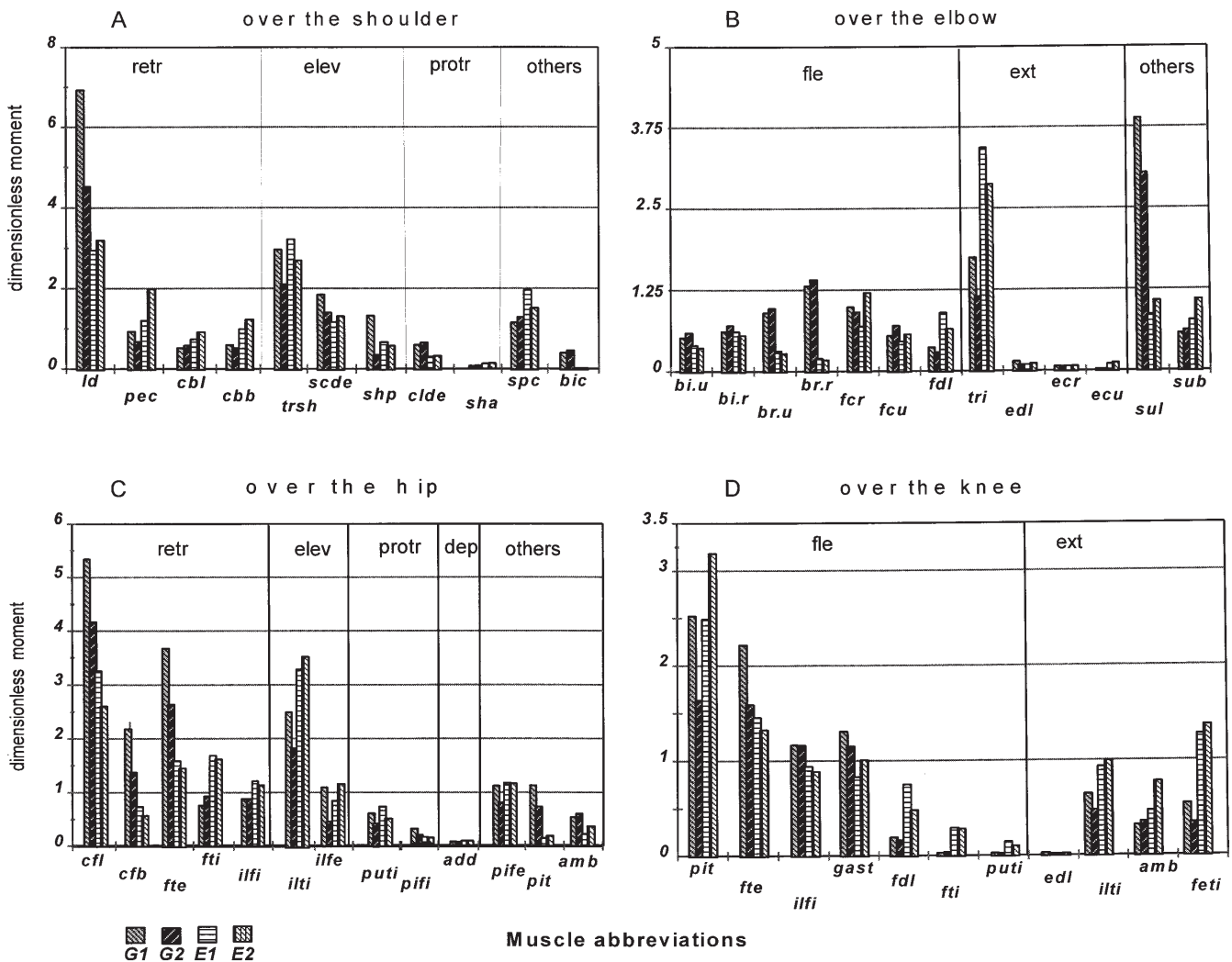


Fig. 5A–D Comparison of dimensionless joint moments in two *G. gecko* (*G1*, *G2*) and two *E. macularius* (*E1*, *E2*). Only the moments over the shoulder (**A**), over the elbow (**B**), over the hip (**C**) and over the knee (**D**) are given. *cbb* m. coracobrachialis brevis, *cfl* m. caudofemoralis longus, *dep* depressor, *elev* elevator, *ext* extensor, *fle* flexor, *pit* m. puboischiotibialis, *protr* protractor, *retr* retractor, for other abbreviations see tables 4, 5 and Figs. 3–5

der retractors deliver higher moments at their respective joints in the specialised climber, the knee and ankle extensors are also capable of delivering higher moments in the cursorial *E. macularius* (Fig. 5). Clearly such strong retractors are important during upward locomotion, especially as *G. gecko* generally keeps the two diagonal limbs in contact with the substrate during the majority of a stride cycle while climbing (Russell 1975; personal observations). By a synchronisation of humeral and femoral retraction, the front limb would exert pull by retraction of the humerus, while the hind limb pushes by retracting the femur of the diagonal limb. In this way, the thrust is shared between the two diagonal limbs. Strong knee and ankle extensors in *E. macularius*, on the other hand, allow the animals to elevate their bodies from the substrate, and assume a more parasagittal gait whereby friction of the body with the substrate is absent. The in-

crease of the joints moments can be and is in fact achieved by altering one or more functional characteristic of the muscles, such as the muscle mass (e.g. the m. iliobtibialis in *E. macularius*), the fibre length (e.g. shorter fibres in the m. caudofemoralis in *G. gecko*), the pennation angle (e.g. the m. biceps which is pennate in *G. gecko* but parallel fibred in *E. macularius*) or the moment arm length (e.g. the increased moment arm length of the m. gastrocnemius in *E. macularius*; see Tables 4–6).

Additionally, for the forearm flexors the results also seem to support the biomechanical predictions. As climbers on vertical substrates tend to push themselves away from the substrate while pushing on the hind legs, pull has to be exerted by the forelimbs. Indeed, the moments of the majority of elbow flexors are higher in *G. gecko*. Finally, unambiguous support for the last prediction (see Introduction) is provided when considering the ankle and wrist joints. All extensors crossing these joints are capable of delivering higher moments in the cursorial species as predicted. The presence of adhesive pads in *G. gecko*, which greatly increase its clinging abilities, apparently constrains the use of wrist/ankle extension to increase propulsive forces. Given the importance of ankle

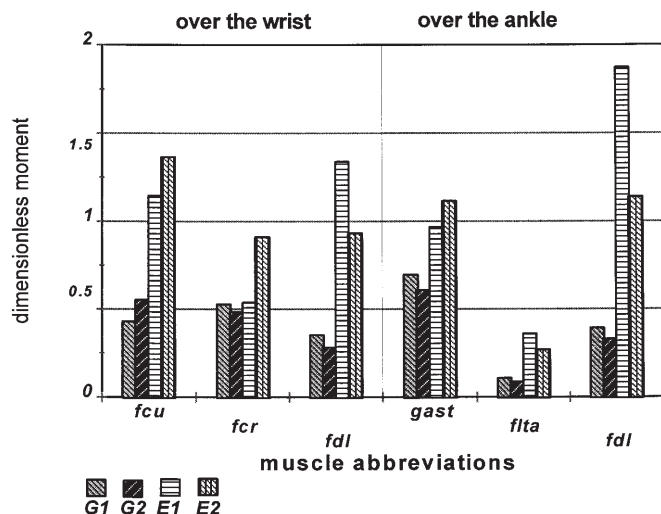


Fig. 6 Comparison of the dimensionless joint moments over the wrist and ankle joints in *G. gecko* and *E. macularius*. Muscles are grouped according to their predominant function during locomotion. *fta* m. flexor tarsi, for others abbreviations see tables 4, 5 and Figs. 2, 4

extension during fast running (Fieler and Jayne 1998), this should result in a decreased performance during level running in *G. gecko*. Although the actual changes in morphological characteristics remain small (Tables 2–6) the effects of these changes result in large differences in the muscular performance across specific joints.

The strong overall morphological similarities in the leg musculature of two closely related gekkotan lizards, supports the well-established view that, in general, the *bauplan* of the appendicular musculature is highly conserved within and among lizard families (Peterson 1984). This apparent phylogenetic inertia masks any direct correlation between morphology and habitat use in the animals considered here. On the other hand, morphological similarities might also be due to the fact that even specialists (e.g. climbers) must be able to use other locomotor habitats too (e.g. level running; see Snyder 1954; Hildebrand 1974; Losos et al. 1993). Yet, despite this morphological rigidity at first sight, the animals seem highly adapted to their preferred substrate when considering the functional parameters of the appendicular musculature. Indeed the functional properties of the limb muscles in both species closely match the a priori predictions based solely on biomechanical principles. Clearly, to pin down adaptations at the morphological level when considering the locomotor apparatus, quantitative components should be taken into account, and the functional or mechanically relevant features should be integrated in a comparative analysis.

These observations may have consequences for other studies where correlations between habitat use and locomotor morphology are examined. If even in extreme specialists, such as the animals considered here, adaptations are masked by the overall conserved nature of the *bauplan* of the appendicular structures, comparisons between less-specialised species are especially prone to

these problems (see also Losos and Miles 1994; Wainwright 1994; Lauder 1996). The risk of classifying animals with different habitat preferences which show no overall morphological differences as generalists (but which may be highly specialised at a functional level) may become real. Again this prompts the need for functional (e.g. including estimates of muscle moments), instead of pure descriptive morphological analyses.

The results gathered here might also have some implications in an evolutionary context. Whereas large changes in the limb musculature (existence or absence of new muscles) might induce sudden and even large decreases in the performance of the organism, more subtle changes in the functional properties of the muscles themselves do not induce such drawbacks and still allow an optimisation of the locomotor morphology to the habitat most used. In such a hypothetical evolutionary scenario, changes would occur gradually and with small increments, without decreases in the performance of the organism. Given the already large variation in some functional characteristics such as fibre lengths, pennation angles and mass, selection might theoretically lead in a relatively short period of time to an increase in the muscular performance which in turn can be expected to be linked to the predominant mode of locomotion of the animals considered.

Although some clear adaptations to the climbing locomotor habitus are thus observed in *G. gecko*, additional kinematic (e.g. Reilly and Delancey 1997a,b; Fieler and Jayne 1998; Irschick and Jayne 1998; Van Damme et al. 1998) and performance (Losos et al. 1993, 1997; Miles et al. 1995; Van Damme et al. 1997) analyses should be conducted to examine how specialised climbers exploit the observed differences in the functional properties of the appendicular musculature.

Acknowledgements We are grateful to Ms. Jeanine Fret for her assistance in preparing and correcting the manuscript and proofs. We are also thankful for the valuable comments of the anonymous referees.

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