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Sesamoid elements in lizards

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This study reviews the morphology and topological distribution of sesamoid elements in the lizard families Gymnophthalmidae, Polychrotidae, Tropiduridae, Corytophanidae, Teiidae, Scincidae and Gekkonidae. We used cleared and stained specimens of 41 species, and describe 18 sesamoids of both fore and hindlimbs, finding a new sesamoid (*fabella lateralis*). The toplogical distribution of these elements is compared among lizard families and other vertebrates (mammals, anurans and birds), and we do not find putative synaphomorphies or autapomorphies. We recognize that the *intermedium* is not yet a clearly defined sesamoid, but state that this is the case for the *pisiform*.

Key words: forelimbs, hindlimbs, lizards, manus, osteology, pes

INTRODUCTION

Hypotheses about relationships of vertebrates based on their skeleton have been largely based on the skull, vertebrae and bones of fore and hindlimbs, whereas sesamoids (floating elements, mostly between joints) have received very little attention. Pearson & Davin (1921) defined these elements as ossifications of the hyaline cartilage, spacings or nodules of cartilage without ossification. Haines (1969) described the sesamoid elements as small fibrous nodules, typically located between tendons in pressure areas close to both elbows and knees. Sesamoid elements generally occur in points of tension in tendons, often where a narrow tendon transmits the force of a muscle through a union. Sesamoids reinforce the tendon to maintain its form under tension and increase the mechanical advantage of the translation of force (Nussbaum, 1982). Olson (2000), and Vickaryous and Olson (2007) used the word "sesamoid" for all small and unusual skeletal elements, and for ectopic mineralizations found in soft or connective tissue. They are generally ovoid, covered by dense regular bands of tissue (tendon or ligament) and located near the prominence of a bone. Olson (2000) also called these elements heterotopic bones or heterotopic cartilages, accessory bones or accessory cartilages, nodules of cartilage or condensation of connective tissue.

Sesamoid or extraskeletal elements represent an anatomical enigma, with high variability in size, form and position within and between taxa (Vickaryous & Olson, 2007). For lizards, sesamoids were broadly defined by Jerez et al. (2010), identifying ontogenetic patterns and classifying them in four types. Vickaryous and Olson (2007), and Maisano (2002c) regard sesamoids as informative elements to determine phylogenetic relationships between Squamata, with Vickaryous and Olson (2007) specifically highlighting the possibility that they could bear phylogenetic information at the level of families; Ponssa et al. (2010) also highlighted the use of sesamoid elements in anuran phylogenies. In the present study we address whether specific sesamoid elements are exclusive to one or several species of lizards, and whether sesamoids in lizards can be regarded as autapomorphic.

MATERIALS AND METHODS

We examined 41 lizard species deposited in the Museo Lorenzo Uribe of the Pontificia Universidad Javeriana (Bogotá, Colombia), Museo de Historia Natural of the Universidad Nacional of Colombia in Bogotá, the Universidad del Valle (Cali, Colombia), the Universidad de Antioquia (Medellín, Colombia) as well as loans from the Pontificia Universidad Católica of Ecuador (Quito, Ecuador) and the Museo Ecuatoriano de Ciencias Naturales. We included the families Gymnophthalmidae, Polychrotidae, Tropiduridae, Corytophanidae, Teiidae, Scincidae and Gekkonidae. Some specimens were cleaned and stained using the method of Dingerkus and Uhler (1977), with the following modifications: We changed tripsin when there was a strong muscle decomposing smell; we added time to each change of KOH-Glycerine solution; we added two or three drops of oxygenated water in each change of KOH-Glycerine; we did not add tymol at the end of the procedure. We did not find sesamoid elements as Alcian blue positive except when considering paraphalangeal elements. Whenever possible we examined both sexes for each species (Table 1).

Our anatomical terminology is based on the Nomina Anatomica Veterinaria (ICVAGN, 2005). We also followed

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Table 1. Presence/absence of sesamoids (including the *intermedium*) in the forelimbs among lizard species. P: Pisiform, PU: *Patella ulnaris*, PM: *Parafalanges manus,* SR: *Sesamum radiale*, I: *Intermedium*, SP: *Sesamoideum palmaria*, SMC: *Sesamoidea metacarpale,* SDM: *Sesamoideo digitorum manus*.

Family	Species	Sesamoid element							
		P	PU	PM	SR	I?	SP	SMC	SDM
POLYCHROTIDAE	*Anolis antonii*	X	X						X
	Anolis auratus	X	X				X		X
	Anolis "anoriensis"	X	X						X
	Anolis "podocarpus"	X							X
	Anolis aequatorialis	X	X				X		X
	Anolis agassizi	X	X				X	X	X
	Anolis apollinaris	X	X				X	X	X
	Anolis calimae	X	X			X	X		X
	Anolis chloris	X	X						X
	Anolis danieli	X	X				X		X
	Anolis eulaemus	X	X						X
	Anolis fitchi	X	X				X		X
	Anolis fraseri	X	X				X		X
	Anolis gemmosus	X	X						X
	Anolis heterodermus	X	X				X		X
	Anolis jacare	X	X				X		X
	Anolis latifrons	X	X				X		X
	Anolis ortonii	X	X				X		X
	Anolis otongae	X	X				X		X
	Anolis peraccae	X	X						X
	Anolis punctatus	X	X				X		X
	Anolis transversalis	X	X				X		X
	Anolis ventrimaculatus	X	X				X		X
	Polychrus marmoratus	X	X				X		X
CORYTOPHANIDAE	*Basiliscus* sp.	X					X		
TROPIDURIDAE	*Stenocercus trachycephalus*	X	X				X		X
SCINCIDAE	*Mabuya mabouya*	X					X	X	X
GYMNOPHTHALMIDAE	*Anadia bogotensis*	X				X			X
	Leposoma rugiceps	X					X		
	Leposoma southi	X					X		
	Pholidobolus montium	X				X	X		X
	Prionodactylus argulus	X				X	X		X
	Prionodactylus vertebralis	X				X	X		X
	Riama striata	X				X	X		
	Ptychoglossus stenolepis	X					X		X
	Tretioscincus bifasciatus	X					X		X
TEIIDAE	*Cnemidophorus lemniscatus*	X				X	X		X
GEKKONIDAE	*Gonatodes albogularis*	X	X		X				
	Gonatodes concinnatus	X	X		X				X
	Hemidactylus brooki	X	X	X	X			X	X
	Thecadactylus rapicauda	X	X		X				

the second principle of the Nomina Anatomica Veterinaria (1973: XII) by the International Committee on Veterinary Anatomical Nomenclature: "Each term should be in Latin in the official list, but the anatomist of each country are free to translate the official Latin terms into the language of instruction". Thus, taking into account that most of the sesamoids do not have Latin names, we used them in this language. We argue that it is important to avoid long and descriptive names (e.g., some names in Ponssa et al. (2010) and Jerez et al. (2010). Using a stereomicroscope attached to a digital camera, photographs were taken using the software Motic (2012).

Abbreviations used in Figures and Appendix

MUJ: Museo Universidad Javeriana, MHUA: Museo de Herpetología, Universidad de Antioquia; QCAZ: Colección de Herpetología, Pontificia Universidad Católica de Ecuador; MECN: Museo Ecuatoriano de Ciencias Naturales; MRC: Field series María del Rosario Castañeda; IAvH: Instituto Alexander von Humboldt; MOA, MYM: Field series Mario Yánez Muñoz, Museo Ecuatoriano de Ciencias Naturales; LFO: Field series Luis Fernando Ortega; JAV: Field series Julián Andrés Velasco.

RESULTS

We characterize 18 sesamoids based on both position and size, describing their number and variability. We found no differences in the presence, absence or form of sesamoids according to sex. Tables 2 and 3 indicate the presence and/or absence of each sesamoid in the elbow, hand, knee and foot among lizard species.

Forelimb sesamoids (Fig. 1; Table 2)

Pisiforme (A): This lengthened sesamoid element was found towards the external face of the *carpalia*, and on the dorsal, distal and external zone of the ulna. Adjacent to the dorsolateral surface of the distal end of the ulna. This element is mineralized. This sesamoid was identified in all species.

Patella ulnaris (C, D): This sesamoid appears in the region of the elbow, immediately adjacent to the humerus and the ulna, and has a spherical form. It was found in all the species of the families Polychrotidae and Gekkonidae. This element is mineralized.

Sesamoidea radiales anterioris and *posterioris* (C): These sesamoids are round, characterized mainly by their reduced size in comparing with the other forelimb sesamoids except those of the fingers. They were found in the elbows and on the proximal zone of the radius of species pertaining to the Gekkonidae family. These elements are mineralized.

Sesamoideum palmaria (E): Depending on the species, these sesamoids dorsally displayed high variability in size and number when compared to the dorsal carpal sesamoids. They are situated in the ventral face, either of the metacarpals or carpals of palms. In *Anolis aequatorialis*, we identified variations in the form of these mainly cubical and spherical elements. We observed the presence of two large sesamoids which covered almost 60% of the palm of *Anolis auratus,* and sesamoids of rectangular cubical shape towards the external face of the palm of *A. transversalis*. Species that did not present this type of sesamoids were *A. antonii*, *A. chloris*, *A.* "*anoriensis*", *A.* "*podocarpus*", *A. eulaemus*, *A. peraccae*, *A. bogotensis*, *Hemidactylus brooki*, *Gonatodes albogularis*, *G. concinnatus* and *Thecadactylus rapicauda*.

Sesamoidea digitorum manus (F): These are rounded and the smallest sesamoid elements of the forelimb. We found two positions for these elements: They are placed in both the distal zone of penultimate phalanges and the first dorsal phalanges of the hand. Species that lack these elements are *Basiliscus* sp., *G. albogularis*, *H. brooki*, *Leposoma rugiceps*, *L. southi*, *R. striata* and *T. rapicauda* (Table 2).

Parafalanges manus: In *H. brooki*, we found lateral elements to the phalanges, the paraphalangeal elements (Russell & Bauer, 1988), although these cartilaginous elements were not explicitly considered by these authors as sesamoids. Here we consider them as possible sesamoids.

Sesamoidea metacarpale (G): These small and rounded elements were found at the distal ends of metacarpals. They are present in *A, agassizi*, *A. apollinaris* and *Mabuya mabouya,* (Table 2). They are mineralized in most species.

Hindlimb sesamoids (Fig. 2; Table 3)

Patella tibialis (C): This *patella* is normally large and rounded, on the distal area of the femur towards its dorsal surface. It is mineralized and present in all species.

Fabella lateralis (C, D): This *fabella* is of medium size in relation to *patella tibialis*, since the latter is large in almost all cases. The fabellae are mineralized, rounded and placed towards the internal face of femur (Table 3).

Fabella mesial (C): This sesamoid is different to the *fabella lateralis* by position and size. It is placed towards the external face of the distal end of the femur,

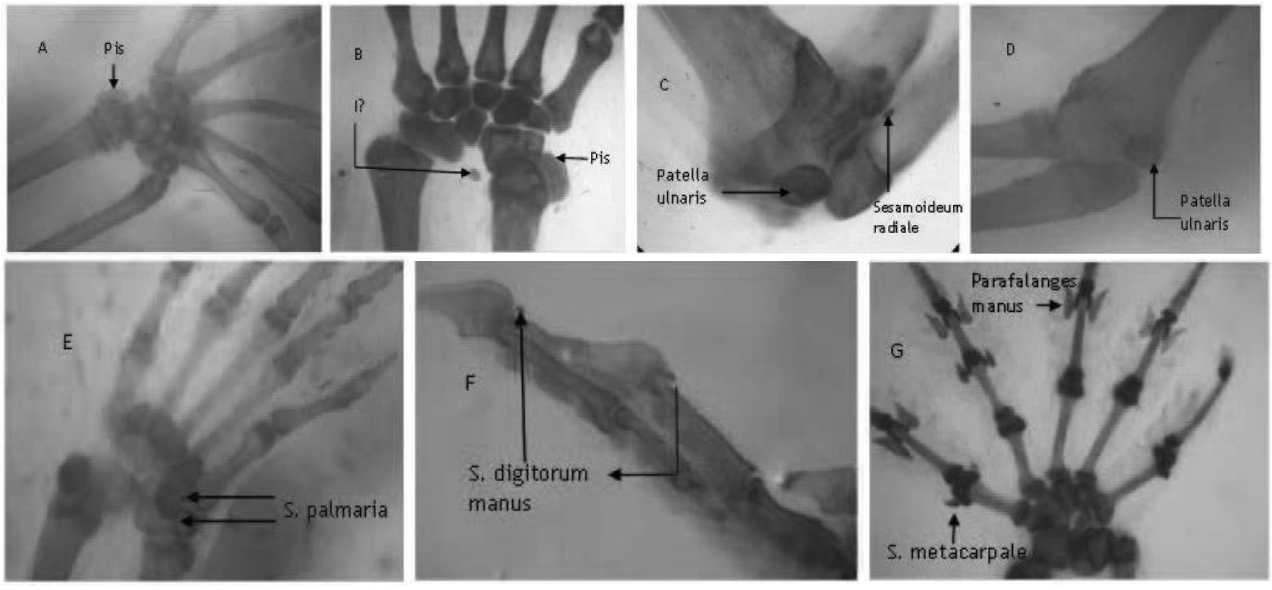

Fig. 1. Forelimb sesamoids. (A) *Anolis ventrimaculatus* (MUJ 338), right forelimb, ventral view of the hand. (B) *Anadia bogotensis* (JMH 174), right forelimb, dorsal view of the hand. (C) *Hemidactylus brooki* (Not catalogued), right forelimb, dorsal view of the elbow. (D) *Anolis ventrimaculatus* (MUJ 338), left forelimb, dorsal view of the elbow. (E) *Mabuya mabouya* (ICN 4322), right forelimb, ventral view of the hand. (F) *Mabuya mabouya* (ICN 4322), right forelimb, lateral view of the hand phalanges. (G) *Hemidactylus brooki* (Not catalogued), left forelimb, ventral view of the hand.

Table 2. Presence/absence of sesamoids in the hind limbs among lizard species. PT: *Patella tibialis*, L: *Lunula*, PP: *Parafalanges pedis*, FL: *Fabella lateralis*, FM: *Fabella mesial*, C: *Cyamella*, SPL: *Sesamoideum plantaria*, ST: *Sesamoideum tarsale,* SMT: *Sesamoidea metatarsale*, SDP: *Sesamoideum digitorum pedis*.

Family	Species	Sesamoid element									
		PT	L	PP	FL	FM	C	SPL	ST	SMT	SDP
POLYCHROTIDAE	*Anolis antonii*	X	X		X	X					X
	Anolis auratus	X	X		X						X
	Anolis "anoriensis"		X						X		X
	Anolis "podocarpus"		X								X
	Anolis aequatorialis								X		X
	Anolis agassizi	X	X						X		
	Anolis apollinaris		X								X
	Anolis calimae		X				X				X
	Anolis chloris	X	X		X						X
	Anolis danieli		X								X
	Anolis eulaemus	X	X								X
	Anolis fitchi		X			X					X
	Anolis fraseri	X	X								X
	Anolis gemmosus		X						X		X
	Anolis heterodermus	X	X						X		
	Anolis jacare		X								X
	Anolis latifrons	X	X		X	X			X		X
	Anolis ortonii		X						X		X
	Anolis otongae		X					X			X
	Anolis peraccae	X	X		X				X		X
	Anolis punctatus	X	X		X	X			X		X
	Anolis transversalis								X		X
	Anolis ventrimaculatus		X					X			X
	Polychrus marmoratus		X					X		X	X
CORYTOPHANIDAE	*Basiliscus* sp.		X								
TROPIDURADAE	*Stenocercus trachycephalus*	X	X					X	X		X
SCINCIDAE	*Mabuya mabouya*	X	X			X		X	X	X	X
GYMNOPHTHALMIDAE	*Anadia bogotensis*	X	X					X			X
	Leposoma rugiceps	X	X					X	X		X
	Leposoma southi	X	X					X	X		X
	Pholidobolus montium	X	X					X			X
	Prionodactylus argulus	X	X						X		X
	Prionodactylus vertebralis	X	X		X			X	X	X	X
	Riama striata	X	X			X					
	Ptychoglossus stenolepis	X	X		X	X	X	X	X		X
	Tretioscincus bifasciatus	X	X		X						X
TEIIDAE	*Cnemidophorus lemniscatus*	X	X		X			X			X
GEKKONIDAE	*Gonatodes albogularis*	X	X		X			X			
	Gonatodes concinnatus	X	X		X			X	X		X
	Hemidactylus brooki	X	X	X				X	X		X
	Thecadactylus rapicauda	X	X								

and is smaller than the *fabella lateralis* (Table 3). This is a mineralized element. *Sesamoideum plantaria* (I): The plantar sesamoid, like the *sesamoideum palmaris*, has a variety of forms and sizes (rounded, oval or elongated) covering almost 50% of the surface of the sole, and on the surface of some of these we also observed small rounded protuberances. This is a mineralized element. *Parafalanges pedis*: As with the *parafalanges manus* in *H. brooki*, we consider them as a possible sesamoid.

Sesamoideum tarsale (F): This extended and flattened element is large and near the proximal zone of the metatarsals; it covers the dorsal surface of the tarsals in almost all species. This is a mineralized element. *Lunula* (D, E): This sesamoid appeared in all studied species. It is placed between the joints of the knee between the femur and the tibia. It displays a triangular or, in some cases, a half-moon shape. This is a mineralized element. *Cyamellae anterioris* and *posterioris* (A, B): They were found in the tibiofemoral articulation of two species, *A. aequatorialis* and *P. stenolepis*. These are mineralized elements. *Sesamoidea digitorum pedis* (H): This sesamoid bears

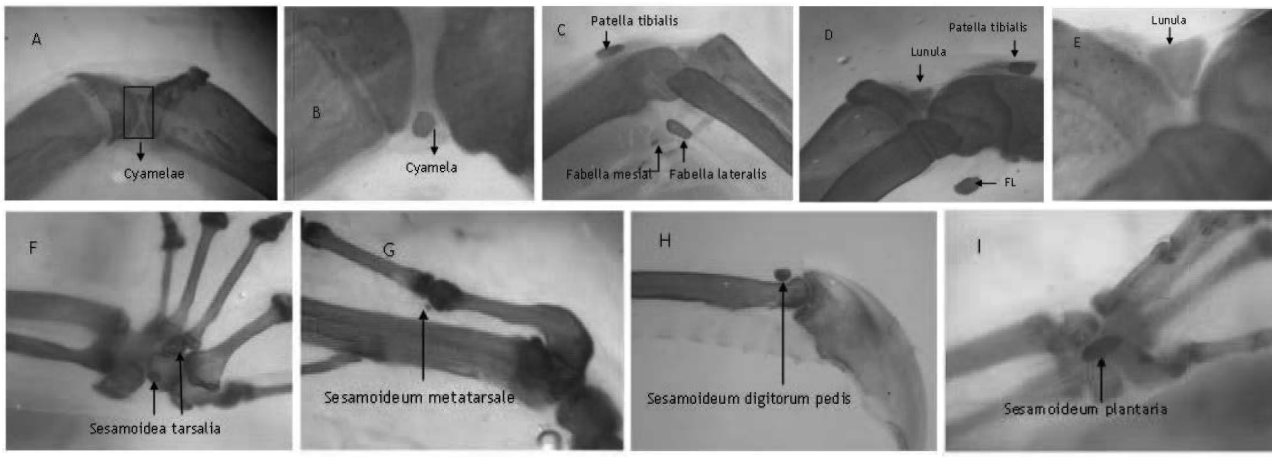

Fig. 2. Hind limb sesamoids. (A) *Anolis aequatorialis* (QCAZ 5375), left hind limb, ventral view of the knee. (B) *Anolis apollinaris* (LavH 3483) right hind limb, ventral view of the knee. (C) *Anolis punctatus* (QCAZ 3010), right hind limb, dorsal view of the knee. (D) *Anolis apollinaris* (lavH 3483), left hind limb, dorsal view of the knee. (E) *Anolis apollinaris* (lavH 3483), left hind limb, dorsal view of the knee. (F) *Hemidactylus brooki* (Not catalogued), right hind limb, dorsal view of the foot. (G) *Anolis antonii* (MUJ 376), left hind limb. (H) *Anolis aequatorialis* (QCAZ 5375), left hind limb, lateral view of the foot. (I) *Mabuya mabouya* (ICN 4322), left hind limb, ventral view of the foot.

the same characteristics as the *sesamoidea digitorum manus*, as it occurs towards the dorsal surface of the toes. It occurs in a large number of species. In almost all species hand and foot sesamoids occur simultaneously. However, *L. rugiceps* and *R. striata* do not have these sesamoids in their penultimate phalanges in their hands. These are mineralized elements. *Sesamoidea metatarsale* (G): We found it in the distal zone of the metatarsals. They are mainly of spherical shape and reduced size. This element was observed only in *P. marmoratus*, *M. mabouya* and *P. vertebralis*. This is a mineralized element.

From the total of the forelimb sesamoids, the pisiform and *Sesamoidea digitorum manus* are the most common, whereas the *Sesamoidea radiales*, and *Sesamoidea metacarpale* are the least common (Table 4). The most common hindlimb sesamoids are the *lunula* and the *sesamoidea digitorum pedis*. The least common are the *cyamella* and the *sesamoidea metatarsale* (Table 4).

We described 18 sesamoids for 41 species of lizards, three of which are common for the seven major groups: the *pisiforme*, the *lunulae* and the *sesamoidea palmaria*, appearing in 100%, 97.56% and 73.17% of samples, respectively (Tables 4 and 5). Four sesamoids appeared

Table 3. Presence/absence of sesamoid elements in anurans, lizards, and mammals. SR: *Sesamum radiale*, P: Pisiform, PU: *Patella ulnaris*, SDM: *Sesamoideo digitorum manus*, I: *Intermedium*, PM: *Parafalanges manus*, SMC: *Sesamoidea metacarpale*, SP: *Sesamoideum palmaria*; C: *Cyamella*, FL: *Fabella lateralis*, FM: *Fabella mesial*, L: *Lunula*, PT: *Patella tibialis*, SDP: *Sesamoideum digitorum pedis*, PP: *Parafalanges pedis*, SMT: *Sesamoidea metatarsale*, SPL: *Sesamoideum plantaria*, ST: *Sesamoideum tarsale*.

Sesamoid element	Anurans (Hoyos, 2003; Ponssa et al. 2010)	Lizards	Mammals (Lewis, 1958; Mivart, 1867; Orhan et al., 2005; Rothwell, 2001)
P		X	X
PU	X	X	X
C		X	X
SR		X	X
I		X	
SP		X	X
SMC	X	X	
SDM	X	X	
PT		X	X
L	X	X	X
FL	X	X	X
FM	X	X	X
SPL	X	X	
ST	X	X	
SMT		X	
SDP	X	X	
PM		X	
PP		X	

Table 4. Comparison of sesamoids found by Jerez et al. (2010) and found in the present work. Lizard major taxa: Aga: Agamidae. Cor: Corytophanidae, Gek: Gekkonidae, Gym: Gymnophthalmidae, Lio: Liolaemidae, Phr: Phrynosomatidae, Pol: Polychrotidae, Sci: Scincidae, Shi: Shinisauridae, Tei: Teiidae, Tro: Tropiduridae, Xan: Xantusidae.

Limb	Jerez et al. (2010)	This paper	Lizard groups (this paper)	Jerez et al. (2010)
Forelimb	Distal phalangeal sesamoid	*Sesamoidea digitorum manus*	Pol, Sci, Tro, Gym, Gek, Tei	Gek, Sci, Gym, Tei, Xan, Shi, Lio, Phr, Pol, Aga
Forelimb	Pisiform	*Pisiform*	Gek, Sci, Pol, Cor, Tro, Gym, Tei	Gek, Scin, Gym, Tei, Xan, Shi, Lio, Phr, Pol, Aga
Forelimb	Sesamoid dorsal to the pisiform. Sesamoid dorsal to the distal ulnar epiphysis; sesamoid dorsal located between humerus, radius and ulna; sesamoid located between proximal radial and ulnar epiphysis	*Sesamoideum radialis*	Gek	Gek, Gym
Forelimb	Ulnar patella	*Patella ulnaris*	Pol, Gek, Tro	Gek, Xan, Shi, Lio, Phr, Pol, Aga
Forelimb	Ventral metacarpophalangeal sesamoids (I–IV) Sesamoid lateral to the distal epiphyses of the metacarpals	*Sesamoidea metacarpale*	Pol, Sci, Gek	Lio
Forelimb	Second and third palmar sesamoid; palmar sesamoid	*Sesamoideum palmaria*	Pol, Gym, Cor, Sci, Tro, Tei	Sci, Gym, Tei, Xan,
Forelimb	Sesamoid ventral to the proximal radial epiphysis	*Sesamoideum radialis posterioris*	Gek	Gek, Gym
Forelimb	Not described	*Intermedium*	Pol, Gym,Tei	
Forelimb	Not described	Metaplasic bone of the ulnar epiphysis	Pol, Gym	
Hind limb	Tibial patella	*Patella tibialis*	Pol, Tro, Sci, Gym, Tei, Gek	Gek, Sci, Gym, Tei, Xan, Shi, Lio, Phr, Pol, Aga
Hind limb	Sesamoid ventral to the proximal fibular epiphysis; sesamoid ventral to the distal femoral epiphysis	*Cyamellae*	Pol, Gym	Gym, Tei, Lio
Hind limb	tibial lunulae; dorsal pre-axial tibiofemoral lunula; ventral pre-axial tibiofemoral lunula	*Lunulae*	Pol, Cor, Tro, Sci, Gym, Gek, Tei	Gek, Sci, Gym, Tei, Xan, Shi, Lio, Phr, Pol, Aga
Hind limb	Parafibula	It is the *patella tibialis*		
Hind limb	Lateral post-axial tarsal sesamoid; dorsal tarsal sesamoid, located between proximal tarsal and distal tarsal IV; sesamoid lateral and distal to the distal epiphysis of metatarsal V; sesamoid dorsal to the metatarsal V; Sesamoid in the pre-axial niche of the proximal head of metatarsal V; dorsal sesamoid located between distal tarsal IV and metatarsal IV; Sesamoid ventral to the articulation of the proximal tarsal and metatarsal; ventral pre-axial tarsal sesamoid	*Sesamoideum tarsale*	Pol, Tro, Sci, Gym, Gek	Gek, Sci, Gym, Tei, Xan, Lio, Phr, Pol, Aga
Hind limb	Ventral metatarsophalangeal sesamoids Sesamoid lateral to the distal epiphyses of the metatarsals	*Sesamoideum metatarsale*	Pol, Sci, Gym	Lio
Hind limb	Plantar sesamoid	*Sesamoideum plantaria*	Pol, Tro, Sci, Gym, Tei, Gek	Gek, Sci, Gym, Tei, Xan, Lio, Aga
Hind limb	Not described	Metaplasic bone of the tibial epiphysis	Pol, Gym	
Hind limb	Not described	*Sesamoidea digitorum pedis*	Pol, Tro, Sci, Gek, Tei, Gym	
Hind limb	Not described	*Fabella lateralis*	Pol, Gym, Tei, Gek	
Hind limb	Not described	*Fabella* mesial	Pol, Sci, Gym	

in most of the species but their distribution was not observed in all groups. The *sesamoidea digitorum manus* and *digitorum pedis* were present in 85.37% and 87.80% of the species studied, respectively. The *patella ulnaris* and the *patella tibialis* were observed in 70.73% and 68.29% of species, respectively. The remaining sesamoids were recorded as follows: the *cyamella* and the *sesamoidea radialis* (14.64%), the *sesamoideum metacarpale* (9.76%), the *fabella lateralis* (36.59%), the *fabella mesial* (17.07%), the *sesamoideum plantaria* (36.59%), the *sesamoideum tarsale* (43.90%), the *sesamoideum metatarsale* (7.32%), the *parafalanges manus* (2.43%) and the *parafalanges pedis* (2.43%).

DISCUSSION

There is a high amount of topological, morphological and taxonomic diversity of sesamoids in vertebrates (Vickaryous & Olson, 2007). More than ten sesamoids have been found in bone joints, of which some are more frequent than others. Jerez et al. (2010) identified 41 sesamoids in lizards based on their forelimb and hindlimb position.

Pearson and Davin's (1921) classification of sesamoids was proposed based on morphology, classifying *patella*, *lunula*, *fabella* and *cyamella*. The *patella* is an important sesamoid for pathological, evolutionary, biomechanical and orthopedic studies (Bland & Ashhurst, 1997; Tecklenburg et al., 2006; Vickaryous & Olson, 2007). This element is ossified, proximally disposed and adjacent to the distal ends of both the femur and the humerus. In the area where this sesamoid is found, tendons are present around the bone, which is frequently swollen and modifies the histological semblance of the sesamoidal structure with more ossification (Haines, 1969). In the mature skeleton, the *patella* possesses two edges: a proximal pole and a distal or inferior pole. It also has two surfaces (external and articular). The *patella* is made up of a crust lamellar bone with a trabecular core and a deep cartilage alignment in the surface. Vickaryous and Olson (2007) stressed that according to some authors the *patella* is not a true sesamoid but a development of the complexity of the tendon in either the knee or the elbow. However, this possibility is dismissed from a developmental and adult position point of view.

Several sesamoids or meniscal ossifications appear in the edges of semi-lunar cartilages (*lunula* according to Pearson & Davin, 1921) at the inferior (or distal) ends of the femur, forming a joint area in the knee (Haines, 1969; Vickaryous & Olson, 2007). This element differs from the rest of sesamoids and from the ossified tendons in both position and development (Vickaryous & Olson, 2007).

Other sesamoids such as the lateral *fabella* have been found in frogs, lizards and mammal species. A medial *fabella* is present in some mammals (Vickaryous & Olson, 2007). This small sesamoid bone is usually found in a position behind the lateral condyle or the femur (where it is generally evident in the frontal view of the knee); is usually not placed in the lateral head of the *gastrocnemius* muscle and almost never in the medial head (Houghton-Allen, 2001). The *cyamella* is the smallest known sesamoid, and has been poorly studied. Vickaryous and Olson (2007) stated that it was only observed in some birds and mammals. Hoyos (2003) and Jerez et al. (2010) did not find this sesamoid in frogs and lizards.

Our aim was to comprehensively describe and present the topological distribution of sesamoids in lizards for the first time. We also aimed to provide information about both unique and shared elements in comparing lizard sesamoids with mammals and amphibians. Fourteen out of the 18 sesamoids described herein have already been reported in reptiles. Besides those described by Jerez et al. (2010; Table 4), we additionally found the *patellae ulnaris* and *tibialis* (Camp [1923: 409] stated that "Banchi (1900) has named this bone *patella tibialis* parafibula"; Pearson & Davin 1921; Haines, 1969; Olson, 2000; Maisano, 2001; Vickaryous & Olson, 2007); they are possibly formed by hyaline cartilage, mineralized fibromuscular tissue or tendon (Haines, 1969). Both elements are considerably variable and can be found in knees and elbows. The *lunulae* of lizards are related to the free rotation of the knee (Pearson & Davin, 1921; Haines, 1969; Maisano 2001, 2002a; Vickaryous & Olson, 2007). We described these elements as *sesamoidea digitorum manus* and *sesamoidea digitorum pedis*, which were referred to as dorsal sesamoids by Haines (1969), Mohammed (1988b, describing the appendicular skeleton of *Bunopus tuberculatus*), and Maisano (2002a, for *Callisaurus draconoides* and *Uta stansburiana*). Russell and Bauer (1988) also described these sesamoids in gekkonids as paraphalangeal elements, and Maisano (2002a) referred to them as *sesamoidea palmaria*. Mohammed (1988a) described the presence of some sesamoids in both the hindlimb (the pisiform, *lunula*, *patella ulnaris* and *sesamoideum plantaris*) and fore limb (*sesamoidea palmaria*).

To our knowledge, the *fabella lateralis* described herein is reported in lizards for the first time. Pearson and Davin (1921) identified the true *cyamellae* and the *fabellae* as parafibula and sesamoid respectively, and the *sesamoidea metatarsale* have not been reported for any other vertebrate taxon. Five further sesamoids have been originally described for other vertebrates, but not yet for lizards. *Cyamellae*, *fabellae*, *mesial* and *lateralis* were reported in several species of mammals (Pearson & Davin, 1921; Budras et al. 1989; Olson, 2000; Hoyos, 2003). The *sesamoideum ulnaris* was reported in rodents (Greene, 1935), and the *sesamoideum tarsale* was previously reported in frogs (Nussbaum, 1982; Olson, 2000; Hoyos, 2003). Jerez et al. (2010) described a sesamoid in the *extensor carpi ulnaris* muscle, in the same position where we found our *sesamoiea radiales anterioris* and *posterioris*. Nussbaum (1982) reported further sesamoids in tarsal segments of the frog hindlimbs (family Pipidae): the *cartilago plantaris* in the subarticulate region of the foot, the *cartilago sesamoides* in the calcaneus ligament of the hindlimb and the *Os* sesamoidum *tarsale* in the proximal end of the *aponeurosis plantaris*. Hoyos (2003) reported the presence of these sesamoids (*cartilago plantaris*, *cartilago sesamoides* and the *Os sesamoidum tarsale*)

and metacarpal sesamoids in further anuran species.

Most but not all of their sesamoids previously described by Jerez et al. (2010) corresponds to what we describe herein, however with differing nomenclature (Table 5). Jerez et al. (2010) claimed that the *sesamoideum palmaria* is present in all lizards except gekkotans, and is associated with the tendon of the *m. flexor digitorum longus* (Zaaf et al. 1999; Maisano 2002c), in accordance with our observations. Russell and Bauer (2008) reviewed the locomotory apparatus of lizards, including brief descriptions of some of the sesamoid elements described by us. The bony element found between the radius and ulna seems a sesamoid in *Anolis calimae*, *A. bogotensis*, *Pholidobulus montium*, *P. vertebralis*, *Prionodactylus argulus*, *Riama striata* and *Cnemidophorus lemniscatus* because it lies in the in the *spatium interosseum*. However, several authors identified it as the *intermedium*, a carpal element. Camp (1923) stated that the *intermedium* is absent in most of the species of lizards, and Stokely (1950) recognized its occurrence in Ascalabotan and Autarchoglossan lizard species. Fabrezi et al. (2007: 908) state that they "failed to find an embryonic *intermedium*" in the lizard carpus, and that they are not sure that the element placed between the *ulnare* and *radiale* is the *intermedium* (see their Fig. 13). Leal et al. (2010) recognized the *intermedium* as a transitory element in both *carpus* and *tarsus* during the development of limbs in *Gonatodes albogularis* (Gekkonidae). They did not find this carpal element "floating" in the *spatium interosseum* in any species studied.

The pisiform was always considered as a sesamoid, however not unambiguously. It has an anomalous position compared to other bones of the carpus (Gillies, 1929; May, 1996). Gillies (1929: 383) suggested that the pisiform appeared because "the most ulnar of the *centralia* was displaced to the lateral margin of the ulnare and became the Pisiform". However, Jerez et al. (2010) sustained this element as a sesamoid by investigating its relationships with the *mm. extensor carpi ulnaris*, *flexor carpi ulnaris*, *flexor retinaculum* and *abductor digitorum*. May (1996) shares the same point of view for humans. Fabrezi et al. (2007: 911) stated that "the pisiform is one of the numerous sesamoids that develop without spatial connectivities with the primary cartilages of the limb". A decision of whether both elements are sesamoids will be based on a unified definition of sesamoids, and on broader ontogenetic studies in lizards.

The presence of these sesamoids in several groups of vertebrates is assumed to represent a primary homology (*sensu* de Pinna, 1991) based on both structure and position. Sesamoid elements are of similar shape, and are found in two or more different organisms. A topographic similarity of limb sesamoids in lizards and other vertebrates is present (Schuh, 2000). Based on primary homology definition, the nomenclature proposed by Pearson and Davin (1921), Greene (1935), Nussbaum (1982), Budras et al. (1989), Olson (2000) and Hoyos (2003) is used in the elements described here, since the morphology and distribution of some sesamoids are apparently identical. Nussbaum (1982), Olson (2000), Hoyos (2003) and Vickaryous and Olson (2007) highlighted the possibility that sesamoid elements could bear phylogenetic information at the level of families in frogs and/or lizards. Lizards are characterized by a large number of ossifications (Maisano, 2002a). According to Olson (2000), sesamoids must be ontogenetically stable and relatively constant within a population in order to be informative; if multiple elements share mechanisms of common development, these ossifications do not have to be treated as independent. Vickaryous and Olson (2007) used sesamoids to establish phylogenetic relationships in frogs of the family Pipidae, considering the *lunulae*, the *fabella*, the cartilago *sesamoides*, the *patella ulnaris* and a radial sesamoid. Vickaryous and Olson (2007), and Maisano (2002c) considered both the *patella ulnar* and *tibial* and the palmar sesamoid to determine phylogenetic relationships in Squamata (Iguania, Gekkota, Teiioidea, Lacertidae, Xantusiidae, Scincidae, Anguidae and Varanoidea). According to these authors, the Scleroglossa possess sesamoids of the preaxial ligament as a shared character, and the Autarchoglossa are characterized by the plantar sesamoid.

Conclusions

Sesamoids occur in all lizards examined, and no sesamoid elements are unique for one species. We could not define families of lizards based on the the absence or presence of unique sesamoid elements. We identified some sesamoid elements not described in other tetrapods, but it is necessary to explore their presence and topological distribution in mammals and birds. Although we do not aim to resolve the problem of the origin of sesamoid elements (mainly Gillies, 1929; May, 1996; Fabrezi et al., 2007 and Leal et al., 2010) we argue that (i) the *intermedium* needs further study to define whether it is a sesamoid element, and (ii) the pisiform is a sesamoid. We furthermore argue that sesamoid elements can be used to resolve relationship hypotheses after more detailed morphological analyses. It is however necessary to expand existing studies across more families and species of lizards, taking morphological and functional aspects of sesamoid elements for locomotion into account.

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APPENDIX

Appendix: Details of species examined

Family	Species	Number of individuals	Sex M=male F=Female	Number of collection
POLYCHROTIDAE	*Anolis antonii*	1	M	MUJ 376
	Anolis auratus	1	M	MUJ 590
	Anolis "anoriensis"	3	M	MHUA 11285
			M	MHUA 11283
			M	MRC 086
	Anolis "podocarpus"	1	F	QCAZ 6047
	Anolis aequatorialis	1	F	QCAZ 5375
	Anolis agassizi	1	M	IavH 5007
	Anolis apollinaris	1	M	IavH 3483
	Anolis calimae	1	F	LFO 009 (MHUA)
	Anolis chloris	1	F	QCAZ 3215
	Anolis danieli	2	F	MHUA 11300
			F	MHUA 11291
	Anolis eulaemus	1	M	JAV 258
	Anolis fitchi	2	M	QCAZ 6742
			M	QCAZ 5715
	Anolis fraseri	1	F	QCAZ 0093
			--	QCAZ 2112
	Anolis gemmosus	5	M	QCAZ 6781
			M	QCAZ 881,
			M	QCAZ 2067
			--	MECN 1494
			--	MECN 1495
	Anolis heterodermus	5	F	MHUA 10504
			--	MHUA 10632
			--	Not catalogued
			M	Not catalogued
			--	Not catalogued
	Anolis jacare	1	F	MHUA 10632
	Anolis latifrons	2	F	JAV 140
			M	JAV 152
	Anolis ortonii	1	--	QCAZ 2160
	Anolis otongae	2	F	QCAZ 3872
			M	QCAZ 2052
	Anolis peraccae	1	--	QCAZ 3132
	Anolis punctatus	2	F	QCAZ 3010
			--	QCAZ 2924
	Anolis transversalis	2	F	MOA 804
			M	QCAZ 5435
	Anolis ventrimaculatus	3	--	MUJ 338
			--	MUJ 336
			--	MUJ 341
	Polychrus marmoratus	1	M	QCAZ 1531
CORYTOPHANIDAE	*Basiliscus sp.*	1	--	Not catalogued
TROPIDURADAE	*Stenocercus trachycephalus*	2	--	MUJ 635
			--	Not catalogued
SCINCIDAE	*Mabuya mabouya*	3	M	ICN 2400
			--	ICN 4322
			--	ICN 4325
GYMNOPHTHALMIDAE	*Anadia bogotensis*	5	--	JMH 174
			--	JMH 194
			--	JMH 812
			--	ICN 2897
			--	ICN 2178
	Leposoma rugiceps	1	F	ICN 637
	Leposoma southi	3	M	UVC 5168
			H	UVC 8990
			M	UVC 8993
	Pholidobolus montium	2	M	ICN 5609
			M	ICN 5603
	Prionodactylus argulus	1	F	ICN 5708
	Prionodactylus vertebralis	3	--	ICN 5719
			M	UVC 5178
			F	UVC 5181
	Riama striata	2	--	ICN 2372
			--	ICN 2373
	Ptychoglossus stenolepis	1	M	UVC 7761
	Tretioscincus bifasciatus	1	--	ICN 5588
TEIIDAE	*Cnemidophorus lemniscatus*	4	M	ICN 5536
			--	ICN 5551
			--	ICN 5546
			M	ICN 5548
GEKKONIDAE	*Gonatodes albogularis*	1	F	MUJ 665
	Gonatodes concinnatus	1	M	MUJ 733
	Hemidactylus brooki	1	F	Not catalogued
	Thecadactylus rapicauda	1	--	Not catalogued