

Full Length Research Paper

Comparative study of the osteology and locomotion of some reptilian species

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The aim of this study is to show the osteological characters of the fore- and hind-limbs and the locomotion features in some reptilian species: *Laudakia stellio*, *Hemidactylus turcicus*, *Acanthodactylus scutellatus*, *Chalcides ocellatus*, *Chamaeleo chamaeleon*, collected from different localities from Egypt desert and *Varanus griseus* from lake Nassir in Egypt. In the studied species, the fore- and hind-feet show wide range of variations and modifications as they play very important roles in the process of jumping, climbing and digging which suit their habitats and their mode of life. The skeletal elements of the hand and foot exhibit several features reflecting the specialized methods of locomotion, and are related to the remarkable adaptations. Locomotion is a fundamental skill for animals. The animals of the present studies can take various forms including swimming, walking as well as some more idiosyncratic gaits such as hopping and burrowing.

Key words: Lizards, osteology, limbs, locomotion.

INTRODUCTION

In vertebrates, the appendicular skeleton provides leverage for locomotion and support on land (Alexander, 1994). The major skeletal elements serving in these roles are collectively known as "long bones" because their longitudinal dimensions typically exceed the transverse ones (Marieb and Mallat, 1992). These bones include the femur, tibia, fibula, metatarsi, and phalanges of the hind limb, and the humerus, radius, ulna, metacarpi, and phalanges of the forelimb, and the femur, tibia, fibula, metatarsi, and phalanges of the hind limb. At the same time, there is a gradual reduction or loss of some bones between reptilian species (Romer, 1956; Stephenson, 1960; Jordan, 1970; Mohammed, 1990a, b).

In the skinks, the pectoral girdle has median cruciform interclavicle and paired clavicles (Mohammed, 1988b, 1990b). Gasc (1984) illustrated that in pygopoidids (Gekkota), scincids (Scincomorpha) and anguids (Angimorpha), the reduction of the dermal pectoral girdle always affects the interclavicle first, which may disappear while the clavicles persist. Stephenson (1960) recorded that the carpus elements consist of the radiale, ulnare, centrale and the carpalia 1 to 5 in several geckos. There is a radiale and an ulnare for the articulation of the radius and ulna, respectively, with a proximal central situated between them in the geckos *Stenodactylus slevini*, *Stenodactylus khobarensis* and *Stenodactylus sthenodactylus* (Mohammed, 1988a).

In most tetrapoda, the pelvic girdle is attached to the axial skeleton through the ilia articulating with the sacral vertebrae (Raynaud et al., 1975a, b; Romer and Parsons, 1977). In reptiles, the pubis, ischium and ilium are quite distinct or indistinguishably fused. Separation of these elements was noted in juvenile forms of different New Zealand geckos (Stephenson, 1960) and in other investigated lizards (Mohammed, 1990a, b; El-Wetery, 1992; EL-Gharib, 1994; Abo-Eleneen, 2005). The elements of pelvic girdle may be completely fused or unfused in geckos (Mohammed, 1988b) as also in lacertids (EL-Wetery, 1992; Abo-Eleneen, 2005).

The primitive tetrapod structure of the tarsus and metatarsus has been associated with the ability to grasp the substratum by opposing digits one and five

(Robinson, 1975). In the markedly asymmetrical foot of most lizards, digits one to four of the pes are essentially parallel and their metatarsals are enclosed in a "common bag of skin" (Robinson, 1975) with digit five being markedly deviant from this (Robinson, 1975; Rewcastle, 1983). Generally, in lizards, the digits have important functions in climbing, burrowing or digging and therefore the anatomy of the feet is a complex one (Russell, 1986; Russell and Bauer, 1988). Russell (1981) demonstrated that the vascular system of the digits of the Tokay *Gekko gekko* is more complex than it has been suspected, which suggests that it is intimately involved in the process of adhesion.

The understandings of phalangeal formula evolution in reptiles (Greer, 1991) has greatly benefited from consideration of comparative data and development at lower taxonomic levels (Shapiro, 2002; Shapiro et al., 2003), rather than comparisons among model organisms. The paraphalangeal elements are unique to gekkonid lizards and were first noted by Wellborn (1933). She provided a reasonably detailed gross morphological account of paraphalanges of five genera (*Ptychozoon*, *Gehyra*, *Uroplatus*, *Hemidactylus* and *Lygodactylus*). Generally, in geckos, the paraphalanges are associated with the pes digits or with digits of the manus and pes. In addition, the paraphalangeal elements are widespread in several geckos but not universal among gekkonid lizards (Wellborn, 1933; Russell, 1981, 1986; Russell and Bauer, 1988; Mohammed, 1988b, c, 1991b). Stephenson (1960) reaffirmed their presence in *Gehyra* and *Hemidactylus*.

In general, lizards are variable in the presence or absence of sesamoids associated with the elbow and knee (Russell and Bauer, 1988; Mohammed, 1991b; Abo-Eleneen, 2005). In some cases, the sesamoids appear to be involved in grasping abilities of foot associated with digging and climbing modifications. The mechanical effect of sesamoids increases the leverage of muscles at the joint which may explain the inverse

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development of some bony prominences and nearly sesamoids as described by Haines (1969) and Alexander and Dimery (1985). Mathur and Goel (1976) showed the ventral sesamoids of the sole in *Calotes vesicolor*. Also, a pisiform was recorded in all early tetrapods with ossified hands (Romer, 1956), New Zealand geckos (Stephenson and Stephenson, 1956), lizards (Haines, 1969) as well as geckos (Mohammed, 1988c). The palm and sole sesamoids are recorded in *Calotes vesicolor* (Mathur and Goel, 1976), and *Gymnodactylus kotschyi*, *Hemidactylus flaviviridis*, *Ptyodactylus hasselquisti*, *Stenodactylus petrii* and *Tarentola annularis* (Mohammed, 1986, 1988c). The present patellae are recorded in *Acanthodactylus boskianus* (Abo-Eleneen, 2005).

Movement in terrestrial tetrapodal vertebrates is brought about by the actions of four, or rarely two, limbs and a corresponding shift in the centre of gravity. The two main phases of limb activity are propulsion (stance, support) and recovery (swing, transport), and together they constitute a full limb cycle (stride). The locomotor cycle encompasses the completion of all four limb cycles (Sukhanov, 1974). Locomotion includes several components which may be important for survival. Maximal attainable speed, acceleration capability, endurance and maneuverability or different locomotor modes (for instance, climbing versus level-running) are examples of locomotion. Evolutionary optimisation of performance of one component may have a negative effect on the performance in another, because two functions might involve radically different requirements with respect to design traits such as muscle type, skeletal proportions, etc. High speeds and accelerations, for instance, can be expected to be important for both prey capture and predator evasion (Arnold, 1984; Garland and Losos, 1994).

The limbs play a very different role in lizards as they do in some robots acting to keep the centre of mass at a constant vertical height through out the stance phase (Alexander, 1990). The limbs of terrestrial tetrapods play a function to support body weight and to regulate forward impulsion (Willey et al., 2003). They also have an important role in enabling energy saving mechanisms to reduce muscular effort during terrestrial locomotion.

The present study may provide a fair knowledge concerning the skeletal elements of the hand and foot in some reptilian species that exhibit several features reflecting the specialized methods of locomotion, and are related to the remarkable adaptations of claws, fringes, scales and sesamoids. This may guide a comparative basis for reptilian phylogeny.

MATERIALS AND METHODS

Adult reptilians of the present study were collected from different locations from Egypt desert and lake Nasser then they were transported to Zoology Department, Faculty of Science, Beni-Suef University. They were identified according to Benton (1997) and Saleh (1997) then the animals were narcotized, labeled, injected with formalin and preserved in glass jars with 10% formalin solution. Pectoral and pelvic girdles, fore- and hind-limbs of reptilian species were dissected and separated under a dissecting microscope by the aid of very fine sessors. To stain the skeletal systems, firstly the skin of the present species was removed by the aid of a fine dissecting instrument. Secondly, the whole mounts of the present lizards were stained with the double-stained alcian blue and alizarin red according to the method of Dingerkus and Uhler (1977).

Alcian blue (Mallory, 1944)

To illustrate the developing cartilaginous pattern of limbs and girdles, the whole reptilians were stained in a solution of 80 ml ethanol (95%), 20 ml glacial acetic acid

and 15 mg alcian blue 8GN. Small specimens were stained for 24 h, hydrated in descending series of ethyl alcohol and in water for a period of 7 days with several changes. The soft tissue was completely destained and the blue cartilage became discernable from the other tissue after maceration in weak 0.1 KOH.

Alcian blue-Alizarin red (Dingerkus and Uhler, 1977)

The previous stained specimens were transferred to 0.1% KOH containing 0.1% Alizarin red-S to turn the solution deep purple, stained for 24 h, until the shafts of the thickest long bones become uniformly deep red. Then the specimens were transferred to a series of 0.1% KOH and glycerin (3:1, 1:1, 1:3), followed by fully glycerin, for approximately 24 h in each step. Few crystals of thymol were added to the pure glycerin to inhibit mold and bacteria, after which the specimens were stored in a cool and dark place. The stained samples were examined and photographed under Leica Sterio microscope. The osteological measurements were recorded for Agamidae (*Laudakia stellio*), Gekkonidae (*Hemidactylus turcicus*), Lacertidae (*Acanthodactylus scutellatus*), Scincidae (*Chalcides ocellatus*), Varanidae (*Varanus griseus*), and Chamaeleontidae (*Chamaeleo chamaeleon*).

The locomotion cycle of the fore- and hind-limbs in the present adult reptilian species were analyzed using video camera. Every amphibian and reptilian animal was filmed when walking on a sheet of paper, then the locomotory sequence was photographed to show the position of fore- and hind limbs during the protraction and retraction phases of the locomotory cycle.

RESULTS

Pectoral girdle (Figures 1A-F)

The pectoral girdle usually consists of single interclavicle, paired clavicles, paired scapulae, paired coracoids, paired epicoracoids and paired suprascapulae. In all the investigated species, the medial interclavicle and the paired clavicles, scapulae and coracoids are bony structures, while the paired epicoracoids and suprascapulae are partially calcified cartilage. The distal end of each clavicle articulates with a particular notch located on the antero-ventral region of the suprascapula. The two epicoracoids are flat plates, convexly curved only at their inner borders. The epicoracoids overlap in the middle line, the left being ventral to the right, and they are able to do this because the sternum is more posteriorly placed in relation to them. The two clavicles are joined at the midline with a cartilaginous zone and are slightly dilated laterally.

According to the observed finding in the studied species, the number of the elements constituting the pectoral girdle is fixed, but there is much variation in the shape of the interclavicle. It is cruciform in the Family Agamidae (*Laudakia stellio*) and dagger-shaped in the Family Gekkonidae (*Hemidactylus turcicus*); however, Families Lacertidae (*Acanthodactylus scutellatus*), Scincidae (*Chalcides ocellatus*), Varanidae (*Varanus griseus*) and Chamaeleontidae (*Chamaeleo chamaeleon*) are greatly similar in the shape of their interclavicle as they are cruciform in shape.

There is a pronounced variation in the presence or absence of the coracoid fenestra and the scapulo-coracoid fenestra. In Agamidae (*Laudakia stellio*), one coracoid fenestra is present. In addition, in Gekkonidae (*Hemidactylus turcicus*), two types of fenestrae are present: coracoid fenestra and scapulo-coracoid fenestra, while in Lacertidae (*Acanthodactylus scutellatus*), Scincidae (*Chalcides ocellatus*) and Varanidae (*Varanus griseus*), only one coracoid fenestra was observed. On the other hand, in Chamaeleontidae (*Chamaeleo chamaeleon*), the two types of fenestrae are absent.

The sternum in Gekkonidae (*Hemidactylus turcicus*) is

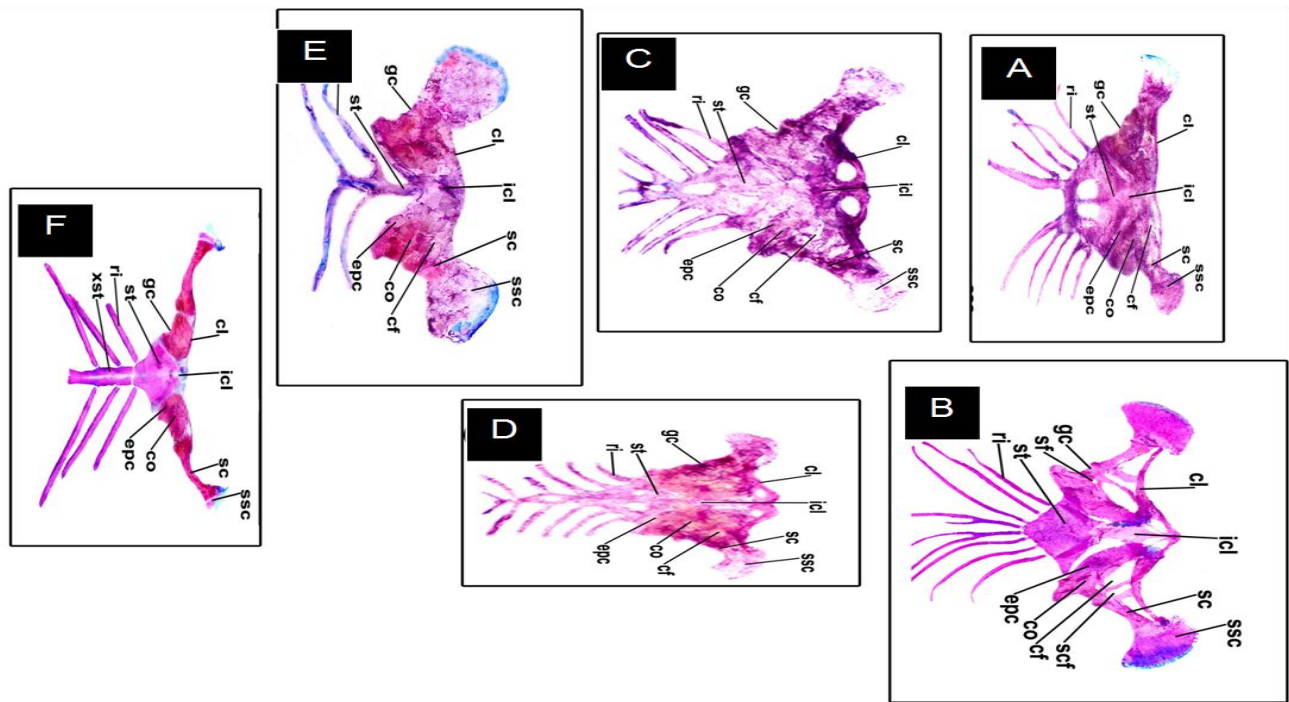


Figure 1. Whole mount preparation of the pectoral girdle of (A) *Laudakia stellio*, (B) *Hemidactylus turcicus* (C)*Acanthodactylus scutellatus* (D) *Chalcides ocellatus* (E) *Varanus griseus* (F) *Chamaeleo chamaeleon* illustrating single fenestra, coracoid fenestra (cf) and the fenestrated sternum (st), the interclavicle (icl) and fenestrated clavicle (cl), coracoid (co) and scapula (sc), epicoracoids (epc), sternum (st), ribs (ri) and xiphisternum (xst) stained with Alcian blue-Alizarin red X2.

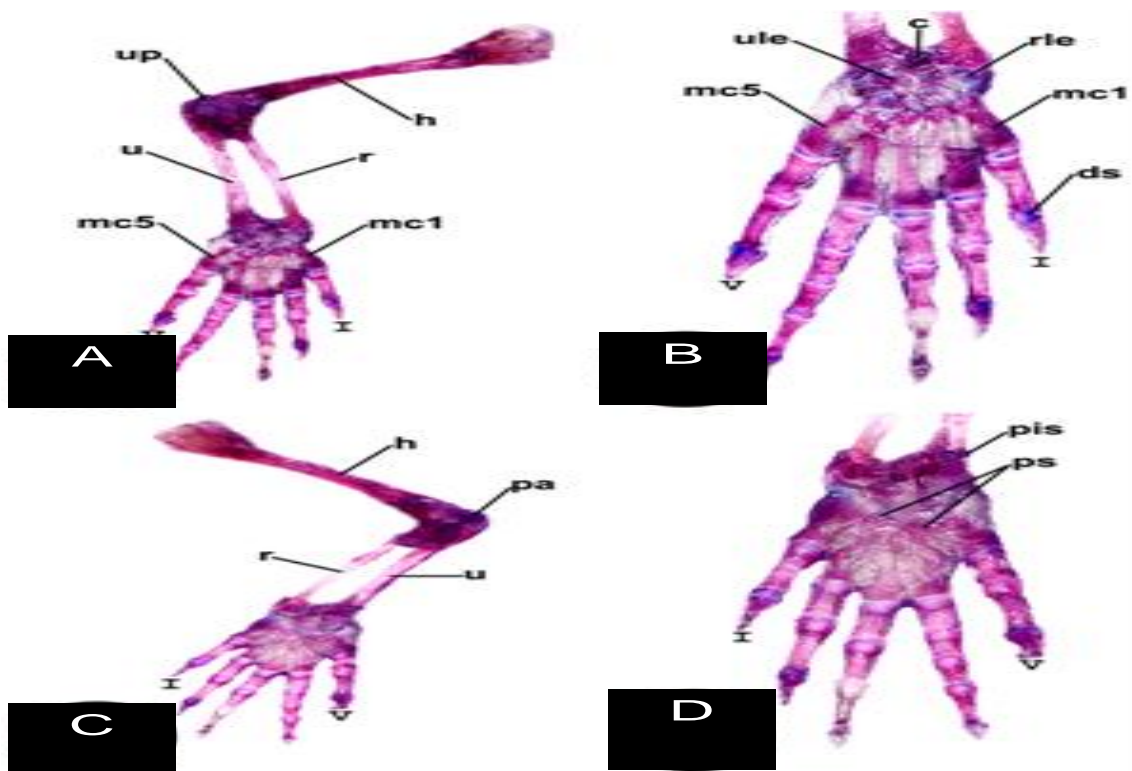


Figure 2. Whole mount preparation of the fore limb (A, C) and manus (B, D) of *Laudakia stellio* showing the cartilaginous carpal elements and ulnar patella (up), dorsal sesamoids (ds) and the ulnare (ule), the patella (pa) pisiform (pis) and the palmar sesamoids (ps). (A, C) "dorsal view", (B, D) "ventral view". Stain with Alcian blue-Alizarin red. X 6

partially calcified and unfenestrated. In the meantime, in Lacertidae (*Acanthodactylus scutellatus*), the structure of the sternum is similar to that found in Agamidae since it is partially calcified and fenestrated. In Scincidae (*Chalcides ocellatus*), the sternum is partially calcified and fenestrated. Finally, in Varanidae (*Varanus griseus*) and Chamaeleontidae (*Chamaeleo chamaeleon*), the sternum is partially calcified and unfenestrated.

Fore Limb (Figures 2A-D, 3A-D, 4A-D, 5A-E, 6A-B and 7A-D; Tables 1, 2)

Generally, in the studied species, the diaphyses of the humerus, radius, ulna, metacarpals and digits are

calcified. The radius and ulna are smaller in length than the humerus, though the radius and ulna are fully separate.

The elements of the carpus of the studied species consist of the radiale, centrale, ulnare and a row of five distal carpals. There is much variation in the phalangeal formula of the manus in the studied species (Tables 1 and 2). The paraphalangeal elements are associated with the basal phalanx of the 3rd and 4th digit in *Hemidactylus turcicus*, whereas in the other studied species, these elements are totally missing.

In the studied species, the epiphyses of phalanges are calcified. These epiphyses are not fused with their shafts and they are separated by a cartilaginous zone. There is

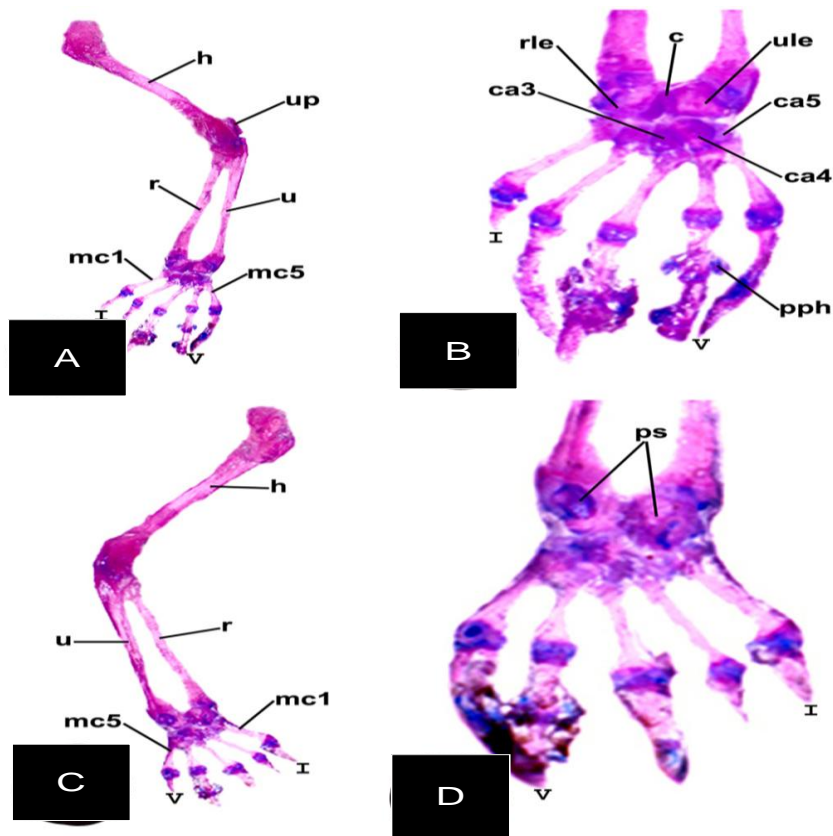


Figure 3. Whole mount preparation of the fore limb(A, C) and manus (B, D) of *Hemidactylus turcicus* illustrating the cartilaginous carpal elements and ulnar patella (up), paracarpals (pph) and the calcified centre in the ulnare (ule) and palmar sesamoids (ps). (A, B)"dorsal view", (C, D) "ventral view". Stain with Alcian blue-Alizarin red. X 6.

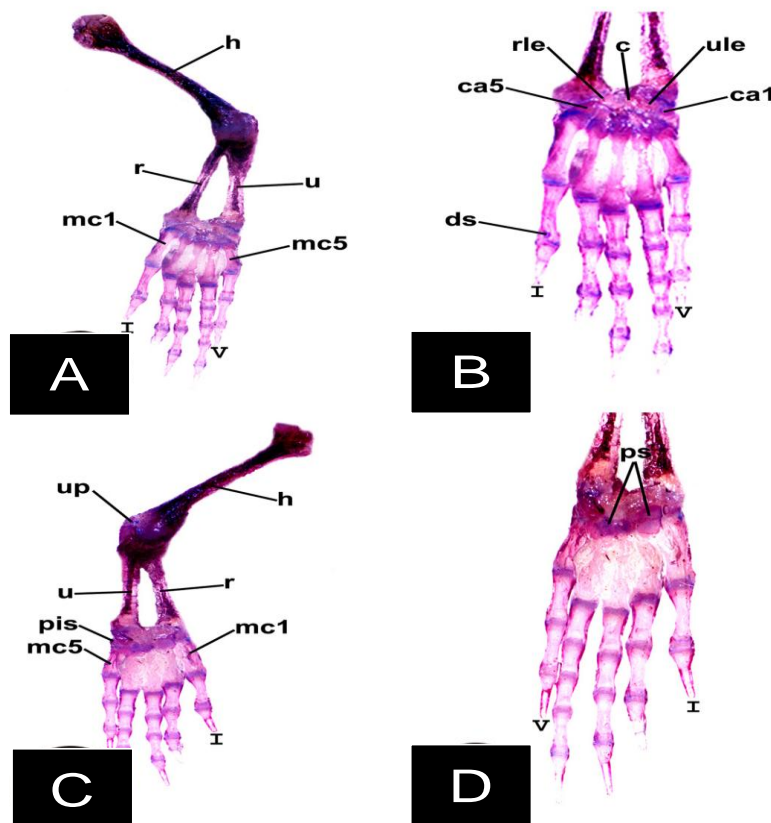


Figure 4. Whole mount preparation of the fore limb (A, C) and manus (B, D) of *Acanthodactylus scutellatus* showing the cartilaginous carpal elements, the carpalia 1 & 5, the calcified centres in the radiale (rle) and the ossified centre in the ulnare (ule), ulnar patella (up) and palmar sesamoids (ps). (A, B)"dorsal view", (C, D) "ventral view". Stain with Alcian blue-Alizarin red. X 8.

a pronounced variation in the sesamoids of the limbs in the studied species.

In *Laudakia stellio* (Figure 2A-D), the ulnar patella is located in a dense fibrous tissue. The pisiform is partially calcified. The palmar sesamoids are located ventral to the palm as two small rounded rudiments in *Laudakia*

stellio. At the proximal end of the humerus, there is a small calcified patella. The dorsal phalangeal sesamoids are present at the distal end of the last phalanges of the digits I to V.

In *Hemidactylus turcicus* (Figure 3A-D), the ulnar patella is located proximal to the olecranon process. The

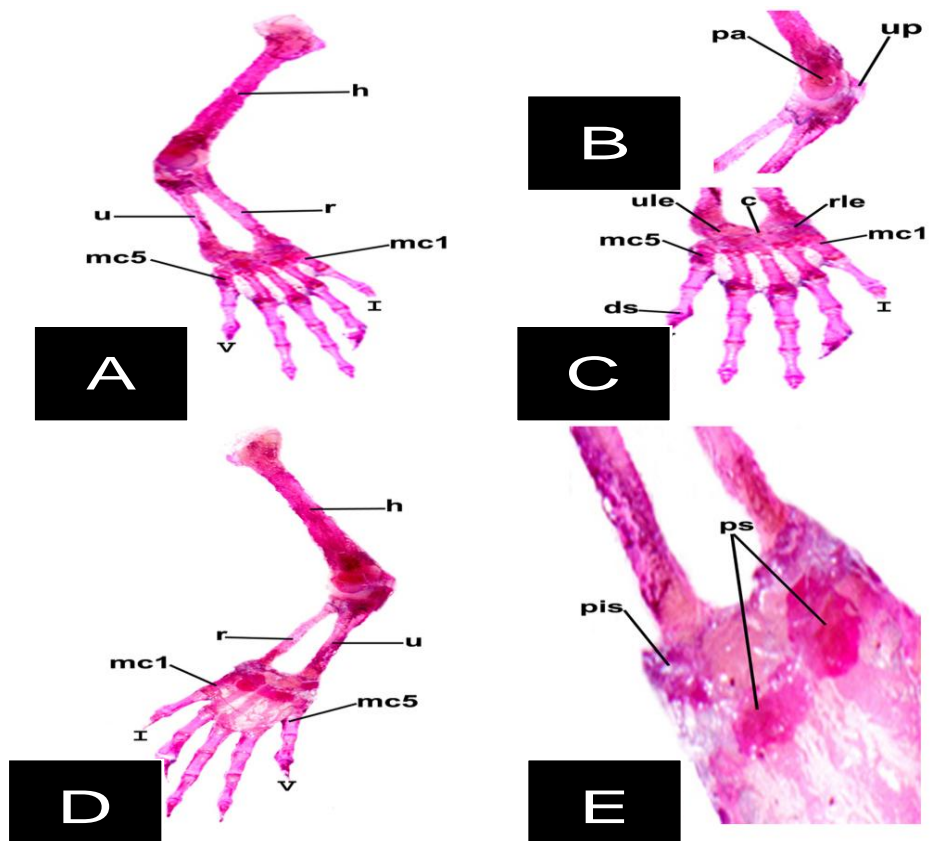


Figure 5. Whole mount preparation of the fore limb(A, D), elbow (B), manus (C) and carpus (E) of *Chalcides ocellatus* showing the cartilaginous carpal elements, patella (pa) and ulnar patella (up), sesamoids (ds), the calcified centres in the radiale (rle) and the ossified centre in the ulnare (ule), pisiform (pis) and the palmar sesamoids (ps). (A, B,C)"dorsal view", (D, E)"ventral view". Stain with Alcian blue-Alizarin red. X 10.

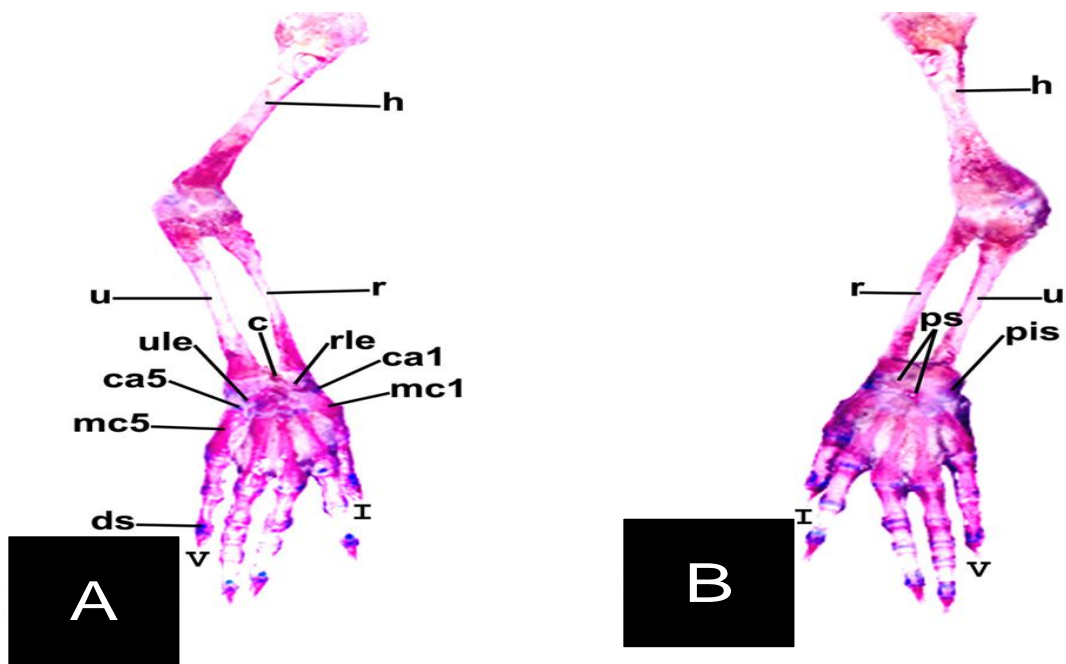


Figure 6. Whole mount preparation of the fore limb(A, B) of *Varanus griseus* displaying the cartilaginous carpal elements, calcified centres in the ulnare (ule), in the radiale (rle) and carpalia 1 and 5 and pisiform (pis) and the palmar sesamoids (ps). (A)"dorsal view", (B)"ventral view". Stain with Alcian blue-Alizarin red. X 8.

pisiform is missing. The palmar sesamoids are located ventral to the palm as two rounded calcified rudiments. The dorsal phalangeal sesamoids are missing.

In *Acanthodactylus scutellatus* (Figure 4A-D), the ulnar patella is located in a dense fibrous connective tissue. The pisiform is partially calcified. The palmar sesamoids are located ventral to the palm as two semitriangular calcified rudiments. The patella is missing. The dorsal phalangeal sesamoids are present at the distal end of the last phalanges of the digits.

The ulnar patella is found only in *Chalcides ocellatus* (Figure 5A-E), where it is located proximal to the olecranon process. The pisiform is fully ossified. The

palmar sesamoids are located as two rounded calcified rudiments ventral to the palm in *Chalcides ocellatus*. At the proximal end of the humerus, there is a small calcified patella found only in *Chalcides ocellatus*. The dorsal phalangeal sesamoids are present at the distal end of the last phalanges of the digits.

In *Varanus griseus* and *Chamaeleo chamaeleon* (Figures 6A-B and 7A-D), the ulnar patella is totally missing. The pisiform is found in *Varanus griseus* and is fully ossified, while it is completely absent in *Chamaeleo chamaeleon*. In the meantime, the palmar sesamoids are found in *Varanus griseus* and *Chamaeleo chamaeleon*.

These palmar sesamoids are located as two rounded

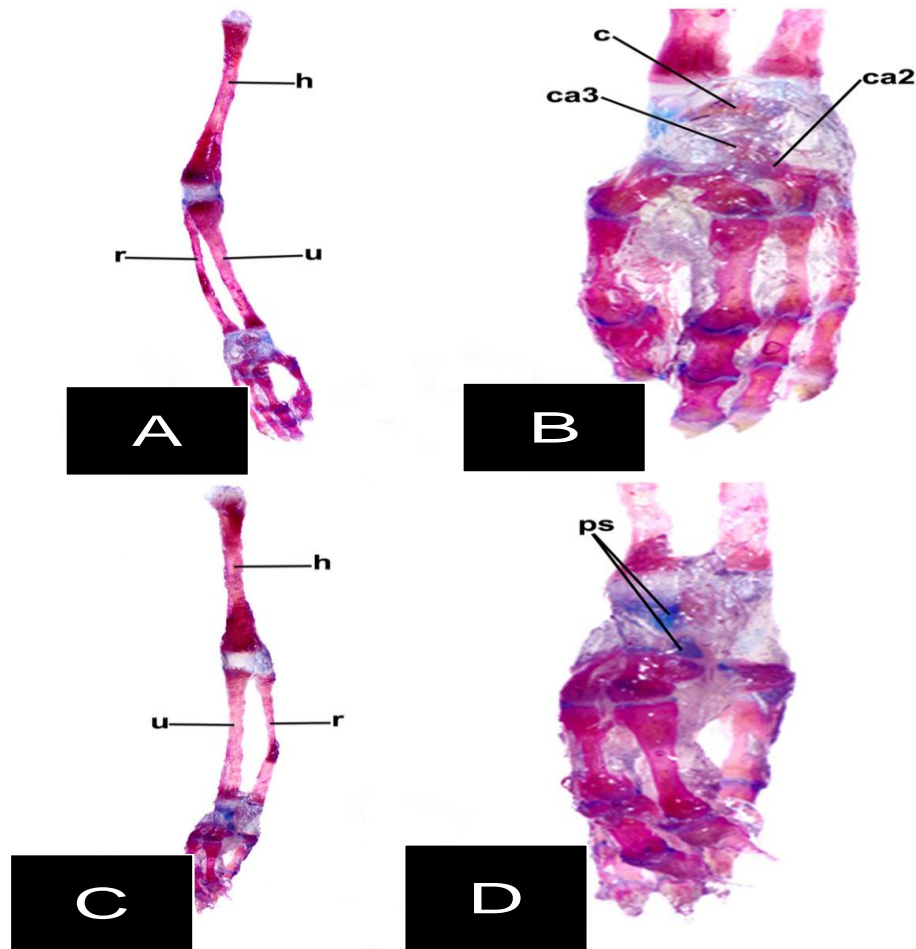


Figure 7. Whole mount preparation of the fore limb (A,C, D) and manus (B) of *Chamaeleo chamaeleon* explaining the cartilaginous carpal elements, the carpalia 2 & 3 and centrale (c) and the palmar sesamoids (ps). (A, B)"dorsal view", (C, D) "ventral view". Stain with Alcian blue-Alizarin red. X 8.

Table 1. The phalangeal formula of the manus and pes in the studied reptilian species.

Species	The manus	The pes
<i>Laudakia stellio</i>	2:3:4:5:3	2:3:4:5:4
<i>Hemidactylus turcicus</i>	2:3:3:4:3	2:3:3:4:3
<i>Acanthodactylus scutellatus</i>	2:3:4:5:3	2:3:4:5:4
<i>Chalcides ocellatus</i>	2:3:4:4:3	2:3:4:5:3
<i>Varanus griseus</i>	2:3:4:5:3	2:3:4:5:4
<i>Chamaeleo chamaeleon</i>	2:3:3:2:2	2:3:4:3:3

Table 2. Morphometrical characterization of the fore-limb skeleton in reptilian species examined.

Species	Humerus length	Radius length	Fore limb length
<i>Laudakia stellio</i>	2.05 ± 0.07	1.55 ± 0.04	3.6 ± 0.1
<i>Hemidactylus turcicus</i>	0.68 ± 0.03	0.58 ± 0.03	1.26 ± 0.06
<i>Acanthodactylus scutellatus</i>	0.61 ± 0.03	0.43 ± 0.04	1.05 ± 0.07
<i>Varanus griseus</i>	3.55 ± 0.312	3.33 ± 0.26	6.88 ± 0.57

Values are means ± SE; N = 4.

calcified rudiments ventral to the palm. The patella is missing in the two latter species. The dorsal phalangeal sesamoids are found in *Varanus griseus*, at the distal end of the last phalanges of the digits, whereas these sesamoids are missing in *Chamaeleo chamaeleon*.

Pelvic girdle (Figure 8A-F)

In the studied species, each half of the pelvic girdle consists of the pubis and ischium; they build together an extensive foramen cordiforme (ischio-pubic fenestra) which is normally undivided. A cartilaginous ischiadic process (*spine ischii*) is developed from the ischium, and a prepubic (pectinael) process from the anterolateral

margin of the pubis. There is a distinct variation in the pubis, ischium and ilium. They meet at the acetabulum in *Varanus griseus* and *Chamaeleo chamaeleon*. Also, variations are found in the epipubis and ischiadic symphysis of the studied animals. They are fully cartilaginous in *Hemidactylus turcicus*, and *Varanus griseus*, while they are fully calcified in *Laudakia stellio*, *Chalcides ocellatus*, and *Chamaeleo chamaeleon*. However, in *Acanthodactylus scutellatus*, the epipubis and ischiadic symphysis are partially calcified. In addition, variation in the shape of the ischiadic symphysis is found among the studied species. In *Laudakia stellio*, *Hemidactylus turcicus* and *Varanus griseus*, it is simple, tapering rod-like. However, in *Acanthodactylus*

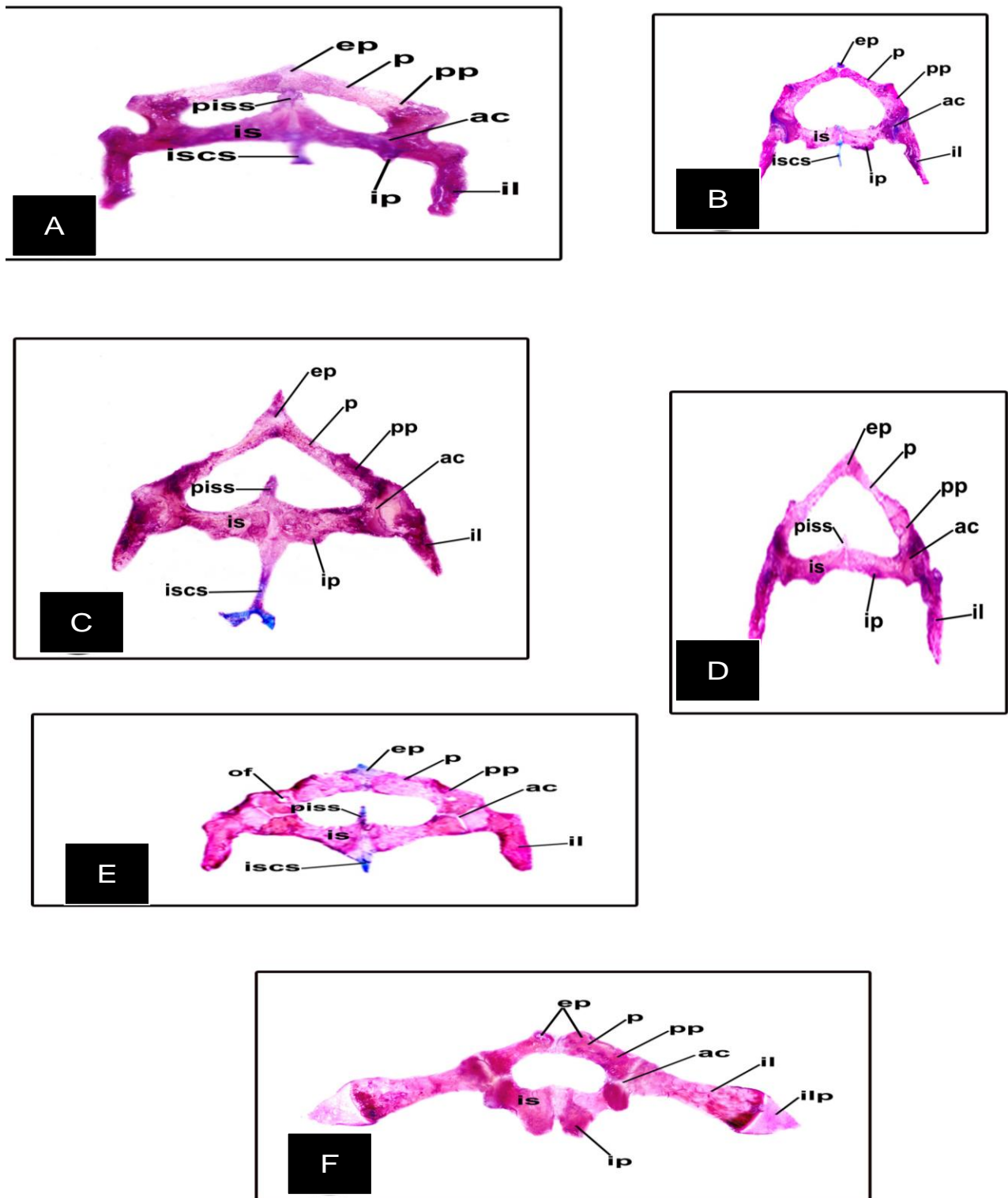


Figure 8. Whole mount preparation of the pelvic girdle of (A) *Laudakia stellio*, (B) *Hemidactylus turcicus* (C)*Acanthodactylus scutellatus* (D) *Chalcides ocellatus* (E) *Varanus griseus* (F) *Chamaeleo chamaeleon*, showing the ilium (il), ischium (is) and pubis (p), ischiadic symphysis (iscs) , epipubis (ep) and ischiadic process (ip), the ischiadic symphysis (iscs), Obturator foramen (of), ilium process (ilp). Stain with Alcian blue-Alizarin red. X 5.

scutellatus, it is rod-like with a distal bifurcate shape, while in *Chalcides ocellatus* and *Chamaeleo chamaeleon*, it is simple. Note that the obturator foramen is present only in *Varanus griseus*, while this foramen is absent in the other studied species. Finally, the distal end of the ilium has cartilaginous epiphysis, which is fully cartilaginous in all species of the present study.

Hind limb (Figures 9, 10A-D, 11A-C, 12A-D and 13A-E; Tables 1 and 3)

In the studied species, the femur bone is, more or less, similar in shape to the humerus. The tibia and fibula are nearly equal in length, distinctly shorter than the femur, and longer than the radius and ulna. The tibia is stouter than the fibula and has an expanded head with single broad surface articulating with the most part of the tibial condyle of the femur.

There is a distinct variation in the tarsus of the studied species. In the meantime, a pronounced variation in the

phalangeal formula of the pes is recorded in Tables 1 and 3.

In *Laudakia stellio* (Figure 9), the tarsus consists of the proximal tarsal element (tarsalia 1, 3 and 4). In *Hemidactylus turcicus* (Figures 10A-D), the tarsus also consists of the proximal tarsal element (tarsalia 1, 3 and 4). In *Acanthodactylus scutellatus* (Figures 11A-C), the tarsus consists of the proximal tarsal element (tarsalia 3 and 4). In *Chalcides ocellatus* (Figure 12A-D), the tarsus consists of the proximal tarsal element (tarsalia 3 and 4). The proximal tarsal element is located as two small calcified rudiments and tarsalia 3 and 4 are fully calcified. In *Varanus griseus* (Figure 13A-C), and *Chamaeleo chamaeleon* (Figures 13D, E), the tarsus consists of the proximal tarsal element (tarsalia 3 and 4). In all studied species, the tarsalia 5, the paraphalangeal elements are missing. Except in *Hemidactylus turcicus*, the paraphalangeal elements are present at the distal end of digit V.

The epiphyses of the femur, tibia, fibula, phalanges and

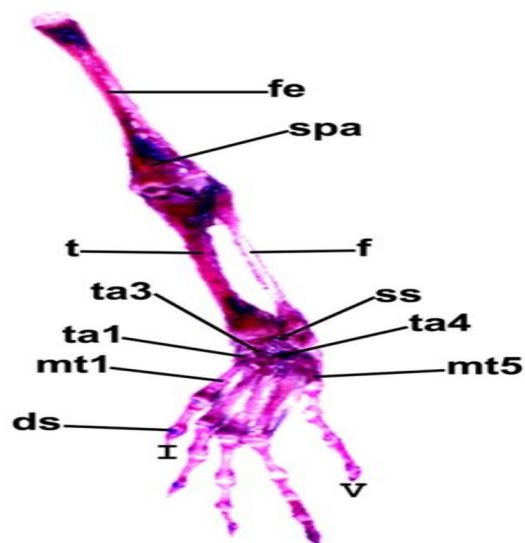


Figure 9. Whole mount preparation of the hind limb of *Laudakia stellio* showing the dorsal sesamoids (ds), the metatarsalia 1 & 5 (mt1 & mt5), the suprapatella (spa), the sole sesamoids (ss) and the tarsalia 1, 3 & 4 (ta1, ta3 & ta4) "dorsal view". Stain with Alcian blue-Alizarin red. X 4.

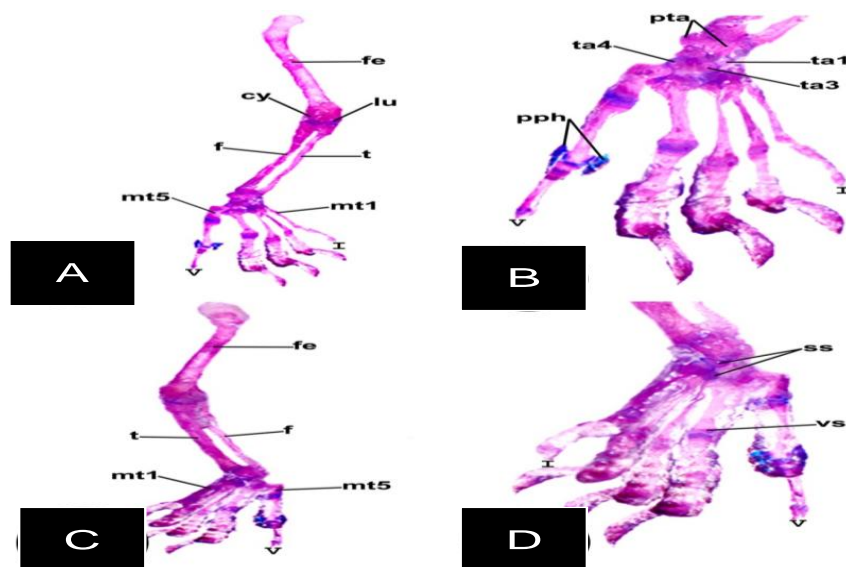


Figure 10. Whole mount preparation of the hind limb (A, C) and pes (B, D) of *Hemidactylus turcicus* explaining the cyamella (cy), the lunula (lu) and the metatarsalia 1 & 5 (mt1 & mt5), paraphalanges (pph), the proximal tarsal (pta) and the tarsalia 1, 3 & 4 (ta1, ta3 & ta4), the metatarsalia 1 & 5 (mt1 & mt5), the sole sesamoids (ss) and the ventral sesamoids (vs). (A, B)"dorsal view", (C, D) "ventral view". Stain with Alcian blue-Alizarin red. X 7.

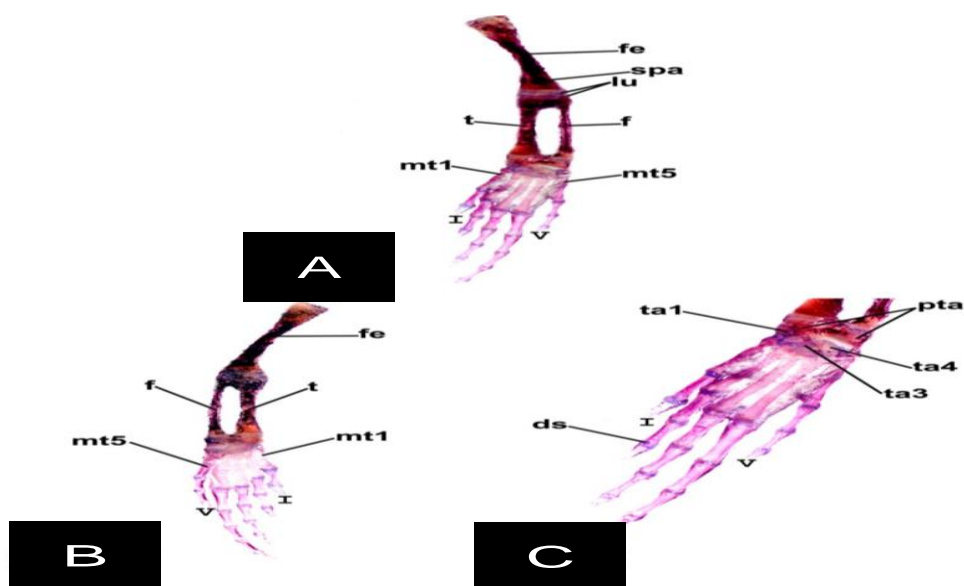


Figure 11. Whole mount preparation of the hind limb (A, B) and pes (C) of *Acanthodactylus scutellatus* exposing the lunula (lu), the suprapatella (spa) and the metatarsalia 1 & 5 (mt1 & mt5), the fibula (f), femur (fe), tibia (t) and the dorsal sesamoids (ds), the proximal tarsal (pta) and the tarsalia 1, 3 & 4 (ta1, ta3 & ta4), (A)"dorsal view", (B, C) "ventral view". Stain with Alcian blue-Alizarin red. X 6.

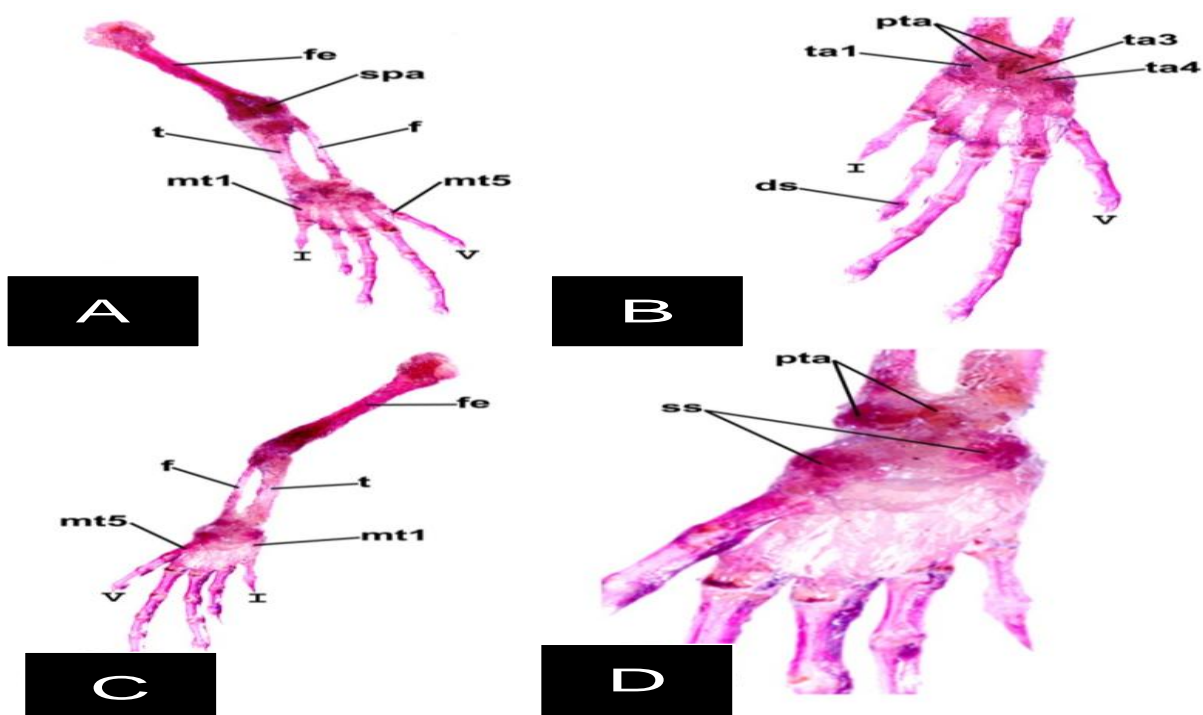


Figure 12. Whole mount preparation of the hind limb (A, C), pes (B) and tarsus (D) of *Chalcides ocellatus* showing the metatarsalia 1 & 5 (mt1 & mt5) and the suprapatella (spa), the dorsal sesamoids (ds), the proximal tarsal (pta) and the tarsalia 1, 3 & 4 (ta1, ta3 & ta4), and the proximal tarsal (pta) and the sole sesamoids (ss). (A,B)"dorsal view", (C, D)"ventral view". Stain with Alcian blue-Alizarin red. X 6.

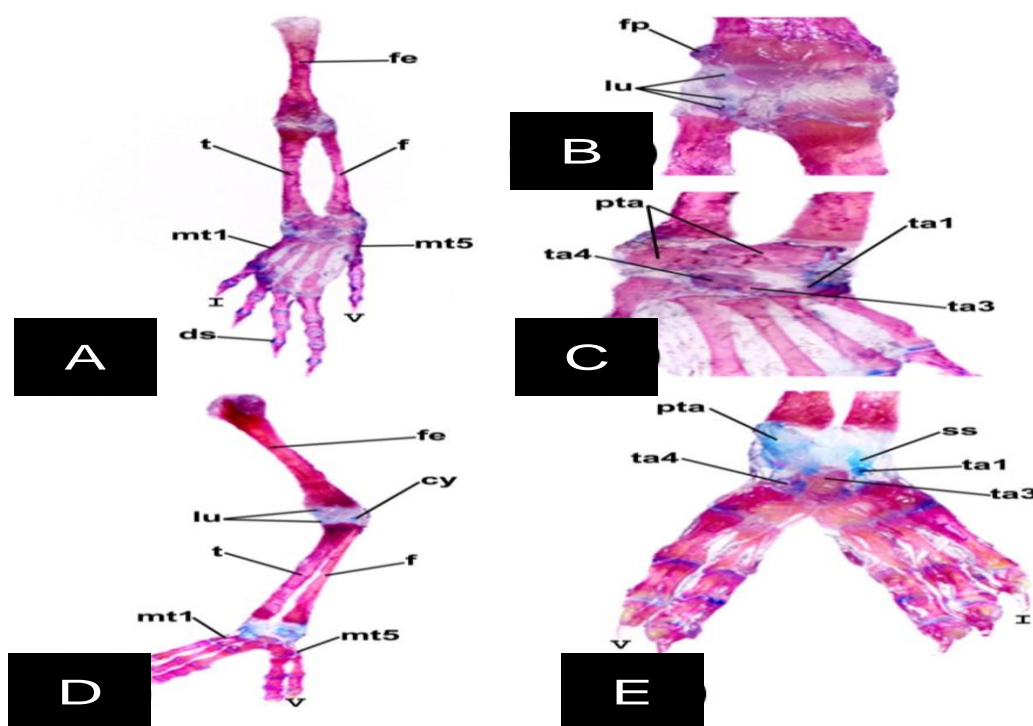


Figure 13. Whole mount preparation of the hind limb(A), the knee joint (B) and the tarsus (C) of *Varanus griseus* and the hind limb (D) and the pes (E) of *Chamaeleo chamaeleon* displaying the dorsal sesamoids (ds) and the metatarsalia 1 & 5 (mt1 & mt5), the fibular patella (fp) and the lunula (lu) and the proximal tarsal (pta) and the tarsalia 1, 3 & 4 (ta1, ta3 & ta4), cyamella (cy), lunula (lu), the proximal tarsal (pta) and the sole sesamoids (ss). (D)"dorsal view", (A, B, C, E)"ventral view". Stain with Alcian blue-Alizarin red. X 6.

Table 3. Morphometrical characterization of the hind-limb skeleton in reptilian species examined.

Species	Femur length	Tibia length	Astragalus and calcaneum	Hind limb length
<i>Laudakia stellio</i>	2.71 ± 0.07	2.58 ± 0.09	— — —	5.3 ± 0.16
<i>Hemidactylus turcicus</i>	0.98 ± 0.03	0.88 ± 0.03	— — —	1.86 ± 0.06
<i>Acanthodactylus scutellatus</i>	0.76 ± 0.06	0.63 ± 0.05	— — —	1.4 ± 0.11
<i>Varanus griseus</i>	4.08 ± 0.35	3.9 ± 0.35	— — —	8.01 ± 0.71

Values are means ± SE; N = 4.

distal tarsals are cartilaginous in *Chamaeleo chamaeleon*, while they are partially calcified in *Laudakia stellio*, *Hemidactylus turcicus*, *Acanthodactylus*

scutellatus, and *Varanus griseus*. However, in *Chalcides ocellatus*, these epiphyses are fully calcified. In the studied species, the epiphyses of femur, tibia and fibula

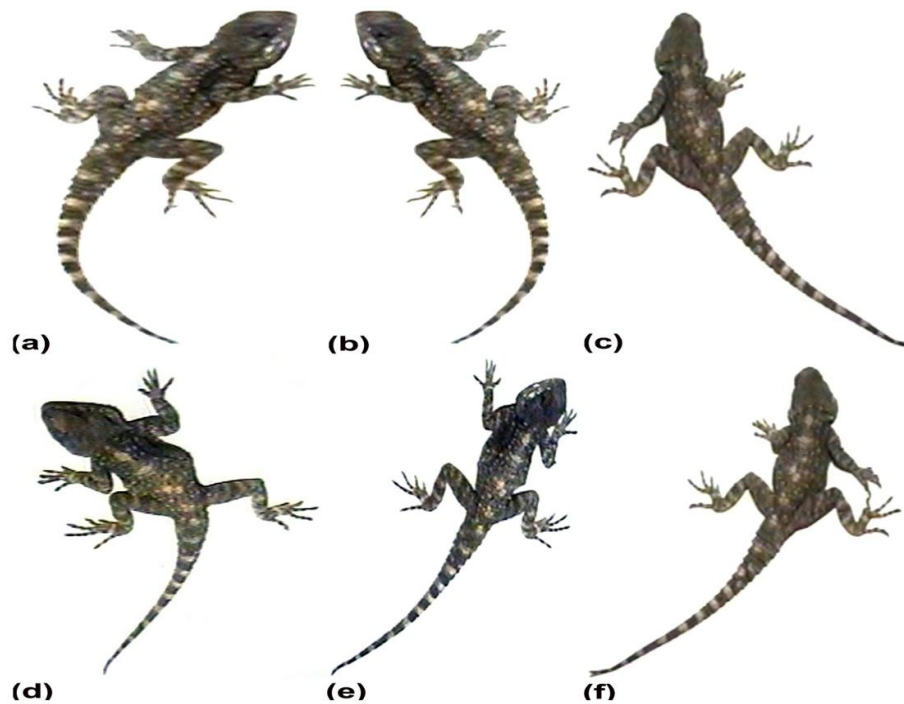


Figure 14. Stages in locomotion of *Laudakia stellio*.

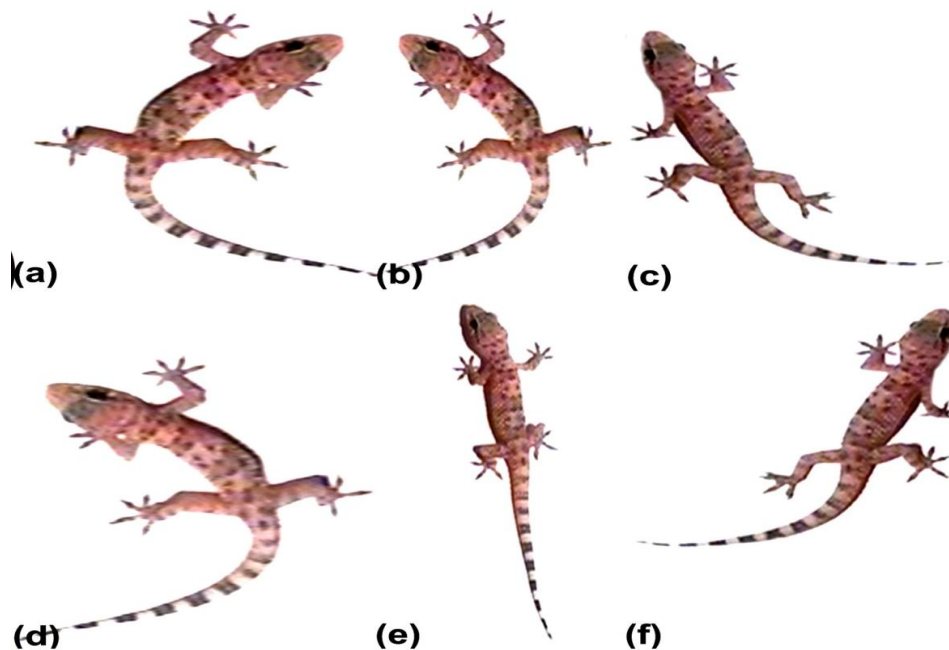


Figure 15. Stages in locomotion of *Hemidactylus turcicus*.

are unfused with their shafts.

There is a pronounced variation in the sesamoids of the hind limbs in the studied species. In *Laudakia stellio*, the fibular patella is missing. The sole sesamoid is recorded as one semirounded calcified rudiment ventral to the sole. The dorsal sesamoids are located at the distal end of the last phalanges, while the proximal end of the epiphyses of the femur has a suprapatella.

In *Hemidactylus turcicus*, the fibular patella is missing. The sole sesamoids are recorded ventral to the sole. On the other hand, the ventral sesamoids are found. The knee joint has one calcified lunulae and one calcified cyamellae. However, the suprapatella is completely missing.

In *Acanthodactylus scutellatus*, the fibular patella is missing. The sole sesamoids are missing. The dorsal sesamoids are calcified and located at the distal end of the last phalanges of digits I to V. The knee joint has two lunulae. The proximal end of the epiphyses of the femur has a suprapatella.

In *Chalcides ocellatus*, the fibular patella is missing. The sole sesamoid is recorded as two semirounded calcified rudiments. The dorsal sesamoids are calcified

and located at the distal end of the last phalanges of the digits. The knee joints are missing. The proximal end of the epiphyses of the femur has a suprapatella.

In *Varanus griseus* and *Chamaeleo chamaeleon*, the fibular patella is calcified and located in the outer side of the femur in *Varanus griseus*, while in *Chamaeleo chamaeleon*, the fibular patella is missing. The sole sesamoid is represented by one oval calcified rudiment in *Chamaeleo chamaeleon*, while it is totally absent in *Varanus griseus*. The dorsal sesamoids are calcified and located at the distal end of the last phalanges of the digits in *Varanus griseus*, while these sesamoids are missing in *Chamaeleo chamaeleon*. The knee joint has three lunulae only in *Varanus griseus*, while in *Chamaeleo chamaeleon*, the knee joint has two lunulae and one cyamellae.

General pattern of locomotion (Figures 14 to 19)

In *Laudakia stellio* (Figure 14), the movement occurred firstly by running at high speeds with the fore limbs above the ground, a case which prevent the fore limbs from interfering with the hind limbs. The longitudinal positions

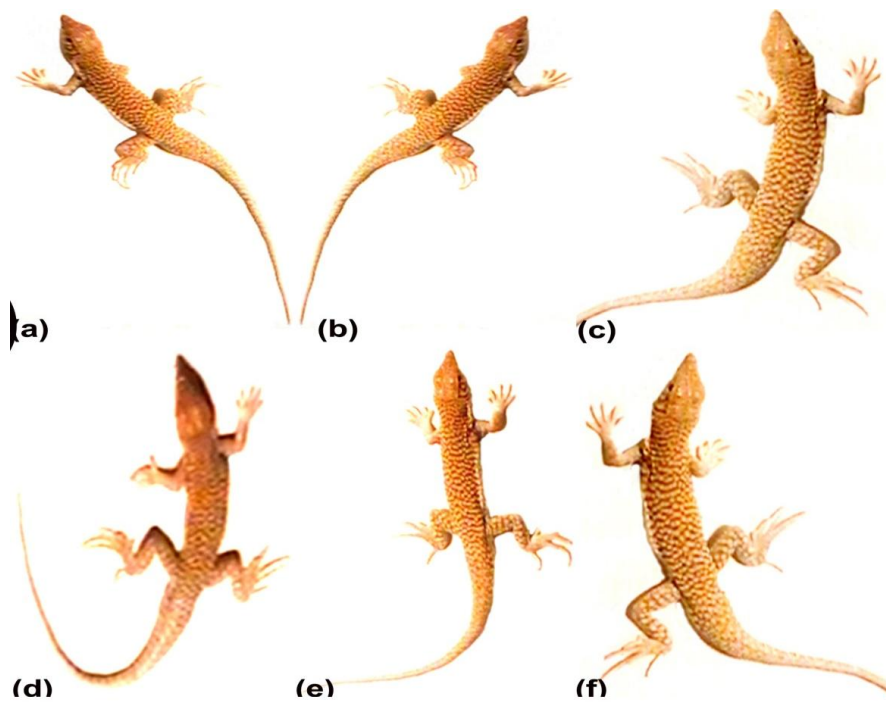


Figure 16. Stages in locomotion of *Acanthodactylus scutellatus*.

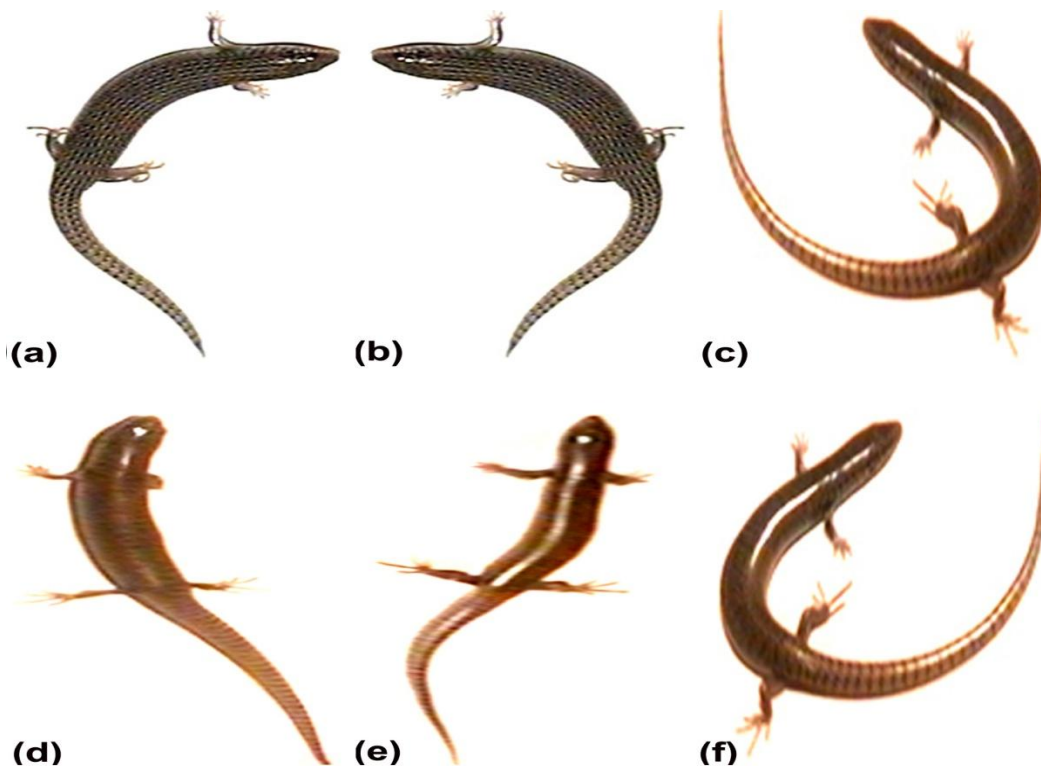


Figure 17. Stages in locomotion of *Chalcides ocellatus*.

of the ipsilateral feet of lizards are commonly overlapped during running. Secondly, they attain velocities that are similar to those produced by the hind limbs. Thirdly, there is increased trunk angles and hence, increased fore limb clearance. There is three species with longer hind limbs that enable lizards to take longer strides, and hence achieve faster speeds.

The present gecko, *Hemidactylus turcicus*, has the ability to move on coarse-grained surfaces. However, the common movement feature of the present gecko is the sinusoidal movement of the vertebral column which has a maximum convex phase towards the limb, being retracted at the end of the protractive phase and becomes straight at the end of the propulsive phase.

At the beginning of the propulsive phase (Figure 15), the right pes and the left manus are applied to the substratum, while the right manus and left pes are undergoing their recovery strokes during the rapid movement. The knee is depressed below the level of the

acetabulum. In addition, there is a flexion of the crus on the end of this phase when the left pes comes in contact with the substratum and at the beginning of the flexion of the crus on the metatarsus. During this phase, the left pes is brought into contact with the substratum. As for the manus, at the end of the recovery stroke, the pes during rapid climbing is rotated towards the sagittal axis of the body, the digit spread and the hyperextension is relaxed as the foot is set down. At this stage, the body is being pulled forward by muscular contraction of the left manus and the right pes, while the recovery stroke of the other two limbs continue. The right manus then reaches the end of its power stroke before the left pes detaches, leaving only the latter in contact with the substratum. Finally, the left manus is brought again into contact with the substratum and both the left and right manus pull the body upwards, while the opposite diagonal pair of the limbs undergoes their stroke.

The steps of locomotion in *Acanthodactylus scutellatus*

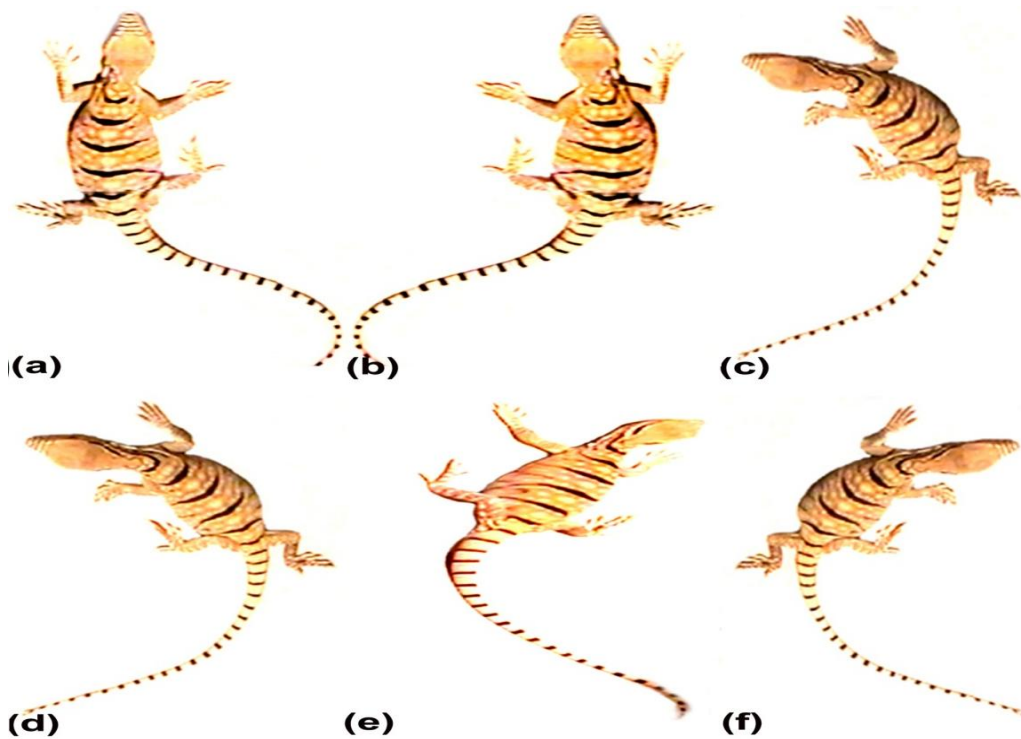


Figure 18. Stages in locomotion of *Varanus griseus*.

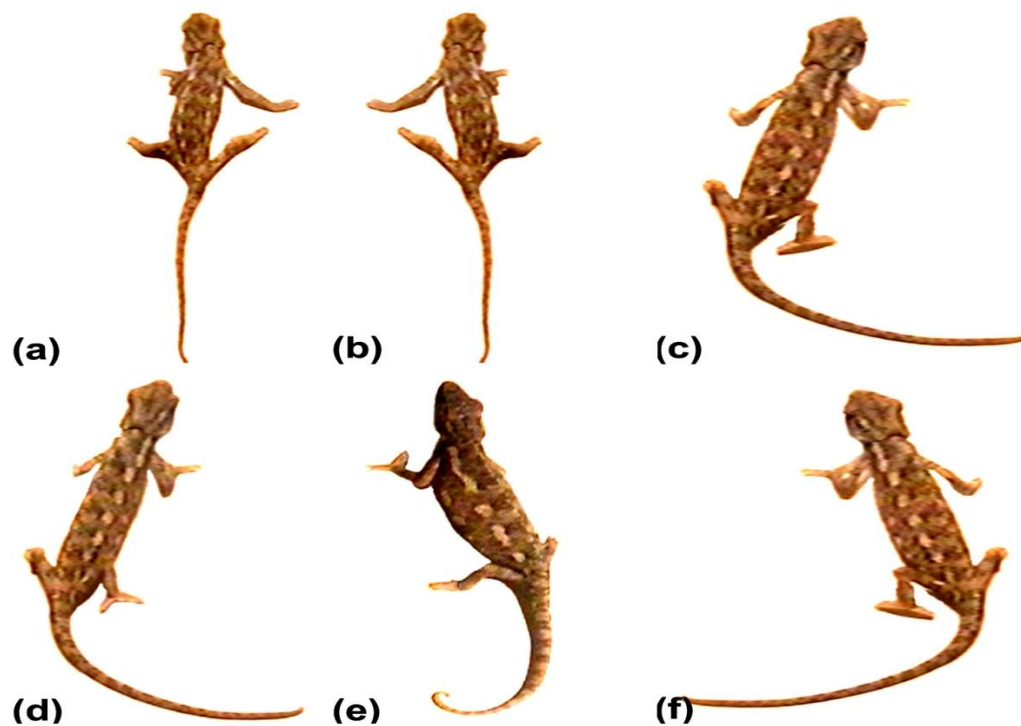


Figure 19. Stages in locomotion of *Chamaeleo chamaeleon*.

(Figure 16) could be described as follows: (a) The left hind foot is firmly affixed to the substratum towards the end of the power stroke of the stance phase. The first three digits are directed anteriorly such that the metatarso-phalangeal part is oriented normally to the long axis of the body. The fourth digit is directed laterally and the fifth postero-laterally. The outlines of the subdigital pads are clearly evident. At this stage, the knee and ankle are flexed and the femur is oriented almost normally to the long axis of the body. (b) The femur has been retracted and the knee and ankle begin to extend. Concomitant with ankle extension, the pes begins to roll onto its mesial border because of extension and conjoint rotation at the mesotarsal joint. This movement is evident by the partial obscuring of the first digit as the foot rolls over. (c) and (f) These stages represent marked protraction of the femur, flexure of the knee, and flexure of the ankle. This movement is rapid. (d) Retraction of the femur and extension of the ankle are more evident, as is the rolling of the pes onto its mesial border, further

obscuring the first three digits. (e) This is followed by a rapid extension of this joint as the pes and digits are placed back into contact with the substratum.

Chalcides ocellatus (Figure 17) is characterized by moving through soil which is usually soft or sandy. Often the substratum is closed behind the animal. Therefore, a permanent burrow is not established, but the soil may instead be compacted. The body is long and slender, which reduces the amount of soil that must be displaced. The sequence of the locomotion occurs when placed on the fine sandy ground. The lizard uses slide-pushing, in which propulsive forces are generated via zones of sliding friction. The head is obviously depressed, the neck is often arched vertically and the snout presses against the substratum. The anterior region becomes almost stationary and the middle and posterior regions of the trunk slide rapidly their contact zones posteriorly. The curvature extends well from head to tail. At the same time, sinusoidal movements of the vertebral column are extended in the form of standing waves with nodes at the

pelvic and pectoral girdles. They are co-ordinated with the limb movements. Therefore, the vertebral column is straight at the end of the propulsive phase and maximally, the convex towards the limb is retracted at the end of the protractive phase. This help in rotating the pelvic region, so the hip of the limb which is being protracted, is moved forward, lengthening the stride. The pelvis then functions as an additional limb segment with its length being equal to the interacetabular width.

The steps of locomotion in *Varanus griseus* (Figure 18) could be summarized as follows: (a) the abdomen is flattened onto the grey concrete surface and the head and neck is raised. (b) The abdomen is dorso-ventrally flattened and directed towards the sun. (c) and (f) Lateral sigmoidal trotting action is shown while walking. (d) Standing erect by balancing on the hind feet and tail. (e) Walking with only the distant end of the tail dragging on the ground.

Chamaeleo chamaeleon (Figure 19) follows the same locomotory pattern as that of most limbed vertebrates, left fore, right hind. It makes many 'jerky' movements for each step. Footfall of the foot of *Chamaeleo chamaeleon* is substantially anterior to the hip as a result of femur protraction and knee extension. Femur protraction is so extreme at footfall that the medial surface of the thigh often touched the body, while femur retraction begins at footfall and continues to a maximum slightly before the end of stance. After footfall, the knee is flexed. The girdles of the chameleon permit the legs to come vertically under the body, so the animal can balance over narrow stems. Chameleon (climbers) that swing or hinge under their support using hook-like appendages are in stable equilibrium.

DISCUSSION

Osteological characters of the fore and hind limbs

The present study shows that the studied species have great differences in the osteology of the appendicular skeletal rudiments.

Pectoral and pelvic girdles

In the present studied species, the elements of the pectoral girdle and their calcification patterns are generally similar to that described in dwelling lizards geckos (Stephenson, 1960; Mohammed, 1986, 1988b; EL-Wetery, 1992; EL-Gharib, 1994; Abo-Eleneen, 2005), as well as in other lizards studied by Romer (1956). In the species of the present study, the interclavicle, clavicles, scapulae and coracoids are fully calcified, while the epicoracoids and suprascapulae are cartilaginous. On the other hand, in the geckos of Australia, New Zealand, New Guinea, Solomon Islands and Jamaica, the elements of the pectoral girdle are fully calcified (Stephenson, 1960). In the present species, the scapula and coracoid are fused. Similar observations were recorded in adult geckos of certain Jamaican genera and in the New Zealand genus *Naultinus*, although these elements were completely separate in young specimens of *Oedura lesueurii*, *Heleronota binoei* and *Phyllurus platurus* (Stephenson, 1960). In addition, similar observations were found in several geckos and skinks (Mohammed, 1988b and 1991b).

In *Hemidactylus turcicus*, the shape of the interclavicle is dagger-shaped. Similar observation was recorded in several geckos (Mohammed, 1988a). However, in the other species of the present study, the shape of the interclavicle is cruciform. This is similarly met with the scincids: *Mabuya aurata* and *Mabuya quinquetaeniata* (Mohammed, 1990a), and the lizards: *Acanthodactylus boskianus*, *Scincus scincus* and *Sphenopus sepsoides* (Abo-Eleneen, 2005).

The pubis, ischium and ilium in *Laudakia stellio*, *Hemidactylus turcicus*, *Acanthodactylus scutellatus*,

Chalcides ocellatus, and *Varanus niloticus* are completely fused. Similar opinion was recorded in *Gymnodactylus kotschy*, *Hemidactylus flaviviridis*, *Ptychodactylus hasselquistii* (Mohammed, 1988b), but in *Varanus griseus* and *Chamaeleo chamaeleon* they are quite distinct, meeting at the acetabulum. Similar remarks were recorded in *Stenodactylus petrii* and *Acanthodactylus boskianus* (Abo-Eleneen, 2005). In addition, these elements are quite distinct in the lizards studied by Raynaud et al. (1975b). The present study demonstrated that the epipubis and ischiadic symphysis are fully cartilaginous in *Hemidactylus turcicus* and *Varanus griseus*, while in *Laudakia stellio*, *Chalcides ocellatus*, *Chamaeleo chamaeleon* and *Varanus niloticus*, they are fully calcified. However, in *Acanthodactylus scutellatus*, the epipubis and ischiadic symphysis are partially calcified. Stephenson (1960) reported that these two rudiments of the juvenile forms may not be, or may be only slightly calcified, although in older specimens, the epipubis becomes strongly calcified as the ischiadic symphysis region. These two elements are fully cartilaginous in the scincids *Mabuya aurata* and *Mabuya quinquetaeniata* and in several geckos (Mohammed, 1988b, 1990a).

Several variations were found in the shape of the ischiadic symphysis of the present species of reptiles, it is tapering rod in *Laudakia stellio*, *Hemidactylus turcicus*, and *Varanus griseus* but it is rod-like with a distal bifurcate shape in *Acanthodactylus scutellatus*. The ischiadic symphysis is simple in *Chalcides ocellatus*, and *Chamaeleo chamaeleon*. Similar observations were recorded by Mohammed (1988a, b, c) in several geckos and scincids.

Fore and hind limbs

The length of the fore-limb skeleton follows the sequence: humerus > radius and ulna. The present sequence corresponds to the appeared limb sequence and differentiated semilaterally in several lizards (Mathur and Goel, 1976; Rieppel, 1992a, b, c; EL-Gharib, 1994; Mohammed and EL-Shershaby, 1995a, b; Mohammed, 1997). The hind limb skeleton follows a particular sequence femur > tibia and fibula. According to the formula of the fore and hind limb, the increased limb length is expected to result in a lower energetic cost of locomotion. This stems from the idea that longer limbs result in longer strides which allow a given distance to be traversed with fewer steps (Fancy and White, 1987; Janis and Wilhelm, 1993). Kram and Taylor (1990) argue that longer limbs reduce the cost by increasing the velocity attained for a given interval of force application.

Carpus and tarsus

The present study proves that there is a marked difference in the carpal elements between the present species. Carpal elements consist of the radiale, ulnare, centrale and the carpalia 1 to 5. Similar observations were recorded in *Calotes versicolor* (Mathur and Goel, 1976), *Ascalobotes fascicularis* (Sewertzoff, 1908), *Varanus* (Porter, 1972), in several geckos (Stephenson and Stephenson, 1956; Stephenson, 1960; Mohammed, 1988a), and in scincids (Romer, 1956; EL-Wetery, 1992; EL-Gharib, 1994; Abo-Eleneen, 2005).

In *Agama colonorum*, Holmgren (1933) reported as many as 12 carpal elements in the embryo as compared with 7 in the adult, the centrale 3, 4 and the intermedium are fused with the ulnare and the carpalia 1 is fused with the metacarpal 1. On the other hand, the cartilaginous elements are not often appeared as independent foci, but usually appeared as branches or buds from the existing chondrogenic or prechondrogenic blastemas (Burke and Alberch, 1985). Therefore, the carpus of the embryonic geckos probably has a certain number of elements; some of them are fused during development which results in

reducing the number of such elements in the adults.

In *Laudakia stellio* and *Hemidactylus turcicus*, the tarsus consists of the proximal tarsal element, tarsalia 1, 3 and 4. But in *Acanthodactylus scutellatus*, *Chalcides ocellatus*, *Varanus griseus*, and *Chamaeleo chamaeleon*, the tarsus consists of the proximal tarsal element, tarsalia 3 and 4. Mohammed (1988c) proved that the tarsus consists of the proximal tarsal element, tarsalia 3 and 4 in *Chalcides ocellatus*. The same situation exists in many skinks and in some agamids and lacertids (Mohammed, 1990a).

The present study and the general accounts reported on other lizards showed that the paraphalangeal characteristics of geckos appear to be generally variable within the genus (Russell, 1986; Russell and Bauer, 1988; Mohammed, 1991b). In addition, the present work displays that the paraphalanges are absent in all studied species except in *Hemidactylus turcicus*. These observations are similarly met with some geckos (Russell and Bauer, 1988). However, the paraphalanges are homoplastic within the Gekkoninae, which is known to possess paraphalanges in all their genera (Kluge, 1987; Mohammed, 1991b).

In the present study, *Hemidactylus turcicus* is divided into scansors and it possesses paraphalanges. As recorded by Russell (1981), this pattern may be associated with applying the requisite pressure to the two banks of the scansors in order to ensure effective contact with a subdivision of the branches of the central blood sinus and consequently to the proximal, expanded regions of the scansors. The primary function of the limbs is to move the body forward as efficiently as possible. The presence of pes paraphalanges may confirm that the hind limbs provide the majority of the power for locomotion in lizards (Snyder, 1962; Urban, 1965). Paraphalangeal elements are widespread, although not universal, among pad-bearing gekkonine geckos.

In discussing *Hemiphyllodactylus*, Kluge (1966) referred to paraphalanges as neomorphic sesamoid bones. Nevertheless, in *Hemidactylus giganteus*, the paraphalanges may represent unossified sesamoids (Haines, 1969). On the other hand, the dorso- and ventro-phalanges of *Hemidactylus turcicus* are recorded as sesamoid bones in several scincid and lacertid lizards (Haines, 1969; Mohammed, 1990a). Accordingly, the paraphalange elements can be considered as modified sesamoids, and the digital sesamoidal control mechanisms in various geckos may differ in a variety of ways. The mechanical effect of sesamoids increases the leverage of muscles at the joints; this may explain the inverse development of some bony prominences and the nearby sesamoids described by Haines (1969) and Alexander and Dimery (1985).

Phalangeal formula

There is much variation in the phalangeal formula of the present species. Romer (1956) found that the typical reptilian phalangeal formula for the manus is 2:3:4:5:3 and for the pes is 2:3:4:5:4, being the primitive formula for reptiles. The phalangeal formula in the present agamid species (*Laudakia stellio*) is 2:3:4:5:3 for the manus and 2:3:4:5:4 for the pes. This is in agreement with the typical reptilian primitive formula reported by Romer (1956). Moreover, similar conclusion was recorded by Mohammed (1988a, b) and the same formula was found in *Acanthodactylus scutellatus*. In addition, the same observation was recorded in *Acanthodactylus boskianus* (Abo-Eleneen, 2005). In addition, similar formula was recorded in the lizards of the present study, *Varanus griseus*. This formula agrees with those recorded for *Calotes* (Mathur and Goel, 1976) and skinks *Mabuya aurata* and *Mabuya quinquetaeniata* (Mohammed, 1990a). In the mean time, the phalangeal formula is different in *Hemidactylus turcicus* of the present study, it is 2:3:3:4:3 in both the manus and the

pes. This latter formula was recorded also in other members of the genus *Stenodactylus* (Arnold, 1980), *Hemidactylus frenatus* (Stephenson, 1960), *Hemidactylus flaviviridis* (Mahendra, 1950), *Stenodactylus slevini*, *Stenodactylus khobarensis* and *Stenodactylus sthenodactylus* (Mohammed, 1988b) and in *Stenodactylus petrii* (Abo-Eleneen, 2005).

Variations are found in the phalangeal formula of the present studied species; in *Chalcides ocellatus*, it is 2:3:4:4:3 for the manus and 2:3:4:5:3 for the pes. However, in *Chamaeleo chamaeleon*, the phalangeal formula is 2:3:3:2:2 for the manus and 2:3:4:3:3 for the pes. Similar observations were recorded by EL-Wetery (1992). These variations in the phalangeal formulae reflect a pattern of incomplete fusion within the normal ontogeny, or that this additional phalanx is a neomorph. However, Maderson (1964) pointed out that such modification in the digits of the gekkonid lizards is to increase the ability of many geckos to adhere to vertical surfaces.

Epiphyses

The present work demonstrates that the studied species display marked differences in the presence or absence of fusion of the epiphyses with their shafts, a condition which may be associated with the mode of bone growth. In the studied reptilians, the epiphyses of the long bones are always separated from the diaphyses by a hyaline growth zone. The same situation exists in *Calotes* (Mathur and Goel, 1976), in several geckos and lizards (Mohammed, 1988a, 1990a, b; Abo-Eleneen, 2005).

The present study shows that in *Chamaeleo chamaeleon*, the proximal and distal epiphyses of the femur, tibia and fibula have calcified centres. In, *Laudakia stellio*, *Hemidactylus turcicus*, *Acanthodactylus scutellatus*, and *Varanus griseus*, there is a calcified centre in the distal epiphysis of the humerus bone, and two centres in the distal epiphyses of the femur. However, in *Chalcides ocellatus*, the epiphyses of long bones are fully calcified. Similar observations were recorded in several lizards (Mohammed, 1986, 1988b; EL-Wetery, 1992; Abo-Eleneen, 2005).

In the present studied lizards, the epiphyseal calcification pattern of the appendicular skeleton is significant. The epiphyses of the phalanges calcify before those of the longer bones, a sequence which was observed also in the agamid lizard *Calotes versicolor* (Mathur and Goel, 1976) and in the gecko *Cryptodactylus* (Mohammed, 1986). This sequence is in contrast with Haine's suggestion (1969) who reported that the larger epiphyses calcify before the smaller ones. In addition, in the present species, the calcified epiphyses may be separated from the diaphyses by cartilaginous zones or fused with them. Such epiphyseal arrangement occurs in most lizards at the approach of maturity agamids and gekkonids (Vialleton, 1919; Mohammed, 1990a), *Lacerta* (Nauch, 1936), *Calotes* (Mathur and Goel, 1976) and *Uromastix microlepis* (Mohammed, 1986). This is in general agreement with the typical lacertilian condition, and supports the observations that the phalanges grow only on their proximal ends (Haines, 1969; Mathur and Goel, 1976) and also the recorded opinion that the metacarpals grow only at their heads (Haines, 1969). Bellairs (1969) noted that some lizards may grow very slowly after maturity if the epiphyses do not fuse completely with the diaphyses. Such phenomena were recorded in *Sphenodon* lizards and in *Gephrosaurus* (Evans, 1981).

Sesamoids

In the present species, there are different types of sesamoids. These are recorded in other lizards and some geckos (Romer, 1956; Stephenson, 1960; Haines, 1969; Mohammed, 1986). The limb of the present species has

a pisiform rudiment in the palmar position relative to the other carpal bones. This element is in every way comparable with the pisiform of anurans (Emery, 1894) and other reptiles (Holmgren, 1933; Schwartz, 1938). Also, the pisiform in the last carpal element is markedly differentiated in turtles (Burke and Alberch, 1985). According to Romer (1956), the pisiform was probably a sesamoid cartilage, a neomorph in reptiles associated with a tendinous insertion. Moreover, the pisiform was recorded in all early tetrapods with well ossified hands (Romer, 1956), New Zealand geckos (Stephenson and Stephenson, 1956), and many lizards (Haines, 1969) and geckos (Mohammed, 1988c).

The other sesamoids associated with the elbow are ulnar patella, the palmar sesamoids, the dorsal sesamoids and the patella. The ulnar patella is found in *Laudakia stellio*, *Hemidactylus turcicus*, *Acanthodactylus scutellatus*, and *Chalcides ocellatus*, while it is missing in *Varanus griseus* and *Chamaeleo chamaeleon*. Similar observations were recorded in *Agama agama* (Haines, 1969), *Calotes* (Mathur and Goel, 1976), *Uromastyx microlepis* (Mohammed, 1986), several geckos (Mohammed, 1988a; EL-Wetery, 1992) and in other reptiles (Abo-Eleneen, 2005).

In all studied species, the palmar sesamoids are represented as two calcified rudiments. Similar observations were recorded in *Acanthodactylus boskianus* and *Scincus scincus* (Abo-Eleneen, 2005). In the present species, the dorsal sesamoids are found in *Laudakia stellio*, *Acanthodactylus scutellatus*, *Chalcides ocellatus*, and *Varanus griseus*. Similar observations were recorded in *Scincus scincus* (EL-Wetery, 1992; Abo-Eleneen, 2005). However, the dorsal sesamoids are totally missing (Mohammed, 1990b; EL-Wetery, 1992; Abo-Eleneen, 2005) in *Stenodactylus petrii*, *Acanthodactylus boskianus* and *Sphenopus sepsoides*.

In the studied species, the patella is found in *Laudakia stellio* and *Chalcides ocellatus*, while the patella is totally missing in the other studied species. Generally, the patella is found in the elbow and in the knee regions of most lizards (Nauch, 1936; Haines, 1969) and in many mammals (Retterer and Vallois, 1912).

The hind limb of the present investigated amphibians and reptilians has sesamoids associated with the knee (cyamellae and lunulae). The knee joint are missing in *Laudakia stellio*. In *Hemidactylus turcicus*, the knee joint has one calcified lunulae and one calcified cyamellae.

In lacertidae, *Acanthodactylus scutellatus*, the knee joint has two calcified lunulae, while in *Chalcides ocellatus* these joints are completely missing. In *Varanus griseus*, the knee joint has one calcified lunulae only. In *Chamaeleo chamaeleon*, the knee joint has two calcified lunulae and one calcified cyamellae.

In general, lizards are variable in the presence or absence of these elements (Russell and Bauer, 1988; Mohammed, 1991b). In these cases, the sesamoids appear to be involved in grasping abilities of foot associated with digging modifications. The mechanical effect of sesamoids increases the leverage of muscle at joint. This may explain the inverse development of some prominences and nearly sesamoids (Haines, 1969; Alexander and Dimery, 1985). In mammals, the digital flexor tendon may modify the effect of sesamoids on the transmission of forces (Alexander and Dimery, 1985). In small lizards, slender tendons are vascular and depend on diffusion for their nutrition; this may be slow under such circumstances and the development of a sesamoid might solve the difficulty (Haines, 1969). The lateral movement is commenced by the extension of the knee joint which results in an anterior movement of the body (Brinkman, 1981). So, it may be concluded that there is a considerable variation in the placement and movements of the limbs in lizards. They seem to be associated with free rotation at the knee (Retterer and Vallois, 1912c). In *Sphendon*, there is a lunula and they appear in *Varanus* like fossils *Ponotsaurus* and *Opetiosaurus* (Nopcsa,

1903). On the other hand, Banchi (1900) considered the cyamella to be a remnant of a finy ray comparable to the tibia or fibula.

Varanus griseus is the only species studied in the present work consisting of the fibular patella. Similar observation was recorded in *Uromastyx microlepis* (Mohammed, 1986).

In the present species, the sole sesamoids are found in *Laudakia stellio*, *Hemidactylus turcicus*, *Chalcides ocellatus*, and *Chamaeleo chamaeleon*, while these sesamoids are totally missing in the other species studied. These sesamoids may play a role in burrowing in sand. In lizards, the hind limbs provide the majority of the power for locomotion (Urban, 1965). Similar observations were recorded in several scincids (Mohammed, 1990a, b). Romer (1956) has indicated the presence of such sesamoids in reptiles.

Finally, the epiphyses of the femur bone of the present species have suprapatellae. A suprapatella is found in *Laudakia stellio*, *Acanthodactylus scutellatus*, and *Chalcides ocellatus*, but totally absent in the other studied species. Similar observation was recorded in *Agama* (Holmgren, 1933), *Calotes* (Mathur and Goel, 1976), *Scincus scincus* and *Scincus mitranus* (Mohammed, 1990b; EL-Wetery, 1992).

General pattern of locomotion

Locomotion is considered one of the major functions within the ecology of an animal because of its importance during activities such as feeding, social interactions and predator avoidance (Brana, 2003). Many animals move through complex and heterogeneous physical environments at varying speeds and using different modes of locomotion (Nauwelaerts and Aerts, 2002). Obviously, animals must modulate their locomotor behaviour to adjust for changes in the external environment, resulting in changes of direction, speed or posture (Irschick and Jayne, 1998; Biewener and Corning, 2001). The changes in locomotor behaviour are expected to be most extreme for species that move through different physical environments such as water and land (Biewener and Gillis, 1999).

Comparison of the movement pattern of the present lizards with that of other previously studied lizards, as *Basiliscus* (Snyder, 1949), *Crotaphytus* (Snyder, 1952), *Varanus*, *Kamodensis*, *Phrynocephalus*, *Teratoscincus* (Sukhanov, 1974), *Gekko gekko* (Russell, 1975, 1981), *Iguana* (Brinkman, 1981), *Amphibolurus nuchalis* (Garland, 1985), *Lacerta vivipara* (Avery et al., 1987), and several other geckos (Mohammed, 1991b, 1992b) showed that the most important variation was present in the arcs described by the movements of the limb segments and in the placement and movements of the manus and the pes. Despite this variation, the pattern of movement of the limb segments is constant in the general features.

In general, the locomotion of species is mostly referred to as the femoral retraction that primitively occurred in a near-horizontal plane (Rewcastle, 1983), with the crus moving in a near vertical plane, resulting in a force with potential posterior and lateral components, since the knee describes an arc about the acetabulum in a horizontal plane. Femoral backswing thus results in a reorientation of the knee joint axis so that it lies parallel to the body long axis (Rewcastle, 1983). As the knee joint does not allow rotation of the crus, the crus rotates on the pes to result in an orientation of the crural long axis perpendicular to the pedal long axis. Without the rotatory movements that occur at the knee and ankle, the lower limb elements would not be able to produce caudally directed thrust. Pedal plantar flexion is important as it enables the pes to act as an additional limb lever (Brinkman, 1981).

Both *Laudakia stellio* and *Acanthodactylus scutellatus* are characterized by bipedal locomotion which is related

to rapid locomotion in the context of escaping from predators. Similar observations were recorded (Belkin, 1961; Snyder, 1967). Also, this observation was discussed by Annandale (1902) in the agamid lizard *Calotes versicolor* and Thomas (1902) in *Lacerta viridis*. Other authors recorded bipedalism in lizards teiids (Urban, 1965), lacertids and varanids (Sukhanov, 1968). The phenomenon of bipedal locomotion in lizards has received considerable attention, beginning with the observations of Cope (1875) on *Basiliscus vittatus*, and de Vis (1884) and Saville-Kent (1898) on *Chlamydosaurus kingi*. Bipeds can be divided into two general groups - primarily terrestrial species living in open, sandy or rocky areas that may be classed as arboreal or semi-arboreal.

Given inoperability of the fifth digit in cursorial locomotion, it is surprising that a greater number of lizards, which do not habitually climb, have lost the fifth digit. As Robinson (1975) has pointed out, however, for a small animal there are few types of terrain which are absolutely level and where a strong grip of the substrate is not of value. While facultative bipedalism appears to occur in ground-dwelling lizards living in open habitats, many bipedal types are also good climbers (*Basiliscus* and *Physignathus*) and thus there is strong selection pressure to retain a functional fifth digit. *Sitana* appears not to climb (Subba-Rao and Rajabai, 1972) but instead seeks out holes located beneath bushes to run into when being pursued (Smith, 1935).

In the present geckos (*Hemidactylus turcicus*), two feet are in contact with the substratum during the rapid movement and three on occasion. Similar observation was recorded in *Gekko gekko* (Russell, 1975). In *Lacerta oxycephala*, four feet are in contact with the substratum for over half of the time and three feet for over three quarter of the time (Arnold, 1998). In all the present geckos, the pes is placed into the locomotor surface with the digits directed anterolaterally. Similar observation was recorded in normal limbed lizards (Schaeffer, 1941). The present geckos have also developed a symmetrical foot in which the line of contact of the distal ends of the metatarsals with the substrate lies approximately perpendicular to the body axis owing to the increase in length of the first to fourth metatarsals. Similar observation was recorded by Brinkman (1981) and Soliman (1997).

Zaff et al. (1999) noted that in the climber, the fore limbs become more important in the production of locomotor thrust and the maintenance of grip and documented more powerful shoulder retractor muscles in *Gekko*, and higher flexion moments across the elbow, preventing the animal from falling backwards when on vertical surfaces. These observations are parallel with the qualitative observations of Arnold (1998).

The locomotor behaviour is affected by a combination of limb movement relative to the girdles and flexion of the spinal cord; the sinusoidal movement is the characteristic movement of these animals. Similar observation was recorded in several lizards (Schaeffer, 1941; Snyder, 1949; Russell, 1975; Brinkman, 1981).

In the present climbing geckos (*Hemidactylus turcicus*), the possession of the setae may employ a distinctive feature for their locomotion; these setae are protected during the locomotion by holding the pad perpendicular to the surface except during climbing where the hyperextension occurs. These findings confirm those obtained by Russell (1975) who stated that the protection of the pad dictates the way to which locomotion can be brought.

It is interesting to conclude that the climbing geckos depend not only on their claws in the process of the climbing, but also on developing distinctive features that characterize most of the climbing geckos, the adhesive pads. The possession of these pads dictates certain morphological and osteological modifications in the digits and also, the way of movement is greatly affected by the

possession of these pads. Generally, these modifications are for supporting, protecting and operation of these pads. On the other hand, the digging geckos do not possess any adhesive pads on their digits as the presence of these pads and their setae may prevent the normal locomotion and digging in the sandy area.

Methods of locomotion in lizards vary according to the nature of the substrate. As regards locomotion on relatively solid substrates, utilizing two or four limbs, many lizards are able to swim (Sukhanov, 1968; Dawson et al., 1977). No aquatic adaptation occurs in the limb structure of living lizards (Romer, 1956). Generally, during swimming, the limbs are held depressed to the body and the tail provides the propulsive force (Tercafs, 1961; Guibe, 1970). This mechanism of propulsion has been referred to as sculling (Seymour, 1982). The only taxa recorded to employ the limbs to affect progression in water are *Tarentola mauritanica* (Gekkonidae), *Chamaeleo dilepis* (Chamaelonidae), and the scincis *Trachydosaurus rugosus* (Tercafs, 1961). Sand swimming occurs in a variety of lizards, with body movements very similar to those seen in swimming in water (Sukhanov, 1968). Sand burial techniques in 23 species of the iguanid *Liolaemus* (Halloy et al., 1998) revealed three distinct modes of burial, and head-first burial. These modes differ primarily in the movements of the head and tail, with limb use across taxa remaining relatively constant.

In the present work, in scincidae (*Chalcides ocellatus*), the plates of limbs are with lateral projections which form fine fringes. They seem to be together with the claws to have an essential function in preventing the limb from sinking into fine loose sand. Similar observations were recorded in several scincids (Mohammed, 1990b, EL-Wetery, 1992; Mostafa and Abo-Eleneen, 2006). It also appears to be used in a controlled way during excavation as in the burrowing webbed gecko *Palmatogecko* which used the digital web (Procter, 1928).

At slow speeds in scincids, three or four limbs support the animal but as the speed increases, fewer limbs are required to support the body simultaneously and the support pattern drops to two or even one limb. Kenins (1977) demonstrated that a true stretch reflex is present in the muscles of the hind limb of the scincid, the response being mediated monosynaptically and resembling the mammalian pattern.

In *Varanus griseus*, all four of the feet are in contact with the substratum for one-quarter of the time during walking. The increased musculature rather than bone compensates for weight support in this taxon. Similar observations were recorded by Christian and Garland (1996) who found that the larger species have longer limbs relative to snout-vent length, but relatively shorter feet and thicker limbs.

In the two species of varanids, bipedalism may also be involved in defensive posturing. Similar observation was recorded by Loveridge (1934) who illustrated a tripod defensive stance in *Varanus gouldii*, in which the erect body is balanced on the hind legs and tail. Allen (1972) reported such posturing in this species as a component of intraspecific ritualized combat. Murphy and Lamoreaux (1978) described bipedal defensive posturing in *Varanus mertensi* and similar bipedal defensive posturing has been reported for *Varanus bengalensis* (Deraniyagala, 1958), *Varanus giganteus* (Waite, 1929) and *Varanus salvator* (Honnegger and Heusser, 1969).

In *Chamaeleo chamaeleon* of the present study, lateral undulatory movements are reduced and the orientation of the pectoral girdle on the sternum is vertical rather than horizontal. Peterson (1984) discussed that the displacement of the scapulocoracoid on the sternum contributes significantly to stride length in place of lateral undulation and replaces the whole body movements of terrestrial forms in enhancing stride length.

Peterson (1984) and Abu-Ghalyun et al. (1988) suggested that the limb posture of *Chamaeleo*

chamaeleon is more erect than that of a general iguanian lizard. When *Chamaeleo chamaeleon* is stationary, the elbow and knee is sometimes lose to the body and hence, the limbs appear to be nearly in a parasagittal plane. Unlike most birds and mammals, during the locomotion of lizards, retraction of the femur changes the position of the limb in a manner that affects the perception of limb erectness.

Peterson (1984) found that chameleons have an increased longitudinal translation of the shoulder joint compared to other lizards, which enables chameleons to reach farther to bridge gaps. *Chamaeleo chamaeleon*, has an unusually large forward reach of the hind limb, which is a result of large amounts of femur protraction and knee extension rather than mobility of the hip joint, unlike the running gaits of many species of lizards, which have a prolonged suspended phase (Jayne and Irschick, 1999; Irschick and Jayne, 1999).

In *Chamaeleo chamaeleon* of the present study, the shift from a sprawling to a semi-erect stance is associated with a narrowing of the trackway, of narrow diameter. This is further associated with the grasping modifications of the manus and pes (Gasc, 1963). Modifications in the antebrachium of it permit manual contact to be maintained while the humerus moves through its semi-erect arc (Peterson, 1984).

Dodson (1975b) denoted that increased relative length of the limbs is the skeletal basis of the adaptation to increased movement. The hind limb provides the majority of the power for locomotion in lizards (Snyder, 1962; Urban, 1965). However, muscle contractile properties and the mechanical advantage are observed during ontogeny (Dodson, 1975a; Sperry, 1981; Carrier, 1983). On the other hand, lizards of the genus *Anolis*, who are branch-dwellers, tend to have shorter hind limbs (Losos et al., 1997; Kohlsdorf et al., 2001).

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