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How common are cranial sesamoids among squamates?

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Abstract

Sesamoids are elements that originate as intratendinous structures due to genetic and epigenetic factors. These elements have been reported frequently in vertebrates, although cranial sesamoids have been recorded almost exclusively in non-tetrapod Osteichthyes. The only tetrapod cranial sesamoids reported until now have been the transiliens cartilage (of crocodiles and turtles), and another one located in the quadrate-mandibular joint of birds. Here, we examined seven squamate species using histological sections, dissections of preserved specimens, dry skeletons, cleared and stained specimens, computed tomographies (CT), and report the presence of other cranial sesamoids. One is attached to the cephalic condyle of the quadrate, embedded in the bodenaponeurosis and jaw adductor muscles of *Ophiodes intermedius* (Anguidae). The other sesamoid is found at the base of the basicranium of several squamates, capping the sphenoccipital tubercle, on the lateral side of the basioccipital–basisphenoid suture. This bone has previously been reported as "element X." We reinterpret it as a basicranial sesamoid, as it is associated with tendons of the cranio-cervical muscles. This bone seems to have the function of resisting tension-compression forces generated by the muscle during flexion the head. This element was previously known in several squamates, and we confirmed its presence in three additional squamate families: Gymnophthalmidae, Gekkonidae, and Pygopodidae. The evidence suggests that cranial sesamoids are a widespread character in squamates, and it is possible that this feature has been present since the origin of the group.

KEYWORDS
basicranial sesamoid, element X, joints, quadrate sesamoid

1 | INTRODUCTION

Sesamoids are organized, intratendinous, or intraligamentous structures, ranging histologically from unmineralized fibrocartilage to bone. They are variable structures and the definition of the term is matter of discussion (Haines, 1969; Jerez, Mangione, & Abdala, 2010; Le Minor, 1987; Maisano, 2002; Pearson & Davin, 1921a, 1921b; Regnault, Hutchinson, & Jones, 2016; Regnault, Jones, Pitsillides, & Hutchinson, 2016; Retterer & Lelièvre, 1911; Romer, 1956; Samuels, Regnault, & Hutchinson, 2017; Sarin, Erickson, Giori, Bergman, & Carter, 1999; Vickaryous & Olson, 2007). Achieving a consensus about a definition of the term sesamoid is beyond the scope of this work. We, therefore, refer to the definition of Vickaryous and Olson (2007): "skeletal elements that develop within a continuous band of regular dense connective tissue adjacent to an articulation or joint." Some sesamoids seem to form as a consequence of mechanical stresses or forces (demonstrated by their absence in paralyzed embryos) (Drachman & Sokoloff, 1966; Hosseini & Hogg, 1991; Kim, Olson, & Hall, 2009), whereas others appear genetically determined (e.g., the patella or the palmar sesamoid) (Eyal et al., 2015; Niven, 1933; Ponssa, Goldberg, & Abdala, 2010; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016; Regnault, Pitsillides, & Hutchinson, 2014). Sesamoids are usually subject to compressive and tensile forces associated with tendons. They can work as a pulley (e.g., the patella in the knee joint), lever, or as a shock absorber (the patella in the knee joint functions as a pulley and seems to protect the tendon from the friction of the distal end of the femur) (Benjamin & Ralphs, 1998).

Biomechanical advantages have been attributed to sesamoids, such as increasing the moment arm of a muscle, protecting tendons as they wrap around joints or bone edges, or improving the ability of tendons to respond to compressive load, among many others (Jerez et al., 2010; Nussbaum, 1982; Otero & Hoyos, 2013; Pearson & Davin, 1921a, 1921b; Ponssa et al., 2010; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016; Samuels et al., 2017; Sarin et al., 1999; Summers, Koob-Emunds, Kajiura, & Koob, 2003; Tsai & Holliday, 2011).

There has recently been a growing interest in sesamoids, and modern techniques have changed the classical view of sesamoids (Haines, 1969; Jerez et al., 2010; Le Minor, 1987; Maisano, 2002; Pearson & Davin, 1921a; Romer, 1956; Sarin et al., 1999), facilitating the detection of these structures, and resulting in new discoveries that challenge previous interpretations (Doherty, 2007; Eyal et al., 2015; Gauthier, Kearney, Maisano, Rieppel, & Behlke, 2012; Ponssa et al., 2010; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016; Tsai & Holliday, 2011). For example, recent papers have presented data on the development of sesamoids, showing that the formation of the patella or the graciella occurs before the formation of the tendon, suggesting possible genetic determination of the formation of these structures (Doherty, 2007; Eyal et al., 2015; Ponssa et al., 2010). Eyal et al. (2015), using an innovative experimental design, showed that the patella is already well developed when the quadriceps tendon is still immature. It is also noteworthy that the near universal presence of some sesamoids such as the palmar sesamoid in tetrapods (Abdala, Manzano, Tulli, & Herrel, 2009; Jerez et al., 2010; Ponssa et al., 2010) or the pisiform in Amniota (Fabrezi, Abdala, & Oliver, 2007; Jerez et al., 2010), challenges the notion of sesamoids being highly variable structures. Previous studies have classified sesamoids according to their relationship with their associated tendons (embedded, glide, etc.) (Jerez et al., 2010; Vickaryous & Olson, 2007) and it cannot be excluded that these functional differences may be correlated with their ontogenetic trajectories.

Sesamoids have been described in several vertebrate groups, including non-tetrapod Osteichthyes (Datovo & Bockmann, 2010; Diogo, Oliveira, & Chardon, 2001; Summers et al., 2003), Anura (Hoyos, 2003; Olson, 2000; Ponssa et al., 2010), Squamata (Haines, 1969; Jerez et al., 2010; Maisano, 2002; Otero & Hoyos, 2013; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016), Aves (Chadwick, Regnault, Allen, & Hutchinson, 2014; Hutchinson, 2002; Regnault et al., 2014; Vanden Berge & Storer, 1995), and Mammalia (Camasta, 1996; Davis, 1964; Doherty, 2007; Flower, 1885; Parsons, 1904; Pearson & Davin, 1921a, 1921b; Samuels et al., 2017; Scott & Springer, 2016; Vickaryous & Olson, 2007). These elements, when compared among different groups, exhibit remarkable differences in their positions. The number of sesamoids is high in non-tetrapod Osteichthyes, where these elements are found mainly in the skull (Datovo & Bockmann, 2010; Diogo et al., 2001; Summers et al., 2003); whereas in tetrapods, sesamoids are primarily known from the appendicular skeleton (Chadwick et al., 2014; Doherty, 2007; Duncan & Dahm, 2003; Hoyos, 2003; Jerez et al., 2010; Joseph, 1951; Mohammed, 1988; Otero & Hoyos, 2013; Parsons, 1904; Ponssa et al., 2010; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016; Regnault et al., 2014; Samuels et al., 2017; Vera, Ponssa, & Abdala, 2015), or in the pelvic girdle (e.g., frogs) (Emerson, 1982; Manzano & Barg, 2005; Ponssa et al., 2010). Among tetrapods there are few reports of putative sesamoids in the skull: in the quadrate-mandible joint in the Kōkako bird *Callaeas cinerea* (Burton, 1973; Stonor, 1942); the transiliens cartilage of crocodiles and turtles (Holliday & Witmer, 2007; Iordansky, 1964; Schumacher, 1973; Tsai & Holliday, 2011); a cartilaginous sesamoid located in the bodenaponeurosis of the adductor muscles of the jaw (Tsai & Holliday, 2011); and between the basipterygoid and pterygoid bones of some squamates (Gauthier et al., 2012).

The marked difference of skull sesamoids of non-tetrapod Osteichthyes compared to Tetrapoda may be due to the number of movable joints (Iordansky, 1989), which require ligamentous and tendinous syndesmoses or sometimes synovial joints. These loose attachments of the cranial bones in Teleostei produce a highly kinetic skull, allowing for the specialized protractile feeding apparatus (Osse, 1985). The skull of tetrapods has a generally reduced number of bones, connected mainly by sutures, with the main movable units being the jaw, tongue, and the head as a whole. Among diapsid reptiles, squamates have developed movable amphikinetic skulls (Frazzetta, 1962, 1983, 1986; Iordansky, 1966, 1990, 1996; Metzger, 2002).

Compared to other tetrapods, squamates possess a highly kinetic skull (Frazzetta, 1962; Metzger, 2002); cranial mobility in squamates may influence the occurrence of sesamoids associated with their different mobile joints. In this article, we present new data of some cranial elements that are widespread in several lizard taxa.

2 | MATERIALS AND METHODS

We examined and dissected adult members of seven squamate species using a diversity of anatomical preparations (Appendix): histological sections; dissections of ethanol preserved specimens; dry skeletons; cleared, and stained specimens; high-resolution computed tomography (HRCT); and optimized protocols for diffusible iodine-based contrast-enhanced computed tomography (diceCT) (Gignac et al., 2016). The main goal of this article is to demonstrate the presence of cranial sesamoids in squamate reptiles, and to show that these elements are developed in several higher-level groups. Our sample size for some of the species is minimal; therefore, we do not intend to evaluate interspecific variation, or to use these elements as traits that can serve to diagnose species or clades.

For histological preparations, one formalin-fixed specimen of *Ophiodes intermedius* (FML 26455) was decalcified with formic acid, followed by tissue dehydration using ascending solutions of ethyl alcohol (75% to absolute). Tissue was cleared in xylene and embedded in paraffin wax. Sagittal serial sections (6 μm thick) were stained using hematoxylin and eosin and Mallory's trichrome (modified from Totty, 2002). We also examined stained histological sections of the head of two specimens of *Diplometopon zarudnyi* from the histological collection of

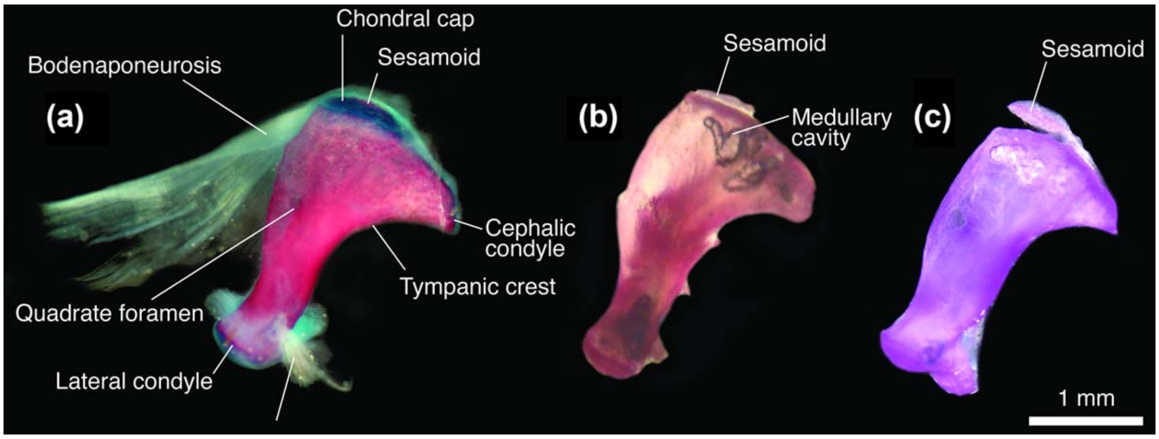

FIGURE 1 *Ophiodes intermedius*, lateral views of cleared and stained disarticulated left quadrates showing the quadrate sesamoids. Cartilages are stained in blue, calcified elements are stained in red. (a) FML 26303. (b) FML 26368. (c) No number, Teaching collection of the Cátedra de Vertebrados of the Universidad Nacional de Salta. Anterior to the left

Angus d'A. Bellairs (currently housed at Museum of Comparative Zoology at Harvard University).

Clearing and staining was conducted following the protocol of Bauer (1986), and we examined multiple specimens prepared with this technique (Appendix).

High-resolution computed tomographies (HRCT) of specimens were obtained at the University of Texas High-Resolution X-ray CT-Facility (Xradia MicroCT-scanner, Pleasanton, CA) and at the American Museum of Natural History in New York City (GE phoenix v|tome|x s240 system, Conroe, TX). All 3D-model rendering was performed using Avizo Lite 9.0.0 (Visualization Sciences Group). DiceCT-techniques were applied to render digital models of soft tissue associated with sesamoids in one *Zygaspis*. CT and diceCT-data sets and the scanning settings are freely available on the online repository MorphoSource (http://morphosource.org/Project "Squamate cranial sesamoids" P338).

Dissections and skeletons of *Amphisbaena bolivica* were examined. Two ethanol preserved specimens of *Amphisbaena bolivica* (FML 29585; 29586) were used to determine the location of element X and its relationship to the connective tissue and muscles of the neck. Four specimens of different sizes were examined to observe changes in element X through ontogeny.

The presence of element X was mapped using parsimony using a pruned metatree based on a recent molecular topology that includes only living taxa (Gamble, Greenbaum, Russell, Jackman, & Bauer, 2012; Gauthier et al., 2012; Martill, Tischlinger, & Longrich, 2015). The tree was assembled in Mesquite Version 3.2 and characters were mapped using pasimony (Maddison & Maddison, 2017).

3 | RESULTS

3.1 | The quadrate element of *Ophiodes intermedius* (putative quadrate transiliens cartilage)

We consistently found an ovoid quadrate element in all examined specimens of *Ophiodes intermedius*, located on the dorsal border of the quadrate (Figure 1). The quadrate of *Ophiodes* is a large bone, with its cephalic condyle capped by hyaline cartilage, and surrounded by a perichondrium formed by fibrous connective tissue (Figure 2a); this perichondrium is covered by the bodenaponeurosis of the jaw muscles and contacts the quadrate sesamoid. The fibers of the bodenaponeurosis originate on the paroccipital process, and extend anteriorly, wrapping around the quadrate border, to end within the fibers of the adductor musculature; they enclose an elongated mineralized fibrous element (Figure 1a) that is loosely attached to the anterior part of the cephalic border of the quadrate, just anterior to the articulation with the paroccipital process. In a disarticulated skull it can be seen to be separate from the bone (Figures 1b,c and 2b). The element consists of fibrocartilage (Figure 2a,b), the collagen fibers of which have been mineralized (Figure 2a); it is stained red by alizarin (in cleared and stained preparations; Figure 1) and by acid fuchsin (in histological sections with Mallory's trichrome stain; Figure 2). In transverse section the quadrate element is lenticular, having a thickened central region and becoming thinner at the anterior and posterior ends where it is continuous with the fibers of the bodenaponeurosis with which it is associated. Ventrally, its smooth articular facet meets the chondral head of the quadrate within a synovial bursa (Figure 2b).

3.2 | Element X of amphisbaenians

The element X is wedged at the lateral margins of the basioccipital-basisphenoid suture. Element X changes ontogenetically, beginning as a cartilaginous structure in embryos, then becoming ossified in adults, or in some cases, it fuses to the surrounding bones. The fusion seems to be related to age (size); in *Amphisbaena bolivica* they are unfused in the young (smaller) specimens, but are fused in the old (larger) specimens (Figure 3).

Element X is the insertion point of the longus colli muscles that originate on the cervical vertebrae (Figure 4a). These muscles have a tendinous attachment (Figures 4 and 5) that fixes the muscular complex to element X. This connection is a fibrocartilaginous enthesis (Apostolakos et al., 2014) (Figure 6). The ventral surface of element X

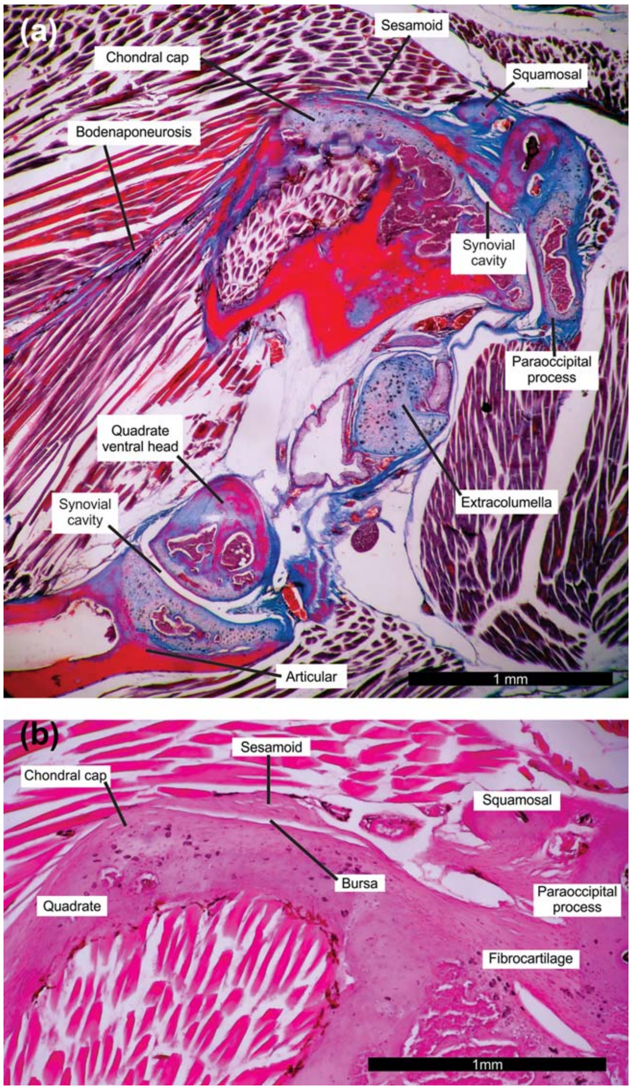

FIGURE 2 *Ophiodes intermedius* (FML 26455), histological section of the left quadrate region showing the quadrate sesamoid. Anterior to the left. (a) General view of the quadrate region; Mallory's trichrome staining. (b) Histological section of the quadrate region showing the quadrate sesamoid and its bursa; hematoxilin and eosin staining

faces slightly posteriorly, providing an almost perpendicular attachment to the muscle fiber direction. This surface of element X is rugose, and remains so even in specimens that undergo fusion to the basicranium. When this element is discrete its osseous core is surrounded by cartilage bands, as seen in *Amphisbaena alba* (Montero & Gans, 1999) and *Diplometopon zarudnyi* (Figure 6). The perimysium surrounding the muscle attaches to element X in a circular way (Figure 4b), whereas on the lateral exposure of the muscle it thickens into a distinct lateral tendon (Figure 4c).

3.3 | Element X of other squamatans

We found evidence of the presence of unfused element X adjacent to the basioccipital (Figure 7) in specimens of Gekkonidae (*Chondrodactylus bibronii* and *Chondrodactylus angulifer*), Pygopodidae (*Paradelma orientalis*), and Gymnophthalmidae (*Calyptommatus leiolepis*). In these additional taxa these ossifications are topologically and functionally equivalent to the amphisbaenian element X.

4 | DISCUSSION

The structures described herein have been recognized as present by earlier authors, but their nature as sesamoids has not been commented on. Both, the quadrate element of *Ophiodes* and element X in a diversity of squamates meet the criteria normally indicative of sesamoids:

1. Sesamoids are embedded within tendons (i.e., Pearson & Davin, 1921a, 1921b; Ponssa et al., 2010; Regnault, Hutchinson, et al., 2016; Regnault, Jones, et al., 2016; Regnault et al., 2014; Retterer & Lelièvre, 1911; Vickaryous & Olson, 2007), excluding the support sesamoids, which serve as attachment of tendons (Jerez et al., 2010). The quadrate element described in *Ophiodes intermedius* is embedded in the bodenaponeurosis, the main tendon of the adductor muscles of the mandible, and element X serves as attachment of the tendons and fibers of the longus colli muscle.
2. Several sesamoids are located in places where tendons bend or wrap around a bony projection (usually, but not limited to, an articulation), acting as a protection or an aide for the gliding of the tendon when it moves (Sarin & Carter, 2000; Sarin et al., 1999). The quadrate element is located where the bodenaponeurosis wraps around the anterodoral corner of the quadrate, possibly acting in a similar way.
3. Sesamoids are related to force-bearing regions, usually near joints (Olson, 2000). The quadrate sesamoid is located where the pressure of muscle contraction is high due to the bending of the tendon; element X is located in the place where the muscles of the neck (longus colli) attach to pull down the head. These muscles are particularly powerful in fossorial organisms such as amphisbaenians (Gans, 1980), in which element X is proportionally large compared to other lizards (Gauthier et al., 2012).
4. Sesamoids are typically related to joints. The quadrate element is related to the quadrate-otooccipital joint (directly affecting the mandibular joint), and element X is related to the cranio-cervical joints.
5. Sesamoids ossify, if at all, late in development (Chapman, 1972; Prokopec, Pfeiferova, & Josifko, 1997). The quadrate element does not ossify, remaining fibrocartilagous and only slightly mineralized in adult specimens and element X remains cartilaginous in late embryos of *Amphisbaena heterozonata* (Montero, Gans, & Lions, 1999), and ossifies only in adults (Gans & Montero, 2008).

Considering the above listed reasons, we infer that both structures, the quadrate element and element X, are in fact sesamoids.

The skeletal element of *Ophiodes intermedius* provides a smooth articular sliding surface for the bodenaponeurosis and is surrounded by this aponeurosis, which is in fact a tendon (as its fibers are parallel and closely packaged). From this reasoning, we describe this sesamoid as

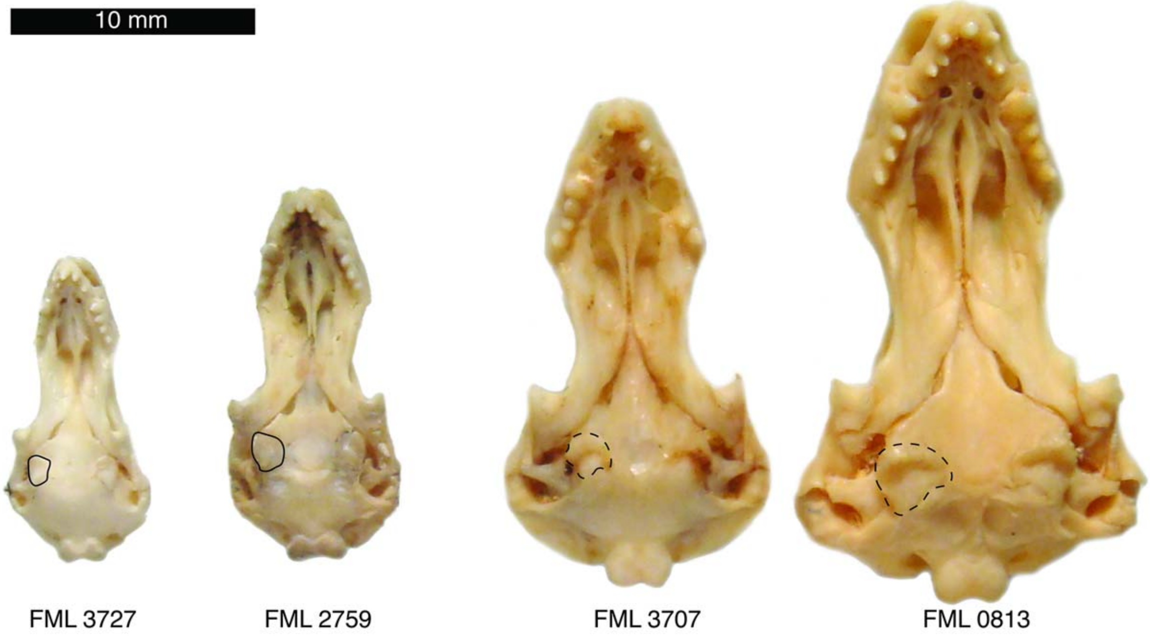

FIGURE 3 *Amphisbaena bolivica*, specimens of different size (age). On the right side of each specimen, independent elements were outlined with solid lines and the presumptive areas of fused element were outlined with dashed lines

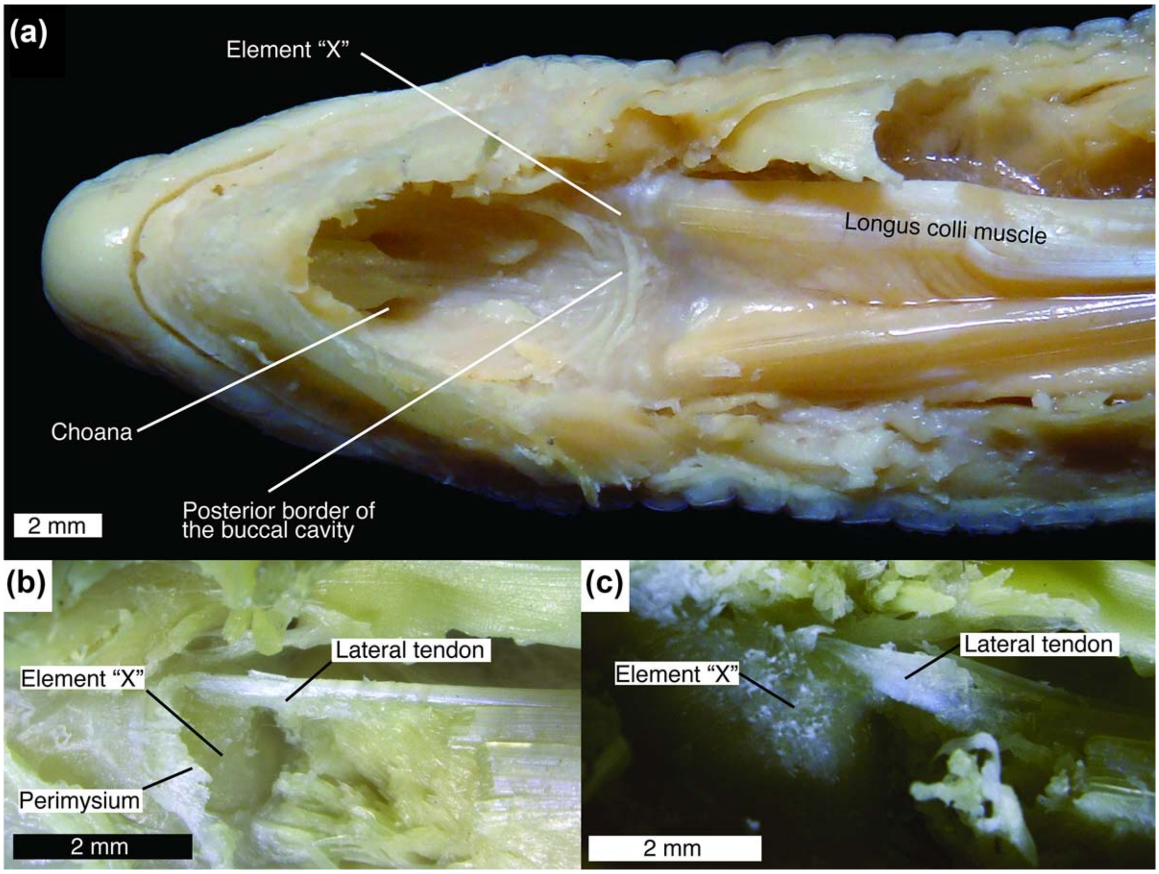

FIGURE 4 *Amphisbaena bolivica* (FML 29586), muscles attached to element X. (a) The tongue and the associated superficial muscles were cut out. (b) The muscle fibers were extracted, leaving the attachment of the perimysium to element X. (c) Most of the perimysium was extracted, exposing the lateral tendon

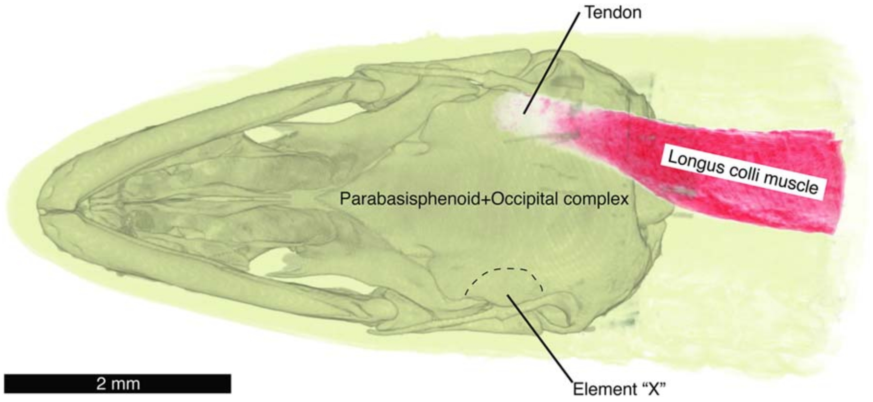

FIGURE 5 *Zygaspis quadrifrons* (FMNH 17751), the muscle longus colli (red colored) attaches, by means of a strong tendon (white), to the area of the sphenoccipital tubercle. In this specimen, the sesamoid (element X) is fused to the basioccipital plate and to the parabasisphenoid. DiceCT preparation, specimen courtesy of Dr. Patrick Lewis and Monte Thies

an embedded sesamoid (Jerez et al., 2010; Vickaryous & Olson, 2007) and we propose to name it the quadrate sesamoid.

The dorsal articulation of the quadrate involves several skeletal elements in squamates: the proximal head of the quadrate itself; the paroccipital process of the exoccipital; the squamosal when present; the supratemporal when present; and the cartilage or intercalary element (Evans, 2008; Jollie, 1960; Oelrich, 1956; Versluys, 1912). The intercalary element is positionally similar enough to the quadrate

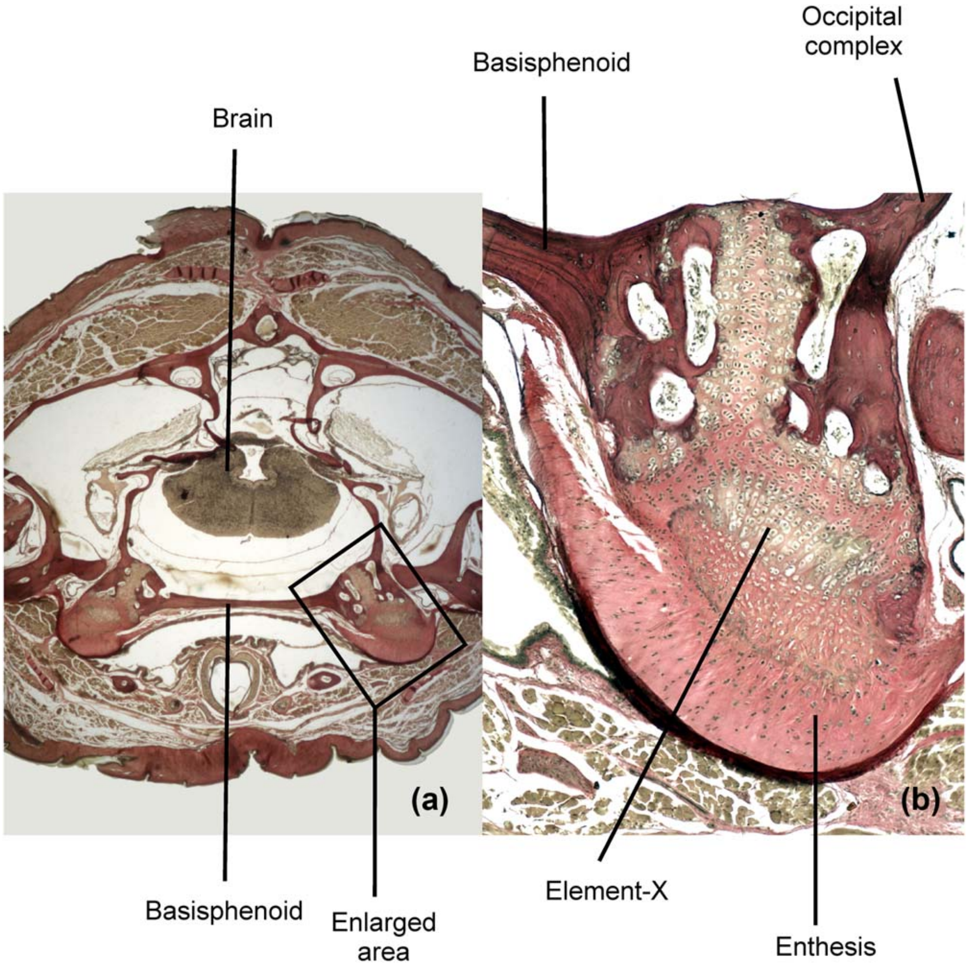

FIGURE 6 *Diplometopon zarudnyi*. (a) General view of a trasverse section of the skull at level of element X. (b) Detail of element X. Note the chondral bands between the element and the surrounding bones. Element X is capped by ligaments. (A. Bellairs histological section; Mallory trichrome; specimen Diplo III, slide 15)

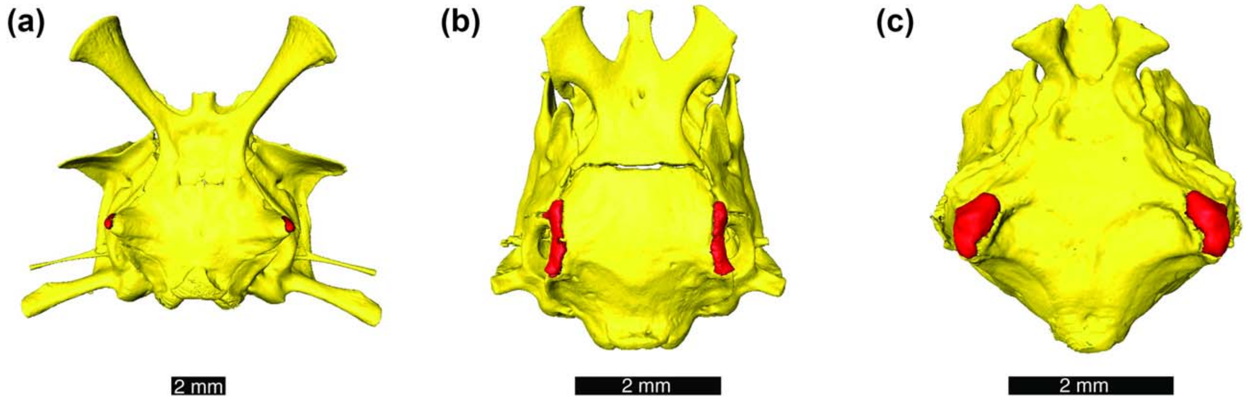

FIGURE 7 HRCT of three squamates showing different developments of Element X (Red). (a) *Chondrodactylus angulifer* (CAS 126466); (b) *Paradelma orientalis* (CAS 77652); (c) *Calyptommatus leiolepis* (MZUSP 71156)

sesamoid to raise the question if they are the same structure. In the literature several structures related to the paroccipital process-quadrate articulation have been called intercalary elements (or intercalare sensu Jollie, 1960); but this does not mean they are necessarily homologous. The intercalary element, or processus paroticus, is a derivate of the dorsal process of the extracolumella (Bellairs & Kamal, 1981; Versluys, 1912). It usually lies over the posterior surface of the quadrate, close to (or covering) the tip of the paroccipital process (Evans, 2008). The intercalary element's posterior position relative to the paroccipital process makes this structure topologically non-homologous to the quadrate sesamoid. Other authors describe an intercalary as an osseus structure located on the dorsal surface of the quadrate, anterior to the paroccipital process (Broom, 1925, in *Tiliqua scinoides*; Brock, 1932, p. 523, in *Lygodactylus*; Kingman, 1932, in *Eumeces schneiderii*; Figure 8). Topologically, this last element agrees with the quadrate sesamoid and, therefore, its identity, homology, and characterization as a sesamoid should be further investigated.

The quadrate sesamoid is in the same position as the cartilage transiliens of chelonians, which is located over the trochlear process (= processus trochlearis oticum of Gaffney, 1972), and may sometimes be ossified (the os transiliens of gopher tortoises) (Bramble, 1974; Ray, 1959). The functional mechanics of the os transiliens of turtles were addressed by Bramble (1974) (Figure 9), and also may apply to the quadrate sesamoid. The anterodorsal corner of the quadrate of *Ophiodes* serves as a supporting point for the bending of the bodenaponeurosis, similar to the turtle trochlear process. The synovial bursa of the quadrate sesamoid would allow the element to slide anteriorly during

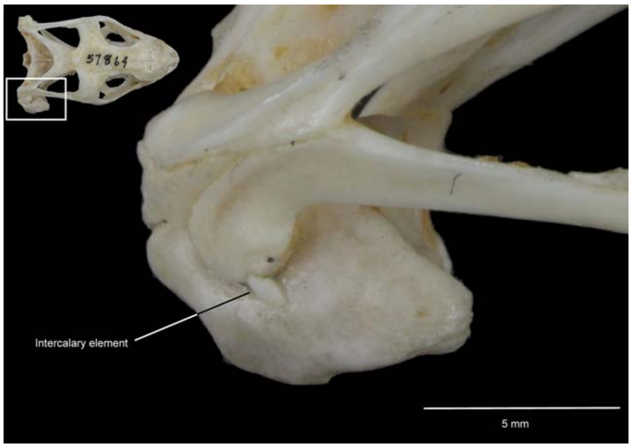

FIGURE 8 *Eumeces schneiderii* (AMNH R-57864), intercalary element. Photo by William Gelnaw

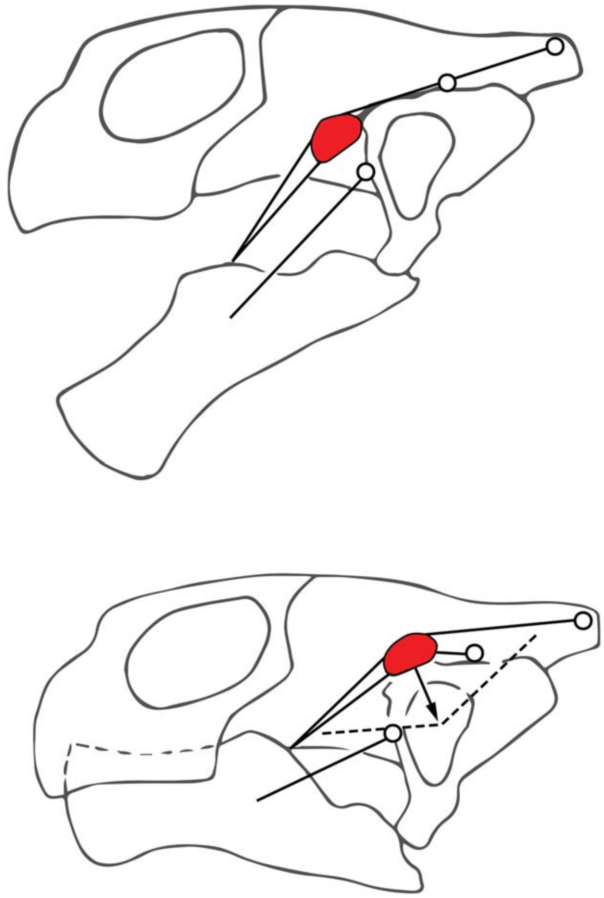

FIGURE 9 Movements of the transiliens cartilage (in red) in turtles with the mandible abducted and closed (Modified from Bramble, 1974). The arrow indicates the resulting force applied by the cartilage on the quadrate, when the mandible is closed

TABLE 1 List of species with basicanial sesamoids (scored as element X by Gauthier et al., 2012)

Iguania	**Anguidae**
Uromastyx aegyptius	*Pseudopus (Ophisaurus) apodus*
Physignathus cocincinus	*Celestus enneagrammus*
Calotes emma	*Elgaria multicarinata*
Leiosaurus catamarcensis	**Helodermatidae**
Urostrophus vautieri	*Heloderma horridum*
Gambelia wislizenii	*Heloderma suspectum*
Dipsosaurus dorsalis	**Lanthanotidae**
Chalarodon madagascariensis	*Lanthanotus borneensis*
Oplurus cyclurus	**Varanidae**
Phrynosoma platyrhinos	*Varanus salvator*
Uranoscodon superciliosus	*Varanus acanthurus*
Insertae sedis	*Varanus exanthematicus*
Sineoamphisbaena hexatabularis	**Dibamidae**
Mosasaurs	*Anelytropsis papillosus*
Platecarpus sp.	*Dibamus novaeguineae*
Teiidae	**Rhineuridae**
Callopistes maculatus	*Spathorhynchus fossorium*
Gerrhosauridae	*Dyticonastis rensbergeri*
Cordylosaurus subtesselatus	*Rhineura floridana*
Scincidae	**Bipedidae**
Plestiodon (Eumeces) fasciatus	*Bipes biporus*
Scincus scincus	*Bipes canaliculatus*
Amphiglossus splendidus	**Trogonophidae**
Shinisauridae	*Trogonophis wiegmanni*
Shinisaurus crocodilurus	*Diplometopon zarudnyi*
Xenosauridae	**Amphisbaenidae**
Xenosaurus grandis	*Geocalamus acutus*
	Amphisbaena fuliginosa

abduction and posteriorly during adduction. These movements may provide a lever system analogous to the patella in the knee. Therefore, we conclude that the quadrate sesamoid is at least an analogue, and potentially a homologue, of the transiliens cartilage of turtles. Crocodylians also have a transiliens cartilage that serves as a junction of the tendon system of the musculature of the mandible but is related to the surangular bone (Schumacher, 1973; Tsai & Holliday, 2011); therefore, the homology of crocodile cartilage with that of turtles and of *Ophiodes* is at least doubtful.

Element X in the basicranium of amphisbaenians and other squamates are related to the ligaments of the neck muscles, because of which we here refer to them as basicranial sesamoids. In amphisbaenians, the identity of these osseous elements in the base of the skull (Figure 6) has been controversial (Gans, 1960, 1978; Jollie, 1960; Kesteven, 1957; Lakjer, 1927; Montero & Gans, 1999; Vanzolini, 1951; Zangerl, 1944). Because the homology of these elements with other bones long remained unresolved, despite being discussed extensively, they were given the name element X (Gans & Montero, 2008; Jollie, 1960; Kesteven, 1957; Montero & Gans, 1999). Element X has been described as a separate element in several species of amphisbaenians (Gans & Montero, 2008; Gauthier et al., 2012), and for other amphisbaenians, in

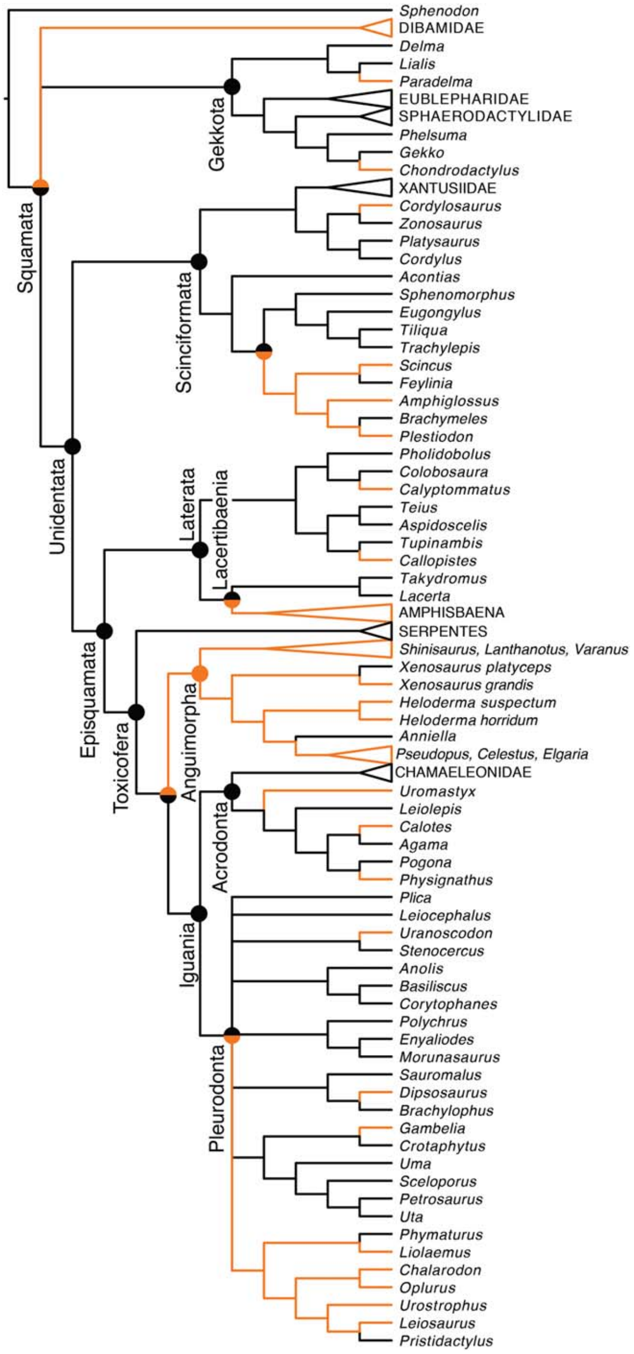

FIGURE 10 Optimization of the presence of basicranial sesamoids (Element X) in a squamate metatree (see methods for details). Orange color indicates the presence of Element X, regardless of size (which is enlarged in Amphisbaenia, Gauthier et al, 2012). Two colored nodes indicate ambiguity for the presence of this element

which they are fused to the occipital complex, their presumptive areas are morphologically distinctive. In the embryology of *Amphisbaena heterozonata*, these elements remain cartilaginous and separated from the nearby ossifications, even in advanced embryos; whereas, in grown adults they appear not only osseous but fused to the basioccipital (Montero et al., 1999). Therefore, fusion seems to be age dependent.

Element X seems to be relatively common in squamates. Gauthier et al. (2012) considered element X as homologous to the bones capping the basal tubera and treated this as an ordered character with different degrees of development, defined as "Apophyseal ossification (Element X) caps basal tubera" (Character 340). Element X was scored as being present in 40 of their 192 species (Table 1); the optimization of the character in their tree shows that element X appears repeatedly and independently in several lineages. To add to these observations, here we report them as being present in some other taxa, including Gymnophthalmidae and, for the first time, in Gekkota (Figure 10). Although these additional observations are scattered, they increase the known scope of the distribution of this character among squamates. However, the restricted number of taxa for which element X has been reported limits our ability to infer the character's presence at some of the squamate nodes. Considering the species listed in Figure 10, it appears that several nodes are ambiguous, including the nodes of Squamata, Lacertibaenia, Anguimorpha, and Pleurodonta. The ambiguity of the squamate node is determined by the presence of this structure in the Dibamidae; however, because this element is also present in some more hierarchically inclusive groups within Squamata, we propose that its origin may be traced to the base of the Squamata clade, and that it has potentially been regained in several clades (e.g., Amphisbaenia, Scincidae, Anguimorpha, among many others; Figure 10). In amphisbaenians it has been postulated that the fusion of element X to the surrounding cranial bones may be age-dependant (Gans & Montero, 2008; Montero et al., 1999). This age-dependent fusion maybe widespread among squamates, therefore, the recorded absence of this element may be biased. More embryological data are needed to test this proposal.

In addition to the apophyseal interpetation of element X of Gauthier et al. (2012), other authors (Gans, 1960, 1978; Montero & Gans, 1999) interpreted it as an epiphysis suitable for muscular attachment, a perspective supported by histological and myological evidence (Al-Hassawi, 2007). Here, we interpret the element X as being a sesamoid. These interpretations are not mutually exclusive and all may be correct. There are many data that indicate that sesamoids are structures that could be fused (Vaughan & France, 1986) or separated from other bones, especially the epiphyses of long bones during ontogeny (Barnett & Lewis, 1958; Broome & Houghton, 1989; Eyal et al., 2015; Hutchinson, 2002; Lewis, 1958; Parsons, 1904, 1908; Pearson & Davin, 1921a, 1921b). There is even a report of sesamoids being fused to each other (Le Minor, 1988). Probably one of the most compelling work supporting the relationships between sesamoids, long bone epiphyses, and apophyses is that of Eyal et al. (2015) which reports that in mouse embryos the sesamoid patella initially develops as a process at the surface of the femoral epiphysis. Later in the ontogeny the patella is separated from the femur by a joint formation process guided by mechanical load. Finally, the patella becomes embedded within the quadriceps tendon. The same process but in the opposite direction has been shown in many avian species (Barnett & Lewis, 1958; Hogg, 1980; Hutchinson, 2002). In these species the tibial tuberosity comes from a separate ossification that fuses with the tibial proximal end (Vickaryous & Olson, 2007). A similar process, finishing with the fusion of the sesamoid and cranial bones, could also explain our observations in amphisbaenians. We, thus, postulate that element X of amphisbaenians begins as a sesamoid at the onset of the ontogeny and, in some species, it becomes fused to the occipital complex. This is congruent with the old hypothesis associating sesamoids with traction epiphyses (Parsons, 1908). Therefore, although our data do not allow us to rule out the possibility that both the quadrate and basicranial sesamoids may be interpreted as apophyseal ossifications or bony prominences, to which tendons attach, the concepts are not mutually exclusive, and it may be possible that element X and the quadrate sesamoid can be both apophyseal ossifications and sesamoids.

The interpretations presented here suggest that cranial sesamoids in squamates are more common than previously thought, and they have remained unrecognized for years. Although these elements are not as numerous as in fishes (Datovo & Bockmann, 2010), the possibility exists that these observations might extend to more groups among tetrapods.

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AUTHOR CONTRIBUTIONS

Design of the article, VA and RM; acquisition of data, VA, RM, AMB, and JDD; data analysis/interpretation, drafting of the manuscript, critical revision of the manuscript, and approval of the article, all authors.

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APPENDIX: EXAMINED MATERIAL

The acronyms used are: AMNH: American Museum of Natural History; CAS: California Academy of Science; FML: Herpetological collection of the Fundación Miguel Lillo; FMNH: Field Museum of Natural History; MZUSP: Museu du Zoologia, Universidade de Sao Paulo.

1. *Ophiodes intermedius* (Anguidae), FML 26303: cleared and stained specimen.
2. *Ophiodes intermedius* (Anguidae), FML no number, Capital-Tucumán-Argentina: cleared and stained specimen.
3. *Ophiodes intermedius* (Anguidae), FML 26368: cleared and stained specimen
4. *Ophiodes intermedius* (Anguidae), Teaching collection of the Cátedra de Vertebrados of the Universidad Nacional de Salta, no number, no data: cleared and stained specimen.
5. *Ophiodes intermedius* (Anguidae), FML 26455: histological sections of the head.
6. *Calyptommatus leiolepis* (Gymnophthalmidae), MZUSP 71156: HRCT-Scanned.
7. *Amphisbaena bolivica* (Amphisbaenidae), FML 29585 and 29586.
8. *Amphisbaena bolivica* (Amphisbaenidae), FML 3727; 2759; 3707; 0813: dry skulls.
9. *Diplometopon zarudnyi*. Two specimens (A. Bellairs histological sections; Mallory trichrome; specimen I, slide 15), held at Museum of Comparative Zoology at Harvard University.
10. *Zygaspis quadrifrons* (Amphisbaenidae), FMNH 17751: DiceCT-Scanned.
11. *Chondrodactylus bibronii*, (Gekkonidae), CAS 173299: HRCT-Scanned.
12. *Chondrodactylus angulifer* (Gekkonidae), CAS 126466: HRCT-Scanned.
13. *Paradelma orientalis* (Pygopodidae), CAS 77652: HRCT-Scanned.
14. *Eumeces schneiderii* (Scincidae), AMNH R-57864: dry skeleton.