Sesamoids in Caudata and Gymnophiona (Lissamphibia): absences and evidence

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An integrative definition of sesamoid bones has been recently proposed, highlighting their relationship with tendons and ligaments, their genetic origin, the influence of epigenetic stimuli on their development, and their variable tissue composition. Sesamoid bones occur mainly associated with a large number of mobile joints in vertebrates, most commonly in the postcranium. Here, we present a survey of the distribution pattern of sesamoids in 256 taxa of Caudata and Gymnophiona, and 24 taxa of temnospondyls and lepospondyls, based on dissections, high-resolution X-ray computed tomography from digital databases, and literature data. These groups have a pivotal role in the interpretation of the evolution of sesamoids in Lissamphibia and tetrapods in general. Our main goals were: 1) to contribute to the knowledge of the comparative anatomy of sesamoids in Lissamphibia; 2) to assess the evolutionary history of selected sesamoids. We formally studied the evolution of the observed sesamoids by optimizing them in the most accepted phylogeny of the group. We identified only three bony or cartilaginous sesamoids in Caudata: the mandibular sesamoid, which is adjacent to the jaw articulation; one located on the mandibular symphysis; and one located in the posterior end of the maxilla. We did not observe any cartilaginous or osseous sesamoid in Gymnophiona. Mapping analyses of the sesamoid dataset of urodeles onto the phylogeny revealed that the very conspicuous sesamoid in the mandibular symphysis of *Necturus beyeri* and *Amphiuma tridactylum* is an independent acquisition of these taxa. On the contrary, the sesamoid located between the maxilla and the lower jaw is a new synapomorphy that supports the node of *Hydromantes platycephalus* and *Karsenia coreana*. The absence of a mandibular sesamoid is plesiomorphic to Caudata, whereas it is convergent in 7 different families. The absence of postcranial sesamoids in salamanders might reveal a paedomorphic pattern that would be visible in their limb joints.

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11
12 ## Abstract

13 An integrative definition of sesamoid bones has been recently proposed, highlighting their

14 relationship with tendons and ligaments, their genetic origin, the influence of epigenetic stimuli

15 on their development, and their variable tissue composition. Sesamoid bones occur mainly

16 associated with a large number of mobile joints in vertebrates, most commonly in the

17 postcranium. Here, we present a survey of the distribution pattern of sesamoids in 256 taxa of

18 Caudata and Gymnophiona, and 24 taxa of temnospondyls and lepospondyls, based on

19 dissections, high-resolution X-ray computed tomography from digital databases, and literature

20 data. These groups have a pivotal role in the interpretation of the evolution of sesamoids in

21 Lissamphibia and tetrapods in general. Our main goals were: 1) to contribute to the knowledge of

22 the comparative anatomy of sesamoids in Lissamphibia; 2) to assess the evolutionary history of

23 selected sesamoids. We formally studied the evolution of the observed sesamoids by optimizing

24 them in the most accepted phylogeny of the group. We identified only three bony or

25 cartilaginous sesamoids in Caudata: the mandibular sesamoid, which is adjacent to the jaw

26 articulation; one located on the mandibular symphysis; and one located in the posterior end of

27 the maxilla. We did not observe any cartilaginous or osseous sesamoid in Gymnophiona.

28 Mapping analyses of the sesamoid dataset of urodeles onto the phylogeny revealed that the very

29 conspicuous sesamoid in the mandibular symphysis of *Necturus beyeri* and *Amphiuma*

30 *tridactylum* is an independent acquisition of these taxa. On the contrary, the sesamoid located

31 between the maxilla and the lower jaw is a new synapomorphy that supports the node of

32 *Hydromantes platycephalus* and *Karsenia coreana*. The absence of a mandibular sesamoid is

33 plesiomorphic to Caudata, whereas it is convergent in 7 different families. The absence of

34 postcranial sesamoids in salamanders might reveal a paedomorphic pattern that would be visible

35 in their limb joints.

36 **Keywords** heterotopic elements, amphibians, homology, mandibular sesamoids, tetrapods

37

38 **Introduction**

39 In a recent review, sesamoids were defined as *"periarticular skeletal elements, which initially*

40 *form in juxtaposition to or independently of bones and joints. They are commonly related to*

41 *tendons and ligaments, have a genetic basis and, once they are formed, epigenetic stimuli drive*

42 *their growth and development to the acquisition of their definitive tissue composition, which can*

43 *be diverse, for example, cartilage, fibrocartilage, or bone*" (Abdala *et al*., 2019). This definition

44 intends to summarize all the skeletal elements considered as sesamoids in the different groups of

45 tetrapods into one description. The definition is quite broad, because sesamoids are associated

46 with diverse functions, such as the mechanical stress exerted on tendons as they wrap around a

47 bony edge or a joint. This stress might improve tendon ability to react to compressive load,

48 pressure, tensile strain, or vibration (Pearson & Davin, 1921ab; Carlsöö, 1982; Nussbaum, 1982;

49 Sarin *et al*., 1999; Benjamin & Ralph, 1998; Jerez *et al*. 2010; Ponssa *et al*., 2010; Tsai &

50 Holliday, 2011; Otero & Hoyos, 2013; Regnault *et al*., 2016; Abdala *et al*., 2017; Zhang *et al*.,

51 2017). Moreover, sesamoids are described in all the large vertebrate groups (Abdala *et al.*, 2019).

52 They occur mainly associated with a large number of mobile joints, most commonly in the

53 postcranium (e.g., Romankowowa, 1961; Vickaryous & Olson, 2007; Ponssa *et al.*, 2010; Jerez

54 *et al.*, 2010; Chadwick *et al.*, 2014; Regnault *et al.*, 2014; Reyes-Amaya *et al.*, 2017; Samuels *et*

55 *al.*, 2017; Denyer *et al.*, 2020), and in the skull of some taxa (e. g., Hofling & Gasc, 1984; Tsai

56 & Holliday, 2011; Montero *et al.*, 2017). The number of cranial sesamoids is notoriously higher

57 in Osteichthyes than in tetrapods (Alexander, 1967; Adriaens & Verraes, 1998; Diogo *et al.*,

58 2001; Summers *et al.*, 2003; Datovo & Bockmann, 2010), possibly due to the higher number of

59 mobile joints in the fish skull (Iordansky, 1989; Montero *et al.*, 2017; Abdala *et al.*, 2019).

60 More than 20 types of osseous, cartilaginous or fibrocartilaginous sesamoids have been

61 described in amphibians (Laurent, 1961; Nussbaum, 1982; Olson, 2000; Hoyos, 2003;

62 Guayasamin, 2004; Avilan & Hoyos, 2006; Fabrezi, 2006; Ponssa *et al.*, 2010; Abdala *et al.*,

63 2017), most of them in 33 extant families of anurans (Ponssa *et al.*, 2010). The earliest records of

64 sesamoids in amphibians include an oval bone lying next to the radial, and distal to the ulnar

65 portion of the radio-ulna in *Xenopus arabiensis* from the Upper Oligocene (Henrici & Báez,

66 2001). This element is located on the dorsal surface of the carpus in the same position as in other

67 *Xenopus* species (Henrici & Báez, 2001). A sesamoid behind the diapophysis, beneath the iliac

68 shaft, was identified in a juvenile anuran from the Lower Cretaceous Jiufotang Formation (Wang

69 *et al.*, 2007).

70 The skeletal anatomy of Caudata and Gymnphiona has been extensively studied (e.g.,

71 Wake, 1963; Bemis *et al.*, 1983; Wake *et al.*, 1983; Restrepo, 1995; Shubin, 1995; Müller, 2006;

72 Schaah, 2010; Wu *et al.*, 2012; Villa *et al.*, 2014; Jia *et al.*, 2018; Cala *et al.,* 2019;

73 Khoshnamvand *et al.*, 2019; Bardua *et al.*, 2019; Marshall *et al.*, 2019; Macaluso *et al.*, 2020).

74   Nevertheless, no work has focused on their sesamoids. This gap of knowledge has attracted our

75   attention, since the Caudata group has a pivotal role in the interpretation of the evolution of

76   sesamoids in tetrapods. Likewise, Gymnophiona cannot be ignored if the evolution of sesamoid

77   in amphibians is to be unveiled.

78   In Caudata, only a cranial sesamoid in the squamosal-collumelar ligament was mentioned

79   (Nussbaum, 1982), with no data or information about the species having been published.

80   Interestingly, cranial sesamoids have been rarely recorded among tetrapods (Bramble, 1974; Tsai

81   & Holliday, 2011; Montero *et al*., 2017; Abdala *et al*., 2019). The sesamoids located in the

82   cranium of tetrapod amniotes include the transilient cartilage or bone in the bodenaponeurosis of

83   the jaw adductor muscles in crocodiles and turtles (Iordansky, 1964; Schumacher, 1973;

84   Holliday & Witmer, 2007; Tsai & Holliday, 2011); elements in the basipterygoid and pterygoid

85   bones in some squamates (Gauthier *et al*., 2012); the quadrate element in Ophiodes; the X

86   element in amphisbaenians (Montero *et al*., 2017); a small bone strengthening the external jugo-

87   mandibular ligament in its retro-articular portion in *Rhamphastos* (Hofling & Gasc, 1984); and

88   the controversial Paaw cartilage in marsupial mammals (Sánchez-Villagra *et al*., 2002). The only

89   records of cranial sesamoids in anuran amphibians belong to *Barbourula busuangensis* (Clarke,

90   1987; Roček *et al*., 2016) and *Chacophrys pierotti* (Fabrezi *et al*., 2017). Considering these data,

91   the report of the sesamoid in the columellar squamous ligament of Caudata is striking, given the

92   notable scarcity of sesamoid records in this area for the entire tetrapod clade. In Gymnophiona,

93   sesamoids are unknown. Data scarcity on sesamoid occurrence in Caudata and Gymnophiona

94   draws our attention, because osteology is considered in several ongoing projects about the

95   morphology of these taxa (Bemis *et al*., 1983; Muller, 2006; Villa *et al*., 2014; Bardua *et al*.,

96   2019; Marshall *et al*., 2019; among others).

97   To evaluate sesamoid evolution in these amphibian groups, and to fill the knowledge gap

98   about them, we present a sesamoid distribution survey. Our main goals were:

99   1. to contribute to the knowledge of the comparative anatomy of bony or cartilaginous

100   sesamoids in Lissamphibia,

101   2. to infer the evolutionary history of selected sesamoids in Lissamphibia.

102   Based on the available evidence of distribution patterns of bony and cartilaginous

103   sesamoids in the remaining tetrapods, we consider that the lack of sesamoid records in urodeles

104   and caecilians is probably due to sampling error. We expect to find bony or cartilaginous

105   sesamoids in both groups: cranial sesamoids in Gymnophiona -due to its lack of limbs- and

106   cranial and postcranial sesamoids in Caudata.

107   To achieve our goals, we studied about 850 specimens belonging to 280 taxa from

108   dissected specimens, scanned specimens from different digital morphological databases, and

109   literature data.

110

Materials and Methods

112   Sesamoids were examined in the skeleton of specimens from the herpetological collections of the

113   Field Museum of Natural History, USA (FMNH), and Fundación Miguel Lillo, Argentina

114   (FML). Material from three morphological databases was also reviewed: Morphosource

115   (morphosource.org), Digimorph (http://digimorph.org/), and Phenome10k (phenome10k.org)

116   (Supplementary Material S1). Adult and juvenile specimens representing all nine extant families

117   (and one extinct family), 73 genera and 212 species (including 12 fossil species) of Caudata (571

118   specimens); nine (one extinct) of 11 families, 29 genera and 44 species (including one fossil

119   species) of Gymnophiona (173 specimens); and 24 species of Temnospondyli and Lepospondyli

120   (17 families) (Supplementary Material S1) were studied in detail. Dry skeletons and cleared and

121   stained specimens of the collections were examined under a Meiji EMZ-5 binocular microscope.

122   Clearing and staining allowed us to distinguish bony and cartilaginous structures. Unfortunately,

123   since specimens were from the skeleton collection, it was not possible to determine age

124   specifications, fixing conditions or loss of bones with soft tissue in the samples. However, our

125   data on high-resolution X-ray computed tomography of specimens from digital databases

126   allowed us to observe the internal structure of organisms without damaging the specimens, thus

127   avoiding the problem of loss of bones with soft tissue.

128   Two individuals of *Pleuredeles waltl* were dissected to corroborate the identity of the

129   ligaments or tendons related to the sesamoids. One specimen (FML30803) was completely

130   cleared, while the other (FML30804) was partially cleared, and both were stained following the

131   protocol of Wassersug (1976), with modifications. Furthermore, some specimens in the FMNH

132   collection were partially transparent (e.g., *Ambystoma mexicanum* FMNH22888), allowing the

133   identification of tendons and associated muscles. Photographs were taken with a Nikon Coolpix

134   P6000 camera, and with a Leica, MZ7.5 stereomicroscope equipped with a Spot Insight Color

135   Model# 3.2.0 camera. The selected specimens were photographed with a DSLR camera,

136   illuminated by light in the blue spectrum. The photos were taken through a yellow long-pass

137   filter (which filters out any reflected light source, allowing only the fluorescent light to pass

138   through). This visualization method of cleared and stained specimens was first described by

139   Smith *et al*. (2018). To compile the sesamoids described for urodeles and caecilians, the

140   literature on myology and osteology of these groups was reviewed.

141   Descriptions of 66 species of Caudata and 40 species of Gymnophiona were also

142   considered (see species and literature cited in Supplementary Material S1). The presence or

143 absence of bony or cartilaginous sesamoids in each of the 280 studied taxa was recorded. Based

144 on both our survey and the literature, the presence, number, and type of bony or cartilaginous

145 sesamoids in urodeles and caecilians were inferred. These relationships were expressed through a

146 probability calculation (Table 1). Our survey included extant species, although descriptions of

147 fossil species were also revised (Supplementary Material S1). Because heterotopic elements are

148 often overlooked in morphological studies, and several of the reviewed studies are descriptions

149 of the skull only, results from literature sources (Supplementary Material S1) should be

150 interpreted with caution. The topology of a suite of anatomical characters (skeletal elements,

151 tendons, ligaments, and muscles) as the main argument to elucidate sesamoid homologies was

152 analyzed (Benjamin & Ralph, 1998; Ponssa *et al.*, 2010; Amador *et al.*, 2018).

153

154 **Character evolution**

155 The obtained data were combined in a character matrix (Supplementary Material S2), where the

156 sesamoids were included as characters and coded as present or absent. For the reconstruction of

157 ancestral states, data from the sesamoid matrix were optimized onto a pruned version of the

158 Caudata phylogeny of Bonnet & Blair (2017), and Pyron & Wiens (2011) for species that were

159 not included in the most recent phylogeny. The tree was generated using TNT software

160 (Goloboff *et al.*, 2008) and the optimization was performed with Winclada software (Nixon,

161 1999), using the default setting (unambiguous mode). Sesamoids terminology follows Ponssa *et*

162 *al.* (2010) and Abdala *et al.* (2019). We included each sesamoid in a different column of our data

163 set (Supplementary Material S2), thus proposing their primary homology, i.e., we propose that

164 all sesamoids belonging to the same column are the same by inheritance (De Pinna, 1991). The

165 proposal of primary homology is based on reasonable assessment, in this case, topology

166 (Agnarsson & Coddington, 2008). However, if they fail the test of congruence and did not

167 constitute synapomorphies on the selected cladogram, then they would not be secondary

168 homologs (De Pinna, 1991). The cladogram allows us to test congruence and the hypothesis of

169 secondary homology of the cranial sesamoid in salamanders.

170

171 **Results**

172 Three bony or cartilaginous sesamoids in Caudata were identified. One sesamoid is located on

173 the mandibular symphysis of *Necturus beyeri* (Fig. 1A) and *Amphiuma tridactylum*. Another is a

174 mandibular sesamoid, adjacent to the jaw articulation. The latter sesamoid is the most frequent

175 and the one that has been most deeply studied. It is embedded in the ligament between the

176 quadrate and prearticular bones (Fig. 2 and 3). The descending ramus of the squamosal is

177 rectangular, flat, and fused to the quadrate. The quadrate is broad; its lateral margins attach to the

178 levator mandibulae muscles anteriorly, and posteriorly to the depressor mandibulae muscle. The

179 ventral margin of the quadrate meets with the terminal end of the mandible. The articular bone is

180 visible as a prominence that articulates dorsally with the quadrate, located between the

181 prearticular and dentary (in addition to sesamoids) in some species. The bony sesamoid is

182 located within the ligament between both the quadrate and the articular or prearticular (Fig. 2C),

183 slightly displaced posteriorly and medially. The sesamoid is present in 12 species of seven

184 families: *Peradactylodon persicus* (Hynobiidae) (Fig. 1D), *Cryptobranchus alleganiensis*

185 (Cryptobranchidae), *Ambystoma jeffersonianum*, *Ambystoma mexicanum*, and *Ambystoma*

186 *tigrinum* (Ambystomatidae), *Notophthalmus meridionalis, Notophthalmus viridescens*, and

187 *Neurergus crocatus, Pleurodeles waltl* (Salamandridae), *Plethodon glutinosus* (Plethodontidae),

188 *Necturus maculosus* (Proteidae), and *Siren intermedia* (Sirenidae) (Figs. 2 and 3). The presence

189 of this sesamoid is variable, and sometimes it is asymmetrically distributed in the same

190 specimen, i.e., being present on one side of the skull (e.g., *Ambystoma mexicanum*,

191 FMNH22888; *Pleuredeles waltl*, FML30804). Another sesamoid was observed between the skull

192 and the lower jaw in *Hydromantes platycephalus* and *Karsenia koreana* (Plethodontidae). It is

193 located at the posterior end of the maxilla (Fig. 1B and C). Isolated structures identified as

194 "occasional elements" are observed, which are present laterally to the terminal and subterminal

195 phalanx of the hands in, e.g., *Ambystoma mexicanum* (FMNH22888) (Fig. 4A) and *Gyrinophilus*

196 *porphyriticus* (UF64645). No other cartilaginous or bony sesamoids are observed in the

197 postcranium of the analyzed sample of urodeles. In the analyzed species of Gymnophiona, no

198 bony or cartilaginous sesamoids are found, but occasional elements are observed surrounding the

199 skull of some species, as in *Ichthyophis bannanicus* (MVZ 236728) (Fig. 4B).

200 The samples of Caudata and Gymnophiona are representative in terms of the number of

201 species, with slightly more than 94% confidence. For a clearer indication that the absence or

202 scarcity of cranial and postcranial bony or cartilaginous sesamoids in Caudata and Gymnophiona

203 can indeed be considered an evidence of absence, a probability calculation based on the dataset is

204 included. Considering the analyzed species, the probability of non-occurrences of bony or

205 cartilaginous cranial sesamoids in Caudata is very high (98%, see Table 1). On the other hand,

206 the probability of non-occurrence of bony or cartilaginous postcranial sesamoids in Caudata and

207 of bony or cartilaginous cranial and postcranial sesamoids in Gymnophiona is 100% (Table 1).

208

Sesamoid evolution

209

210 The survey resulted in a very representative dataset, since all nine families of Caudata were

211 studied. Optimization of the sesamoid in the mandibular symphysis shows that it is a convergent

212 acquisition (Fig. 5). The mapping analyses of the mandibular sesamoid dataset onto the

213 phylogeny reveal its convergent appearance in seven families (Fig. 5), thus rejecting the

214 secondary homology proposal. The optimization was ambiguous at the base of the clades of the

215 *Notophthalmus* species, and at (*Ambystoma tigrinum + A. ordinarium*). In the *Hydromantes*

216 *platycephalus + Karsenia koreana* (Plethodontidae) clade, the presence of the sesamoid between

217 the maxilla and the lower jaw wasoptimized as a putative synapomorphy (Fig. 5).

218

219 **Discussion**

220 Our survey of sesamoids in Caudata indicates that the only three bony or cartilaginous sesamoids

221 present in the group are associated with the mandible: one with the symphysis, another with the

222 quadrate-articular joint of the skull, and another between the maxilla and the lower jaw. As far as

223 we know, this report provides the first record of sesamoids in the mandibular symphysis and at

224 the posterior end of the maxilla of tetrapods. No sesamoids were observed in the postcranial

225 joints. Furthermore, in Gymnophiona, no bony or cartilaginous sesamoids were observed.

226   The very conspicuous sesamoid in the mandibular symphysis suggests some kind of

227 particular mechanical stress acting on the mandible of *Necturus beyeri* and *Amphiuma*

228 *tridactylum*, although its presence in only these two taxa makes the ecological or biomechanical

229 inferences excessively speculative. On the contrary, the sesamoid located between the maxilla

230 and the lower jaw is a new synapomorphy that supports the node of *Hydromantes platycephalus*

231 and *Karsenia coreana*.

232   The pool of species reviewed in this study showed that the mandibular sesamoid is

233 present in seven of the nine families included in the order. However, that sesamoid is infrequent

234 at the specific level, since it is present in only 16 of the 212 examined species (the order includes

757 recognized species; Frost, 2020). The skulls of some species in which sesamoids were observed were previously described, but those descriptions included no reference to sesamoids; e.g., *Siren intermedia* (Reilly & Altig, 1996), *Ambystoma tigrinum* (Naylor, 1978; Pedersen, 1993; Reilly & Lauder, 1990), *Notophthalmus viridiscens* (Naylor, 1978; Reilly, 1986); *Pleurodeles waltl* (Corsin, 1966). Buckley *et al.* (2010) described the skull of *Karsenia koreana* based on the same specimen reviewed in this work (DRV5033). However, they did not mention the sesamoid between the maxilla and the lower jaw, although it is very conspicuous in their illustrations (see fig 2 A-D of Buckley *et al.* 2010).

The optimization of the mandibular sesamoid reveals its convergent appearance in the different families; thus, the secondary homology proposal is rejected. According to our optimization, the absence of this sesamoid is plesiomorphic to Caudata. Three and 15 species of the most basal families, Cryptobranchidae (including four species; Frost, 2020) and Hynobiidae (including 81 species; Frost, 2020), respectively, were reviewed and one species with a bony or cartilaginous mandibular sesamoid was recorded in each family. The descriptions of 12 Caudata fossil species were reviewed, and none of them mentioned the presence of sesamoids. The stem-group of salamanders occurred during the Middle Jurassic, and was represented by species such as *Karaurus sharovi* (Karauridae), *Kokartus honoraius* (Karauridae), and *Marmorerpeton kermaki* (Incertae sedis) (Ivakhnenko, 1978; Evans *et al.*, 1988; Gao & Shubin, 2003; Carroll, 2007). These specimens and the first crown-group of Caudata, represented by *Chunerpeton* (Cryptobranchidae) of the Middle Jurassic and *Beiyanerpeton* and *Qinglong triton* (Salamandroidea) of the Late Jurassic (Gao & Shubin, 2013; Gao *et al.*, 2013; Jia & Gao, 2016), are remarkably well-preserved fossils and do not present sesamoids. Even when more hynobiidae should be sampled, the available evidence of the basal clade Hynobiidae + Cryptobranchidae and

258 the fossil record support the hypothesis of the absence of sesamoids as a plesiomorphic state in

259 Caudata.

260   We propose the mandibular sesamoid of Caudata as a primary homology to that of

261 anurans. However, in this group, the sesamoid has only been reported in *Barbourula*

262 *busuangensis* (Clarke, 1987; Roček *et al.*, 2016) and *Chacophrys pierotti* (Fabrezi *et al.*, 2017)

263 and, based on our findings, now in *Alytes obstetricans* (Alytidae, see

264 https://www.morphosource.org/Detail/MediaDeandtail/Show/media_id/13730), *Kassinula witei*

265 (Hyperoliidae, see https://www.morphosource.org/Detail/MediaDetail/Show/media_id/21067)

266 *Silvertoneia flotator* (Dendrobatidae, see

267 https://www.morphosource.org/Detail/MediaDetail/Show/media_id/63791); *Barycholos pulquer*

268 (Craugastoridae, see https://www.morphosource.org/Detail/MediaDetail/Show/media_id/14710);

269 *Ansonia mcgregori* (Bufonidae, see https://www.morphosource.org/

270 Detail/MediaDetail/Show/media_id/14201). It is likely to be present in a wider sample of

271 anurans and might be considered present in the developmental program of the group. In

272 *Barbourula busuangensis*, the sesamoid was described in the ligament, passing from the

273 squamosal shaft to the posterior end of the angular bone of the mandible (Clarke, 1987; Roček *et*

274 *al.*, 2016). According to its topology and related ligament, in salamanders and anurans the

275 sesamoid would meet the proposed primary homology criterion. However, a wider taxon

276 sampling is needed to test the secondary homology of this sesamoid in Caudata and Anura.

277   Three groups of hypotheses about the origin of frogs, salamanders and caecilians persist

278 in the literature: the "temnospondyl hypothesis", the "lepospondyl hypothesis", and the

279 "polyphyly hypothesis", of which the former was the most widely supported for a long time

280 (Ruta & Coates, 2007). However, recent re-analyses strongly support the lepospondyl origin of

281   lissamphibians (Marjanović & Laurin, 2013, 2019). Whatever the affinities of the three modern

282   orders with Paleozoic amphibians, the records of temnospondyls and lepospondyls do not

283   include sesamoids (e.g., Walsh, 1987; Gardner, 2003, Carrol, 2007; Fortuny *et al*., 2016; see

284   species in Supplementary Material S1). Further research is needed to find out whether

285   fibrocartilaginous sesamoids are absent in these groups as well. Sesamoids are identified "in

286   relation to" other anatomical elements, such as ligaments, tendons, and joints (Fontanarrosa *et*

287   *al*., 2020). In disarticulated fossil remains, sesamoids are challenging to identify, which might

288   explain their report in association with postcranial joints in only two fossils of the anuran

289   *Xenopus* (Henrici & Báez, 2001; Wang *et al*., 2007).

290   The proposed functions of sesamoids include protecting tendons against friction,

291   compression, tension, or injuries (Sarin *et al*., 1999; Otero & Hoyos, 2013; Regnault *et al*., 2016;

292   Abdala *et al*., 2017; Zhang *et al*., 2017). The integration of the mandibular sesamoids with other

293   elements of the mandibular joint (bones, muscles, tendons, and ligaments) would be crucial to

294   generate the strength for feeding through complex and coordinated movements. Interestingly, it

295   is not possible to propose a direct relationship between dietary selection or feeding habits and the

296   presence of a mandibular sesamoid. Species with a mandibular sesamoid have a similar diet to

297   that of species without sesamoids: they are predators with a wide range of prey types and sizes,

298   from macroinvertebrates to small vertebrates, including annelids, mollusks, ants, spiders,

299   centipedes, snails, sowbugs, beetles, mayflies, stoneflies, fish, amphibians, etc. (Hamilton, 1932;

300   Bardwell *et al*., 2007). In a physiological position, the sesamoid fits between the squamosal and

301   the prearticular, and is located among the jaw bones instead of covering the joint, the most

302   common position of sesamoids. More comparative data is necessary to test the hypothesis of

303   biomechanical restrictions linked to feeding and development of the mandibular sesamoids.

304   We prefer not to include among sesamoids the occasional elements found in of

305   *Ambystoma mexicanum*, *Gyrinophilus porphyriticus*, and *Ichthyophis bannanicus*, among others,

306   due to their somewhat anecdotal record. Thus, we believe they should be considered occasional

307   structures (see also Kunc *et al*., 2020) until their location embedded in a tendon is confirmed

308   with histological studies.

309   The absence of bony or cartilaginous postcranial sesamoids in salamanders is striking and

310   would be another particular characteristic of their limbs. Limbs of salamanders have a unique

311   development among extant tetrapods, since they are characterized by the absence of the apical

312   ectodermal ridge and the formation of the distal mesopodial and autopodial elements without a

313   continuous condensation linking them to more proximal cartilages (Shubin & Alberch, 1986;

314   Franssen *et al*., 2005; Fröbisch & Shubin, 2011; Kumar *et al*., 2015; Kearney *et al*., 2018). In the

315   context of limb development of urodeles, several morphological patterns resulting from

316   heterochrony –timing differences in development– have been described (e.g., Wake *et al*., 1983;

317   Blanco & Alberch, 1992; Shubin, 2002). These patterns consist of variations in the stages at

318   which the fore and hind limbs develop (Smith, 1912; Hanken, 1982; Babcock & Blais, 2001;

319   Nye *et al*., 2003; Bininda-Emonds *et al*., 2007), or in the sequences in which several skeletal

320   elements develop in the limbs (Shubin & Alberch, 1986). In the absence of the AER, the small

321   plethodontid *Bolitoglossa occidentalis* lacks phalangeal elements, which is interpreted as a

322   paedomorphic character (Alberch & Alberch, 1981). Sesamoids develop later than the other

323   skeletal elements of anuran limbs (Ponssa *et al*., 2010; Vera & Ponssa, 2014; Vera *et al*., 2015);

324   thus, their absence in the salamander clade (both in large and small species), can be speculated to

325   be a paedomorphic pattern, as a consequence of a truncated development. Whether this pattern is

326   produced by the absence of the AER or any other changes in developmental mechanisms remains

327 to be investigated. Interestingly, the limb joints of urodeles are also highly paedomorphic. The

328 articular surfaces of the long limb bones are rather simple, remain cartilaginous, and lack

329 secondary ossification centers (Haines, 1942; Meng *et al.*, 2019) and the complexities present in

330 the concave bony epiphyses of other tetrapods (see e.g., Hanken 1982, Fig. 4B) (Fig. 6). These

331 simple structures might explain the lack of bony or cartilaginous sesamoids, since the tendons

332 would not be subjected to the pressure and effort of sliding on a hard and sculpted surface.

333 There are no records of postcranial sesamoids in salamanders, caecilians,

334 branchiosaurids, or other lepospondyls and temnospondyls (Walsh, 1987; Carrol, 2007; Fortuny

335 *et al.*, 2016; Gardner, 2001; Gruntmejer *et al.*, 2016). An excellent fossil record of Paleozoic

336 branchiosaurids presents a clear view of the limb ossification pattern in the Temnospondyli

337 *Apateon* (Fröbisch *et al.*, 2007), which lacks sesamoids. The process of limb ossification in

338 *Apateon* is similar to that of urodeles in some aspects, such as the preaxial dominance in limb

339 development or the limb ossification sequence, which has been discussed as a critical character

340 to elucidate the relationship of these taxa (Fröbisch *et al.*, 2007; Fröbisch, 2008). When plotted

341 on the hypothesis of lissamphibian relationships to basal tetrapods, postcranial sesamoids require

342 two steps to achieve a convergent evolution with postcranial sesamoids present in frogs and

343 amniotes (Fig. 7). The absence of postcranial sesamoids results in the plesiomorphic state in

344 tetrapods.

345 Caecilians are elongated, snake-like amphibians, completely lacking limbs and girdles.

346 They have a terrestrial, surface-cryptic, or burrowing lifestyle, except for Typhlonectidae, whose

347 members are secondary aquatic or semi-aquatic (Taylor, 1968; Estes, 1981; Wilkinson &

348 Nussbaum, 1999). The lack of postcranial sesamoids could be a logical consequence of the lack

349 of postcranial joints of the crown group Gymnophiona. However, in the two putative stem-

350　groups of caecilians, *Eocaecilia micropodia* from the Lower Jurassic, which has reduced limbs

351　(Jenkins & Walsh, 1993), and *Rubricacaecilia monbaroni* from the Lower Cretaceous, to which

352　a left femur showing a trochanteric crest has been tentatively attributed (Evans & Sigogneau-

353　Russel, 2001), no sesamoids have been reported. According to the dynamic model proposed in

354　Abdala *et al*. (2019), sesamoids can attach to and detach from the long bone epiphyses and

355　diaphyses during both ontogeny and phylogeny (see also Parsons, 1904; Manners-Smith, 1908;

356　Barnett & Lewis, 1958; Cheong *et al*., 2017, among many others). Thus, the observed

357　trochanteric crest could be interpreted as an attached sesamoid. New fossil evidence could fill the

358　information gap about sesamoid evolution in this group.

359　　Since caecilians are limbless and mainly fossorial animals, the diversification of their

360　cranium might have been conditioned by the functional demands of head burrowing (Sherratt *et*

361　*al*., 2014). This fossorial mode of life might have been the most substantial influence on the

362　parietal and quadrate-squamosal modules (Bardua *et al*., 2019). This strong integration of the

363　skull bones could explain the lack of sesamoids in the quadrate-squamosal module. Moreover,

364　the rearrangement of jaw-closing muscles across Gymnophiona influences the jaw joint (Bardua

365　*et al*., 2019). The involved tendons would not be subjected to the necessary tension threshold for

366　the development and evolution of sesamoids in this group.

367　　The tissue composition of sesamoids can be diverse and can include cartilage, bone, or

368　fibrocartilage. In the latter case, histological samples would be necessary to corroborate its

369　presence or absence in salamanders and caecilians.

370

371　Conclusions

372   Our data show the presence of three cranial bony sesamoids in Caudata, which is

373   remarkable considering that cranial sesamoids are rare among tetrapods. Our data also indicate

374   that Caudata lacks bony or cartilaginous postcranial sesamoids, whereas Gymnophiona lacks

375   bony or cartilaginous cranial and postcranial sesamoids. Our ancestral state reconstruction

376   indicates that the plesiomorphic state to the Caudata is the absence of bony or cartilaginous

377   cranial sesamoids.

378

387

388   **Literature Cited**

389   **Abdala V, Vera MC, Ponssa ML. 2017**. On the presence of the patella in frogs. *The*

390   *Anatomical Record* **300**:1747–1755.

391   **Abdala V, Vera MC, Amador LI, Fontanarrosa G, Fratani J, Ponssa ML. 2019.** Sesamoids

392   in tetrapods: the origin of new skeletal morphologies. *Biological Reviews* **94**:2011–2032.

393   **Adriaens D, Verraes W**. 1998. Ontogeny of the osteocranium in the African catfish, *Clarias*

394   *gariepinus* Burchell (1822) (Siluriformes: Clariidae): ossification sequence as a response to

395   functional demands. *Journal of Morphology* **235**:183–237.

396   **Alberch P, Alberch J. 1981**. Heterochronic mechanisms of morphological diversification and

397   evolutionary change in the neotropical salamander, *Bolitoglossa occidentalis* (Amphibia:

398   Plethodontidae). *Journal of Morphology* **167**:249–264.

399   **Alexander R. 1967**. The functions and mechanisms of the protrusible upper jaws of some

400   acanthopterygian fish. *Journal of Zoology* **151**:43–64.

401   **Amador L, Giannini NP, Simmons N, Abdala V. 2018.** Morphology and

402   evolution of sesamoid elements in bats (Mammalia: Chiroptera). *American Museum Novitates*

403   **3905**:1–40.

404   **Avilan P, Hoyos JM. 2006**. Osteología de *Eleutherodactylus bogotensis* (Amphibia, Anura,

405   Leptodactylidae) del parque nacional natural Chingaza (Cundinamarca, Colombia). *Caldasia*

406   **28**:89–109.

407   **Babcock SK, Blais JL. 2001.** Caudal vertebral development and morphology in three

408   salamanders with complex lifecycles (*Ambystoma jeffersonianum*, *Hemidactylium scutatum*,

409   and *Desmognathus ocoee*). *Journal of Morphology* **247**:142–159.

410   **Bardua C, Wilkinson M, Gower DJ, Sherrat E, Goswani A. 2019**. Morphological evolution

411   and   modularity   of   the   caecilian   skull.   *BMC   Evolutionary   Biology*   **19:30**

412   doi.org/10.1186/s12862-018-1342-7.

413   **Bardwell JH, Ritzi CM, Parkhurst JA. 2007.** Dietary selection among different size classes of

414   larval *Ambystoma jeffersonianum* (Jefferson Salamanders). *Northeastern Naturalist* **14(2)**:

415   293–299.

Barnett CH, Lewis OJ. 1958. The evolution of some traction epiphyses in birds and mammals. *Journal of Anatomy* **92**:593–601.

Bemis WE, Schenk K, Wake MK. 1983. Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). *Zoological Journal of the Linnean Society* **77**:75–96.

Benjamin M, Ralphs JR. 1998. Fibrocartilage in tendons and ligaments-an adaptation to compressive load. *Journal of Anatomy* **193**:481–494.

Bininda-Emonds ORP, Jeffery JE, Sánchez-Villagra MR, Hanken J, Colbert M, Pieau C, Selwood L, Ten CC, Raynaud A, Osabutey CK, Richardson MK. 2007. Forelimb–hind limb developmental timing changes across tetrapod phylogeny. *BMC Evolutionary Biology* **7**:182.

Blanco M, Alberch P. 1992. Caenogenesis, developmental variability, and evolution in the carpus and tarsus of the marbled newt *Triturus marmoratus*. *Evolution*, **46(3)**: 677–687. http://doi.org/10.1111/j.1558-5646.1992.tb02075.x

Bonnet RM, Blair AL. 2017. Evidence for complex life cycle constraints on salamander body form diversification. *Proceedings of the National Academy of Science* doi.org/10.1073/pnas.1703877114.

Bramble DM. 1974. Occurrence and significance of the ostransiliens in gopher tortoises. *Copeia* **1**:102–109.

Cala CJD, Tarazona OA, Ramírez-Pinilla MP. 2019. The morphology and post-hatching development of the skull of *Bolitoglossa nicefori* (Caudata: Plethodontidae): developmental implications of recapitulation and repatterning. *Zoology* **112**:227–239.

Carlsöö S. 1982. The effect of vibration on the skeleton, joints, and muscles: a review of the literature. *Applied Ergonomics* **13(4)**:251–258.

Carroll RL. 2007. The palaeozoic ancestry of salamanders, frogs, and caecilians. *Zoological Journal of the Linnean Society* **150**:1–140.

Cheong I, Kang H, Ko H, Sung J, Song Y, Hwang, J. 2017. Genetic influence on accessory navicular bone in the foot: a Korean twin and family study. *Twin Research and Human Genetics* **20**: 236–241.

Clarke BT. 1987. A description of the skeletal morphology of *Barbourula* (Anura: Discoglossidae), with comments on its relationships. *Journal of Natural History* **21**:879–891.

Corsin J. 1966. The development of the osteocranium of *Pleurodeles waltl* Michahelles. *Journal of Morphology* **119**:209–216.

Chadwick KP, Regnault S, Allen V, Hutchinson J R. 2014. Three-dimensional anatomy of the ostrich (*Struthio camelus)* knee joint. *PeerJ, 2,* e706.

Datovo A, Bockmann FA. 2010. Dorsolateral head muscles of the catfish families Nematogenyidae and Trichomycteridae (Siluriformes: Loricarioidei): Comparative anatomy and phylogenetic analysis. *Neotropical Ichthyology* **8:**193–246.

Denyer AL, Regnault S, Hutchinson JR. 2020. Evolution of the patella and patelloid in marsupial mammals. *PeerJ*8:e9760https://doi.org/10.7717/peerj.9760

Diogo R, Oliveira C, Chardon M. 2001. On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium. *Belgian Journal of Zoology* **131**:93–109.

Diogo R, Walsh S, Smith C, Ziermann JM, Abdala V. 2015. Towards the resolution of a long-standing evolutionary question: muscle identity and attachments are mainly related to

460 topological position and not to primordium or homeotic identity of digits. *Journal of Anatomy*

461 **226**:523–529.

462 **Estes R. 1981.** Gymnophiona, Caudata. In *Handbuch der Palaeoherpetologie*. **Vol. 2**.Kuhn O

463 (coord). Gustav Fischer Verlag. Stuttgart. 115 pp.

464 **Evans SE, Milner AR, Musset F. 1988**. The earliest known salamanders (Amphibia, Caudata):

465 a record from the Middle Jurassic of England. *Geobios* **21**:539–552.

466 **Evans SE, Sigogneau-Russel D. 2001.** A stem-group caecilian (Lissamphibia: Gymnophiona)

467 from Lower Cretaceous of North Africa. *Paleontology* **44**:259–273.

468 **Fabrezi M. 2006**. Morphological evolution of Ceratophryinae (Anura, Neobatrachia). *Journal of*

469 *Zoological Systematics and Evolutionary Research* **44**:153–166.

470 **Fontanarrosa G, Fratani J, Vera MC. 2020.** Delimiting the boundaries of sesamoid identities

471 under the network theory framework. *PeerJ*, DOI 10.7717/peerj.9691.

472 **Fortuny J, Marce-Nogue J, Steyer JS, De Esteban-Trivigno S, Mujal E, Gil L. 2016**.

473 Comparative 3D analyses and palaeoecology of giant early amphibians (Temnospondyli:

474 Stereospondyli). *Scientific Reports* **6**:1–10.

475 **Franssen RA, Marks S, Wake D, Shubin N. 2005**. Limb chondrogenesis of the seepage

476 salamander, *Desmognathus aeneus* (Amphibia: Plethodontidae). *Journal of Morphology*

477 **265**:87–101.

478 **Fröbisch NB, Carroll RL, Schoch RR. 2007**. Limb ossification in the Paleozoic branchiosaurid

479 *Apateon* (Temnospondyli) and the early evolution of preaxial dominance in tetrapod limb

480 development. *Evolution & Development* **9:**69–75.

481 **Fröbisch NB, Shubin NH. 2011.** Salamander limb development: integrating genes, morphology,

482 and fossils. *Developmental Dynamics* **240**:1087–1099.

483 **Frost DR. 2020.** Amphibian Species of the World: an Online Reference. Version 6.0 (Date of

484 access).   Electronic   Database   accessible   at

485 http://research.amnh.org/herpetology/amphibia/index.html.   American   Museum   of   Natural

486 History, New York, USA. doi.org/10.5531/db.vz.0001

487 **Gao KQ, Shubin NH. 2003.** Earliest known crown-group salamanders. *Nature* **422**:424–428.

488 **Gao K, Chen J, Jia J. 2013.** Taxonomic diversity, stratigraphic range, and exceptional

489 preservation of Juro-Cretaceous salamanders from northern China. *Canadian Journal of Earth*

490 *Sciences* **50**:255–267.

491 **Gardner JD. 2003.** The fossil salamander *Proamphiuma cretacea* Estes (Caudata;

492 Amphiumidae)   and   relationships   within   the   Amphiumidae.   *Journal   of   Vertebrate*

493 *Paleontology* **23**:769–782.

494 **Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke AD. 2012.** Assembling the

495 squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the*

496 *Peabody Museum of Natural History* **53**:3–308

497 **Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis.

498 *Cladistics* **24**:774–786.

499 **Gruntmejer K, Konietzko-Meier D, Bodzioch A. 2016**. Cranial bone histology of

500 *Metoposaurus krasiejowensis*(Amphibia, Temnospondyli) from the Late Triassic of Poland.

501 *PeerJ* DOI 10.7717/peerj.2685

502 **Guayasamin JM. 2004.** A new species of *Eleutherodactylus* (Anura: Leptodactylidae) from the

503   northwestern lowlands of Ecuador. *Herpetologica* **60**:190–191.

504 **Gussekloo WS, Bout RG. 2005.** Cranial kinesis in paleognathous birds. *Journal of*

505   *Experimental Biology* **208**:3409–3419.

506 **Haines RW. 1942**. The evolution of epiphyses and of endochondral bones. *Biological Reviews*

507   **17**:267–292.

508 **Hamilton WJ Jr. 1932**. The food and feeding of some eastern salamanders. *Copeia* **1932**:83–86.

509 **Hanken J. 1982**. Appendicular skeletal morphology in minute salamanders, genus *Thorius*

510   (Amphibia: Plethodontidae): growth regulation, adult size determination, and natural

511   variation. *Journal of Morphology* **174**:55–77.

512 **Henrici AC, Baéz AM. 2001.** First occurrence of *Xenopus* (Anura: Pipidae) on the Arabian

513   Peninsula: a new species from the upper Oligocene of Yemen. *Journal of Paleontology*

514   **75**:870–882.

515 **Hofling E, Gasc JP. 1984.** Biomechanics of the skull and the beak in *Ramphastos*

516   (Ramphastidae, Aves) I. Description of anatomical elements. *Gegenbaurs Morphologisches*

517   *Jahrbuch* **130**:125–147.

518 **Holliday CM, Witmer LW. 2007**. Archosaur adductor chamber evolution: Integration of

519   musculoskeletal and topographical criteria in jaw muscle homology. *Journal of Morphology*

520   **268**:457–484.

521 **Hoyos JM. 2003.** Additions to our knowledge of anuran sesamoids. *Herpetological Review*

522   **34**:112–116.

523 **Iordansky NN. 1964**. The jaw muscles of the crocodiles and some relating structures of the

524   crocodilian skull. *Anatomischer Anzeiger* **115**:256–280.

525 **Iordansky NN. 1989**. Evolution of cranial kinesis in lower tetrapods. *Netherlands Journal of*
526   *Zoology* **40**:32–54.

527 **Ivakhnenko MF. 1978.** Urodelans from the Triassic and Jurassic of Soviet Central Asia.
528   *Paleont. Zhurnal*, Moscow **1978** (3):84–89 (in Russian). *Paleontological Journal* **12(3)**:362–
529   368 (in English).

530 **Jenkins DT, Walsh DM. 1993**. An Early Jurassic caecilian with limbs. *Nature* **365**:246–249.

531 **Jerez A, Mangione S, Abdala V. 2010**. Occurrence and distribution of sesamoid bones in
532   squamates: a comparative approach. *Acta Zoologica Stockholm* **91**:295–305.

533 **Jia J, Gao K. 2016.** A new basal salamandroid (Amphibia, Urodela) from the Late Jurassic of
534   Qinglong Province, China. *PLoS One* **11(5)**:1–35. DOI: 10.1371/journal.pone.0153834.

535 **Jia J, Jiang JP, Zhang MH, Gao KQ. 2018.** Osteology of *Batrachuperus yenyuanensis*
536   (Urodela, Hynobiidae), a high-altitude mountain stream salamander from western China.
537   *PLoS One* **14(1)**: e0211069.

538 **Kearney RR, Hanken J, Blackburn DC. 2018**. Early limb patterning in the direct-developing
539   salamander *Plethodon cinereus* revealed by *sox*9 and *col*2a1. *Evolution and Development*
540   **20**:100–107.

541 **Khoshnamvand H, Malekian M, Keivany Y, Zamani-Faradonbe MZ, Amiri M. 2019**.
542   Descriptive osteology of an imperiled amphibian, the Luristan newt (*Neurergus kaiseri,*
543   Amphibia. Salamandridae). *Acta Herpetologica* **14**:51–56.

544 **Kumar A, Gates PB, Czarkwiani A, Brockes JP. 2015**. An orphan gene is necessary for
545   preaxial digit formation during salamander limb development. *Nature Communications*
546   **6**:8684–8688. http://doi.org/10.1038/ncomms9684

547 **Kunc V, Kunc V, Černý V, Polovinčák M, Kachlík D. 2020.** Accessory bones of the elbow:
548   Prevalence, localization and modified classification. *Journal of Anatomy* **237**:618–622.
549   https://doi.org/10.1111/joa.13233

550 **Laurent RF. 1961**. Notes on Some South African Amphibians, Edition (Volume 1), pp.197–
551   209. Publications de l'Universite de l'Etata Elisabethville, Lubumbashi.

552 **Laurin M. 1998**. The importance of global parsimony and historical bias in understanding
553   tetrapod evolution. Part I. Systematics, middle ear evolution, and jaw suspension. *Annales des*
554   *Sciences Naturelles. Zoologie* (13 Ser.) **19**:1–42.

555 **Laurin M, Reisz RR. 1997**. A new perspective on tetrapod phylogeny. In Sumida S, Martin K.
556   (eds). Amniote Origins. Completing the Transition to Land. Academic Press, San Diego, 9–
557   59.

558 **Macaluso L, Villa A, Pitruzzella G, Rook L, Pogoda P. Kupfer M, Delfino, M.**
559   **2020.**Oteology of the Italian endemic spectacled salamanders, *Salamandrina* spp. (Amphibia,
560   Urodela, Salamandridae): selected skeletal elements for palaeontological investigations.
561   *Journal of Morphology* DOI: 10.1002/jmor.21254

562 **Manners-Smith T. 1908**. A study of the cuboid and os peroneum in the primate foot. *Journal of*
563   *Anatomy and Physiology* **42**:397–414.

564 **Marjanović D, Laurin M. 2013.**The origin(s) of extant amphibians: a review with emphasis on
565   the "lepospondyl hypothesis". *Geodiversitas* **35**:207–272.

Marjanović D, Laurin M. 2019. Phylogeny of Paleozoic limbed vertebrates reassessed thorough revision and expansion of the largest published relevant data matrix. *PeerJ*DOI 10.7717/peerj.5565.

Marshall AF, Bardua C, Gower DJ, Wilkinson M, Sherrat E, Goswami A. 2019. High-density three-dimensional morphometric analyses support conserved static (intraspecific) modularity in caecilian (Amphibian: Gymnophiona) crania. *Biological Journal of the Linnean Society* **126:**721–742.

Meng X, Goldin P, Herdina AN, Estefa J, Medvedeva EV, Li L, Newton PT, Kotova S, Shavkuta B, Saxena A, Shumatel LT, Metscher B, Großschmidt K, Nishimori S, Akovantseva A, Linares Arregui I, Tafforeau P, Fried K, Carlström M, Simon A, Gasser C, Kronenberg HM, Bastepel M, Cooper K, Timashev P, Sanchez S, Adameyko I, Eriksson A, Chagin AS. 2019. Secondary ossification centers evolved to make endochondral bone growth possible under the weight bearing demands of a terrestrial environment. *Bio Rxiv* preprint doi: https://doi.org/10.1101/571612.

Milner AR. 1993.Amphibian-grade Tetrapoda, in Benton MJ (ed.). The Fossil Record 2. Chapman & Hall, London, 665–679.

Montero R, Daza JD, Bauer AM, Abdala V. 2017. How common are cranial sesamoids among squamates? *Journal of Morphology* **278**:1400–1411.

Müller H. 2006. Ontogeny of the skull, lower jaw, and hyobranchial skeleton of *Hypogeophis rostratus* (Amphibia: Gymnophiona: Caeciliidae) Revisited. *Journal of Morphology* **267**:967–987.

Naylor BG. 1978. The frontosquamosal arch in newt as a defense against predators. *Canadian Journal of Zoology* **56:**2211–2216.

589 **Nussbaum RA. 1982.** Heterotopic bones in the hindlimbs of frogs of the families

590   Pipidae, Ranidae, and Sooglossidae. *Herpetologica* **38**:312–332.

591 **Nye HL, Cameron JA, Chernoff EA, Stocum DL. 2003**. Extending the table of stages of

592   normal development of the axolotl: limb development. *Developmental Dynamics* **226**:555–

593   560.

594 **Olson WM. 2000**. Phylogeny, ontogeny, and function: Extraskeletal bones in the

595   tendons and joints of *Hymenochirus boettgeri* (Amphibia: Anura: Pipidae). *Zoology* **103**:15–

596   24.

597 **Otero T, Hoyos JM. 2013**. Sesamoid elements in lizards. *Journal of Herpetology* **23**:105–114.

598 **Parsons FG. 1904.** Observations on traction epiphyses. *Journal of Anatomy* **38**:248–258.

599 **Pearson K, Davin AG. 1921a**. On the sesamoids of the knee-joint. Part I. Man. *Biometrika* **13**:

600   133–175.

601 **Pearson K, Davin AG. 1921b.** On the sesamoids of the knee-joint. Part II.

602   Evolution of the sesamoids. *Biometrika* **13**:350–400.

603 **Pedersen SC. 1993.** Skull growth in cannibalistic tiger salamanders, *Ambystoma tigrinum. The*

604   *Southwestern Naturalist* **38(4)**:316–324.

605 **Ponssa ML, Goldberg J, Abdala V. 2010.** Sesamoids in anurans: new data,

606   old issues. *The Anatomical Record* **293**:1646–1668.

607 **Pyron RA, Wiens JJ. 2011**. A large-scale phylogeny of Amphibia including over 2800 species,

608   and a revised classification of extant frogs, salamanders, and caecilians. *Molecular*

609   *Phylogenetic and Evolution* **61**:543–583.

Regnault S, Pitsillides AA, Hutchinson JR. 2014. Structure, ontogeny, and evolution of the patellar tendon in emus (*Dromaius novaehollandiae*) and other palaeognathae birds. *PeerJ* 2, DOI: 10.7717/peerj.711.

Regnault S, Hutchinson JR, Jones ME. 2016. Sesamoid bones in tuatara (*Sphenodon punctatus*) investigated with X-ray microtomography and implications for sesamoid evolution in Lepidosauria. *Journal of Morphology* **278**:62–72.

Reilly SM. 1986. Ontogeny of cranial ossification in the eastern newt, *Notophthalmusviridescens*(Caudata: Salamandridae), and its relationship to metamorphosis and neoteny. *Journal of Morphology* **188**:318–326.

Reilly SM, Lauder GV. 1990. Metamorphosis of cranial design in tiger salamanders (*Ambystoma tigrinum*): a morphometric analysis of ontogenetic change. *Journal of Morphology* **204**:121–137.

Reilly SM, Altig R. 1996. Cranial ontogeny in *Siren intermedia* (Caudata: Sirenidae): paedomorphic, metamorphic, and novel patterns of heterochrony. *Copeia* **1996(1)**:29–41.

Restrepo AE. 1995. Comparación de la osteologìa de la salamandra *Bolitoglossa adspersa* (Urodela: Plethodontidae) con otros urodelos. *Universitas Scientiarum* **2**:43–50.

Reyes-Amaya N, Jerez A, Flores D. 2017.Morphology and postnatal development of lower hindlimbs in *Desmodus rotundus* (Chiroptera: Phyllostomidae): A Comparative Study. *The Anatomical Record* **300**:2150–2165.

Roček Z, Balleva N, Vazeille A, Bravin A, van Dijk E, Nemoz C, Přkryl T, Smirina EM, Boiste R, Claessens L. 2016. Contribution to the head anatomy of the basal frog *Barbourula busuangensis* and the evolution of the Anura. *Russian Journal of Herpetology* **23(3)**:163–194.

632 **Romankowowa A. 1961**. The sesamoid bones of the autopodia of bats;

633   Trzeszczkiodcinkawolnego (autopodium) konczynnietoperzy. *Acta Theriologica* **5**:125–140.

634 **Ruta M, Coates MI, Quicke DLJ.** 2003. Early tetrapod relationships revisited. *Biological*

635   *Reviews* **78**: 251–345.

636 **Ruta M, Coates MI. 2007**. Dates, nodes, and character conflict: addressing the lissamphibian

637   origin problem. *Journal of Systematic Palaeontology* **5**:69–122

638   doi.10.1017/S1477201906002008.

639 **Samuels ME, Regnault S, Hutchinson JR. 2017**. Evolution of the patellar sesamoid bone in

640   mammals. *PeerJ* 5:e3103 doi.10.7717/peerj.3103.

641 **Sarin VK, Erickson GM, Giori NJ, Bergman AG, Carter DR.**

642   **1999.** Coincident development of sesamoid bones and clues to their evolution. *The*

643   *Anatomical Record* **257**:174–180.

644 **Sherratt E, Gower DJ, Klingenberg CP, Wilkinson M. 2014**. Evolution of cranial shape in

645   caecilians (Amphibia: Gymnophiona). *Evolutionary Biology* **41**:528545.

646 **Schumacher GH. 1973**. The head muscles and hyolaryngeal skeleton of turtles and crocodilians.

647   In C. Gans, A. D. Bellairs, & T. S. Persons (Eds.), Biology of the Reptilia 4. Morphology D

648   (pp. 101–200). New York: Academic Press.

649 **Shubin NH, Wake DB, Crawford AJ. 1995.** Morphological variation in the limbs of *Taricha*

650   *granulosa* (Caudata: Salamandridae): evolutionary and phylogenetic implications. *Evolution*

651   **49(5)**:874–884.

652 **Shubin NH. 2002**. Origin of evolutionary novelty: Examples from limbs. *Journal of*

653   *Morphology* **252**:15–28. doi:10.1002/jmor.10017

654 **Shubin NH, Alberch P. 1986**. A morphogenetic approach to the origin and basic organization of
655   the tetrapod limb. *Evolutionary Biology* **20**:319–387.

656 **Smith BG. 1912.** The embryology of *Cryptobranchus alleganiensis*, including comparisons with
657   other vertebrates. *Journal of Morphology* **23**:579.

658 **Smith WL, Chesney AB, Ornay GS, Davis MP, Martin RP, Gibson SZ, Girard MG. 2018.**
659   Improving vertebrate skeleton images: fluorescence and the non-permanent mounting of
660   cleared and stained specimens. *Copeia* **106(3)**:427–435.

661 **Summers AP, Koob-Emunds MM, Kajiura SM, Koob TJ. 2003.** A novel fibrocartilaginous
662   tendon from an elasmobranch fish (*Rhinoptera bonasus*). *Cell and Tissue Research* **312**:221–
663   227.

664 **Taylor EH. 1968.** The caecilians of the world: a taxonomic review. Lawrence: University of
665   Kansas Press. 848 p.

666 **Trueb L., Cloutier R.**1991.A phylogenetic investigation of the inter- and intrarelationships of
667   the Lissamphibia (Amphibia: Temnospondyli), in Schultze HP, Trueb L. (eds), Origins of the
668   Higher Groups of Tetrapods. Controversy and Consensus. Cornell University Press, Ithaca,
669   223–313.

670 **Tsai HP, Holliday CM. 2011.** Ontogeny of the *Alligator* cartilage transiliens and its significance
671   for sauropsid jaw muscle evolution. *PLoSOne* **6**, e24935.

672 **Vallin G, Laurin M. 2004**. Cranial morphology and affinities of Microbrachis, and a reappraisal
673   of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology*
674   **24**:56–72.

Vera MC, Ponssa ML. 2014. Skeletogenesis in anurans: Cranial and postcranial development in metamorphic and postmetamorphic stages of *Leptodactylus bufonius* (Anura: Leptodactylidae). *Acta Zoologica (Stockholm)* **95(1)**:44–62 doi.org/10.1111/azo.12007

Vera MC, Ponssa ML, Abdala V. 2015. Further data on sesamoid identity from two anuran species. *The Anatomical Record* **298**:1376–1394.

Vickaryous MK, Olson WM. 2007. Sesamoids and ossicles in the appendicular skeleton. In: Hall BK, editor. Fins into Limbs. pp. 323–341. The University of Chicago Press, Chicago.

Villa A, Andreone F, Boistel R. Delfino M. 2014. Skull and lower osteology of the Lanza´s salamander, *Salamandra lanzai* (Amphibia, Caudata). *Scripta Herpetologica. Studies on Amphibians and Reptiles in honor of Benedetto Lanza*, pp.171–200.

Wake DB. 1963. Comparative osteology of the plethodontid salamander genus *Aneides*. *Journal of Morphology* **113**:77–118.

Wake T, Wake D, Wake M. 1983. The ossification sequence of *Aneides lugubris*, with comments on heterochrony. *Journal of Herpetology* **17(1)**:10–22. doi:10.2307/1563775

Walsh DM. 1987. Systematics of the Caecilians (Amphibia: Gymnophiona). A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy. 335 p.

Wang Y, Jones MEH, Evans SE. 2007. A juvenile anuran from the Lower Cretaceous Jiufotang Formation, Liaoning, China. *Cretaceous Research* **28**:235e244.

Wassersug RJ. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. *Stain Technology* **51**:131–134.

696   **Wilkinson M, Nussbaum RA. 1999**. Evolutionary relationships of the lungless

697   caecilian Atretochoana eiselti (Amphibia: Gymnophiona: Typhlonectidae). *Zoological*

698   *Journal of the Linnean Society* **126**:191–223.

699   **Wu Y, Wang Y, Hanken J. 2012.** Comparative osteology of the genus *Pachytriton* (Caudata:

700   Salamandridae) from Southeastern China. *Asian Herpetological Research* **3(2)**:83–102.

701   **Zhang R, Han D, Luo G, Ling L, Li G, Ji Q, Li J. 2017**. Macroscopic and microscopic

702   analyses in flexor tendons of the tarso metatarso-phalangeal joint of ostrich (*Struthio camelus*)

703   foot with energy storage and shock absorption. *Journal of Morphology* **279**:302–311.

705

Figure Captions

Fig. 1. Sesamoid in the mandibular symphysis of *Necturus beyeri* (UF177187), view of stl surface model of a cranial CT scan from MorphoSource, dataset https://doi.org/10.17602/M2/M39589 (A). Skulls of: *Hydromantes platycephalus* (uncatalogued), image credit: Digimorph.org (B), and *Karsenia koreana* (DRV5033) with a sesamoid between the posterior end of the maxilla and the lower jaw joint, image credit: Digimorph.org (C); *Peradactylodon persicus* (MVZ241494) with a sesamoid in the quadrate-prearticular joint, image credit: Digimorph.org. (D). The largest arrows show the sesamoids. dent=dentary, max=maxilla, preart=preartricular, sq=squamosal.

Fig. 2. Mandibular sesamoid in the quadrate-prearticular joint of the skull of *Siren intermedia* (FMNH84082) (A), *Neurergus crocatus* (FMNH19629)(B), *Ambystoma mexicanum* (FMNH22888) under white (C) and fluorescent lighting (photo credit: Jennifer Y. Lamb) (D), *Ambystoma jeffersonianum* (FMNH196112) (E), *Necturus maculosus* (FMNH21523) (F). Scale bar = 1mm. White arrow = indicates the ligament surrounding the sesamoid in detail of the *Ambystoma mexicanum* mandibular joint.

Fig. 3. Mandibular sesamoid in the quadrate-prearticular joint of the skull of *Notophthalmus viridiscens* (FMNH93537) (A), *Notophthalmus meridionalis* (FMNH93536) under white (B) and fluorescent light (photo credit: Jennifer Y. Lamb) (C, D). Scale bar = 1mm.

Fig. 4. Accessory structure lateral to the terminal and subterminal phalanx of hands in *Ambystoma mexicanum* (FMNH22888) (A), and surrounding the skull of *Ichthyophis bannanicus* (MVZ236728) image credit: Digimorph.org (B).

Fig. 5. Salamander phylogeny used in the optimization analysis of mandibular sesamoid character follows relationships proposed by Bonnet & Blair (2017) and Pyron & Wiens (2011) for species not included in the most recent phylogeny. Mapping of sesamoid of the mandibular symphysis is indicated in green; mapping of mandibular sesamoid, located between the quadrate and prearticular bone is indicated in red; mapping of sesamoid between the skull and the lower jaw, located at the posterior end of the maxilla is indicated in blue.

Fig. 6. Examples of joints in salamanders and frogs showing the difference in the complexity of the joint surfaces. (A) Manus of the facultative paedomorphic species *Pleurodeles waltl* (FML30803) (B) Manus of the paedomorphic species *Siren intermedia* (FMNH84082) (C) Manus of the anuran species *Leptodactylus latinasus* (FML S/N), showing the glide sesamoids in the inter-phalangeal joints. (D) Hindlimb of *Pleurodeles waltl* (FML30803), the simple articular surfaces of the knee and ankle joints are evident. (E) Ankle and (F) Knee joints of *Leptodactylus bufonius* (FML S/N) where the related sesamoids are visible. Scale bar = 1mm.

Fig. 7. The three discussed hypotheses of interrelationships of the three modern amphibian groups and their relationships to possible Paleozoic records. (A) Polyphyly hypothesis simplified from Ruta & Coates (2007); (B) temnospondyl hypothesis (Trueb & Clouthier, 1991; Milner, 1993; Ruta *et al*., 2003); (C) lepospondyl hypothesis (Laurin & Reisz, 1997; Laurin, 1998; Vallin & Laurin, 2004). Red bars indicate the presence of postcranial sesamoids (PS) as has been known until present.

Figure 1

Cranial sesamoids in salamanders

Sesamoid in the mandibular symphysis of *Necturus beyeri* (UF177187), view of stl surface model of a cranial CT scan from MorphoSource, dataset https://doi.org/10.17602/M2/M39589 (A). Skulls of: *Hydromantes platycephalus* (uncatalogued), image credit: Digimorph.org (B), and *Karsenia koreana* (DRV5033) with a sesamoid between the posterior end of the maxilla and the lower jaw joint, image credit: Digimorph.org (C); *Peradactylodon persicus* (MVZ241494) with a sesamoid in the quadrate-prearticular joint, image credit: Digimorph.org. (D). The largest arrows show the sesamoids. dent=dentary, max=maxilla, preart=preartricular, sq=squamosal.
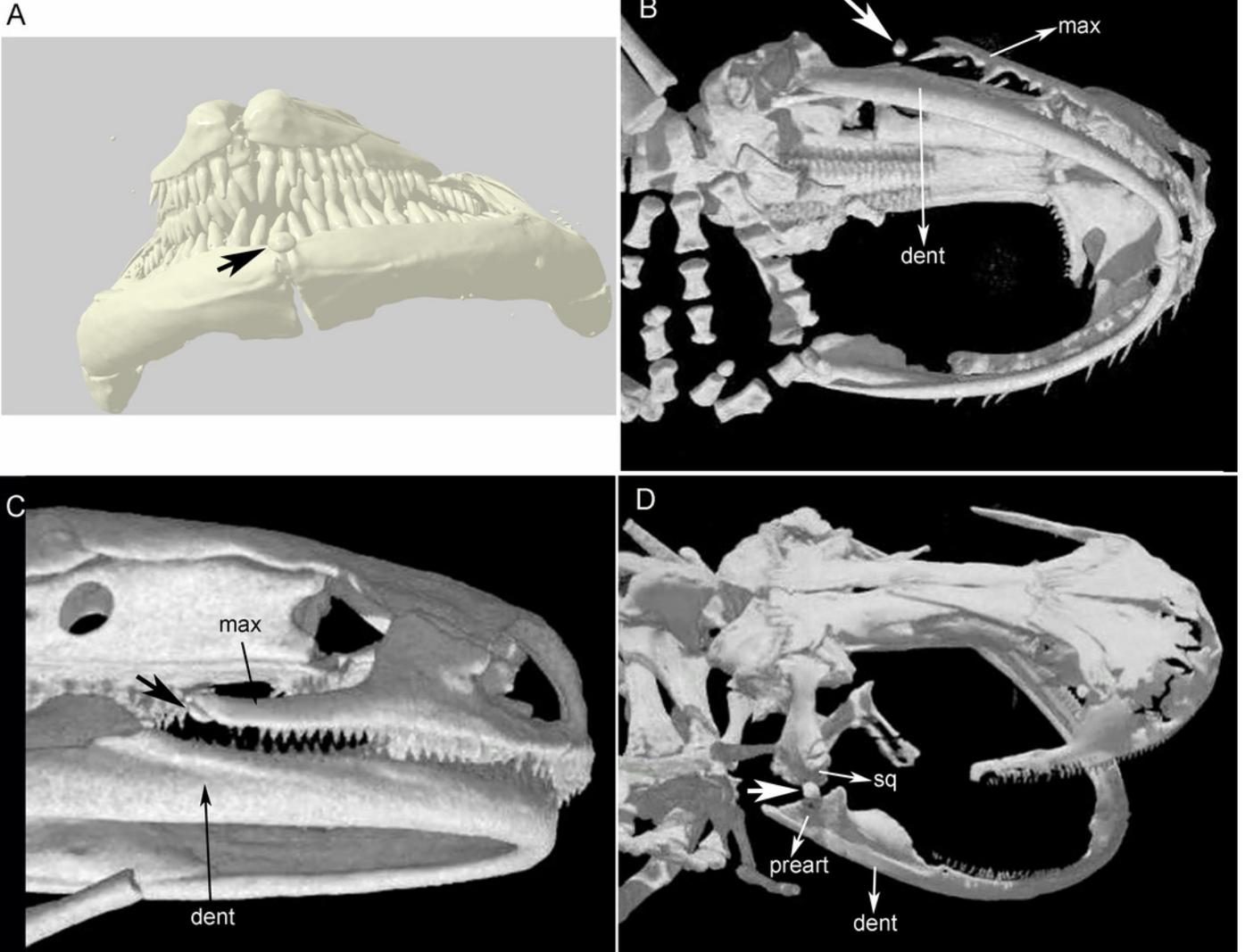
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A

parietal

otic capsule

frontal

orbitosphenoid

squamosal

sesamoid

articular

ceratohyal

prearticular

dentary

B

squamosal

quadrate

articular

sesamoid

ceratohyal

prearticular

C

squamosal

quadrate

sesamoid

articular

prearticular

dentary

D

sesamoid

E

sesamoid

F
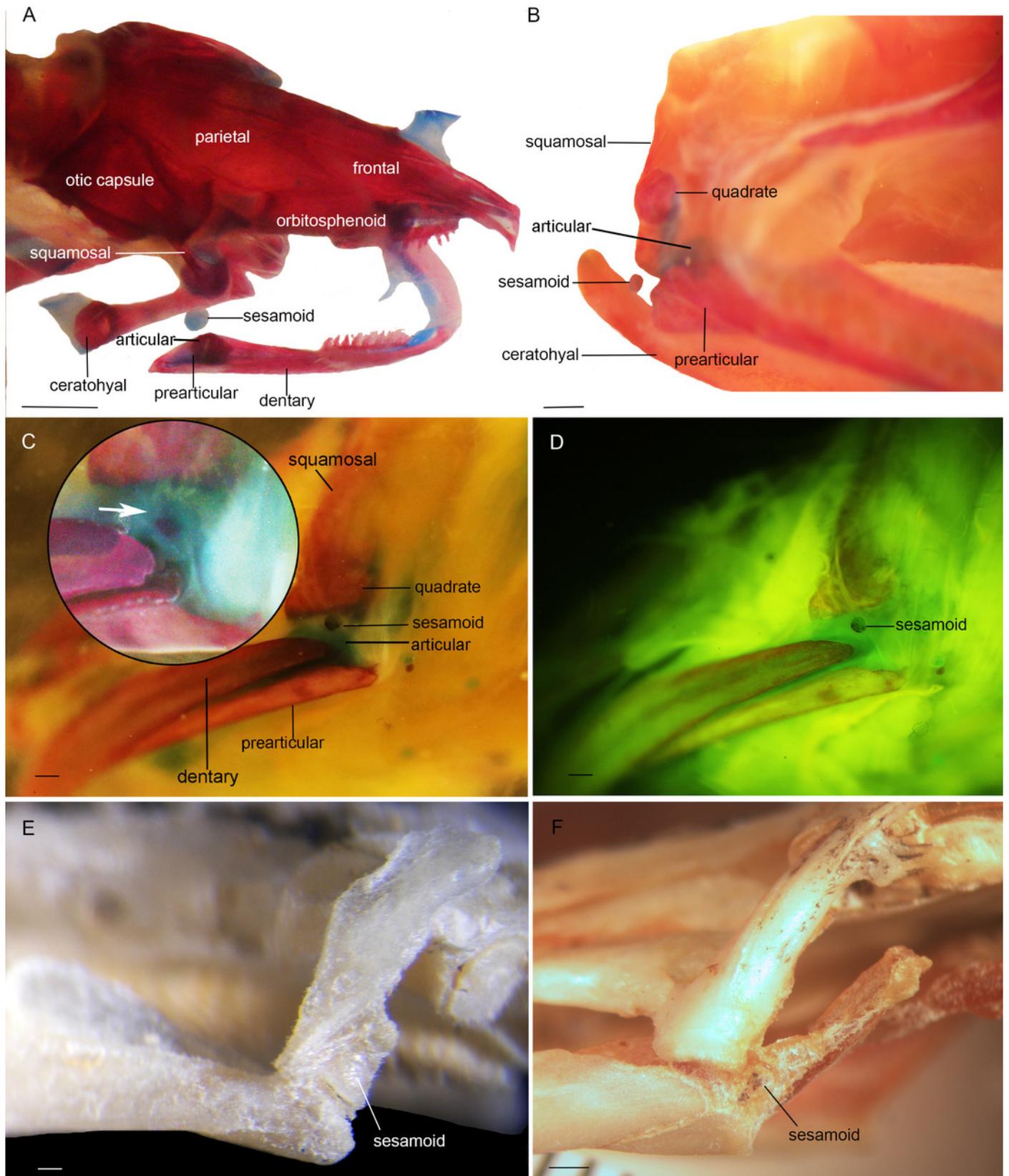
sesamoid

Figure 3

Mandibular sesamoid in the quadrate-prearticular joint of the skull of *Notophthalmus viridiscens* (FMNH93537) (A), *Notophthalmus meridionalis* (FMNH93536) under white (B) and fluorescent light (photo credit: Jennifer Y. Lamb) (C, D). Scale bar =

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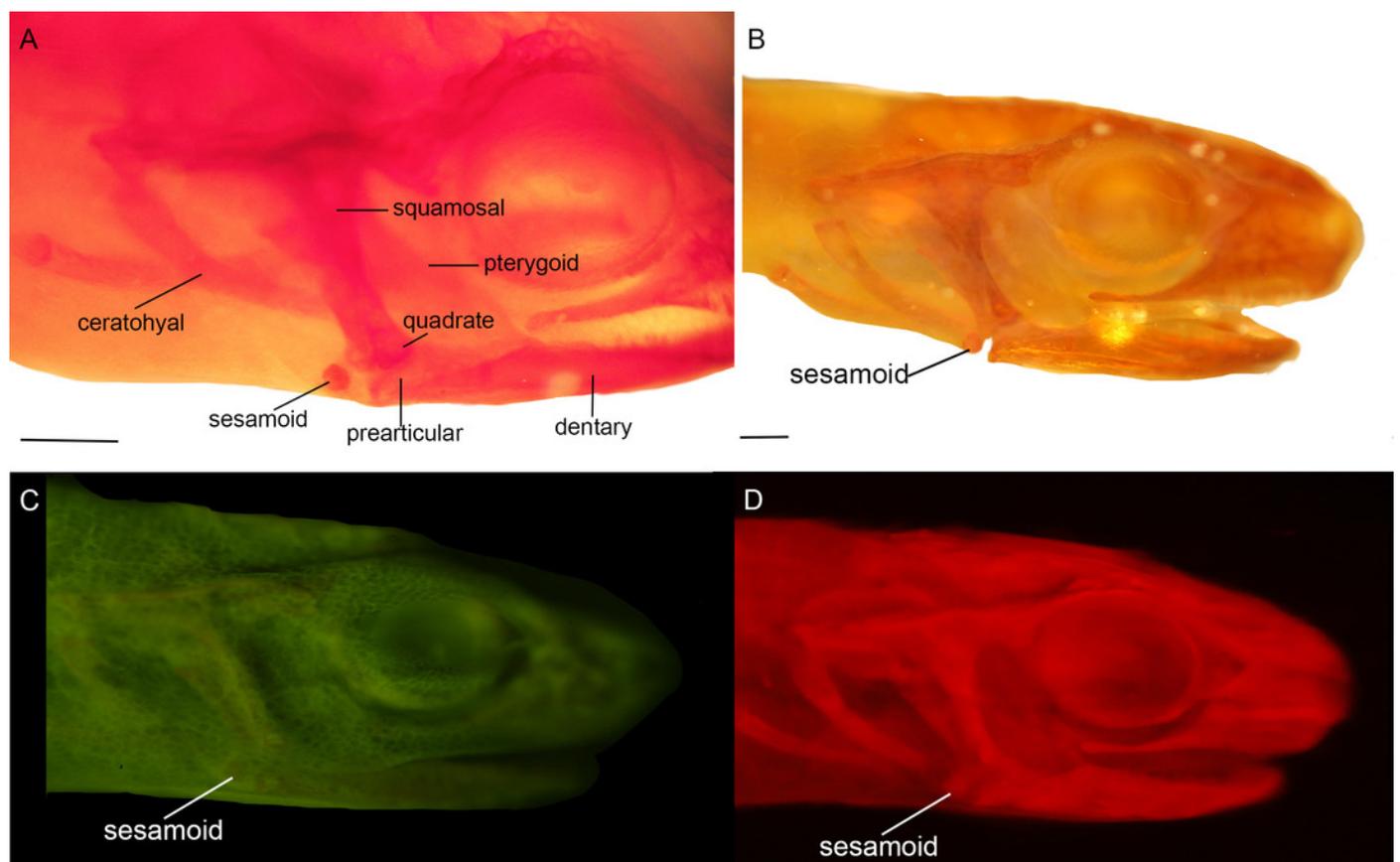
Figure 4

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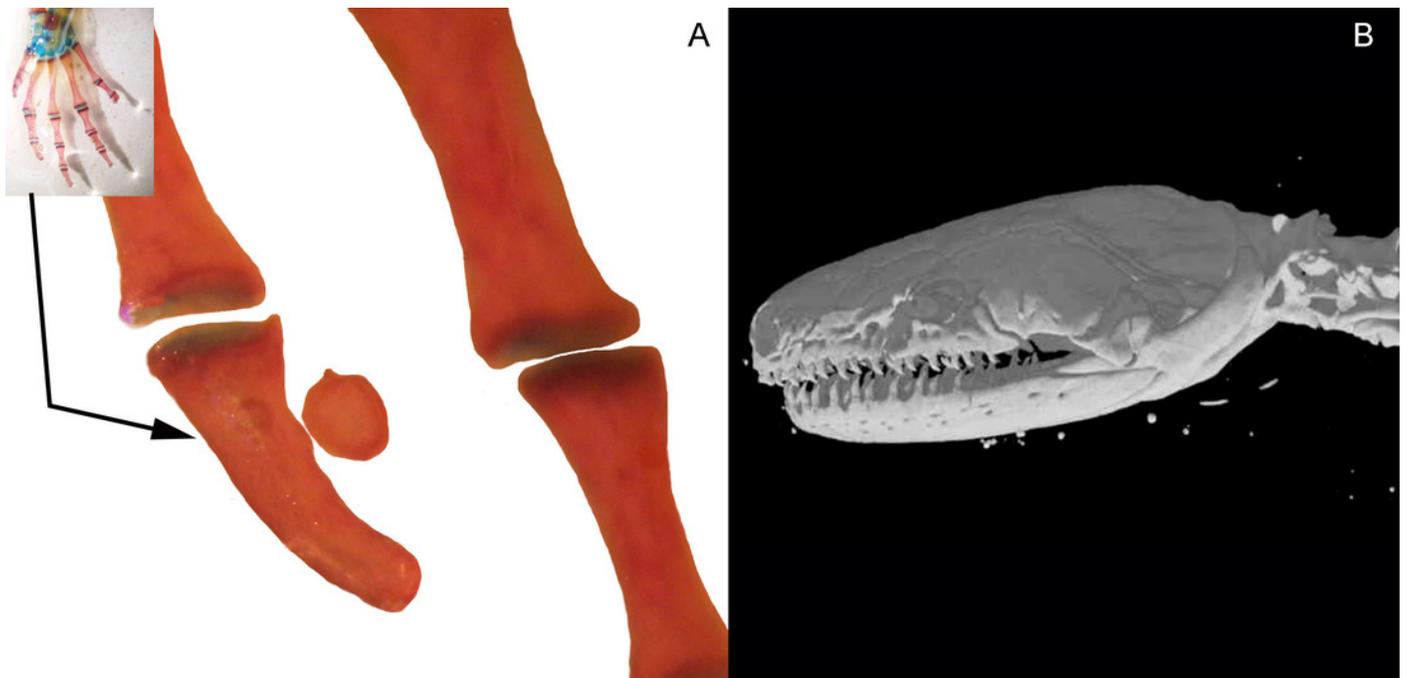
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Cryptobranchus alleganiensis
Andrias davidianus
Andrias japonicus
Onychodactylus japonicus
Onychodactylus fischeri
Salamandrella keyserlingii
Paradactylodon persicus
Ranodon sibiricus
Hynobius naevius
Hynobius leechi
Hynobius nebulosus
Batrachuperus londongensis
Batrachuperus pinchonii
Pseudohynobius flavimaculatus
Liua shihi
Liua tsinpaensis
Siren intermedia
Siren lacertina
Pseudobranchus axanthus
Pseudobranchus striatus
Dicamptodon tenebrosus
Dicamptodon ensatus
Ambystoma talpoideum
Ambystoma gracile
Ambystoma maculatum
Ambystoma macrodactylum
Ambystoma opacum
Ambystoma jeffersonianum
Ambystoma laterale
Ambystoma tigrinum
Ambystoma mexicanum
Ambystoma dumerilii
Ambystoma ordinarium
Ambystoma annulatum
Ambystoma texanum

Cryptobranchidae

Hynobiidae

Sirenidae

Ambystomatidae

Lyciasalamandra atifi
Salamandrina perspicillata
Salamandrina terdigitata
Salamandra algira
Salamandra salamandra
Salamandra infraimmaculata
Salamandra lanzai
Salamandra atra
Salamandra corsica
Echinotriton andersoni
Pleurodeles waltl
Pleurodeles poireti
Taricha torosa
Taricha granulosa
Taricha rivularis
Notophthalmus meridionalis
Notophthalmus perstriatus
Notophthalmus viridescens
Euproctus montanus
Euproctus platycephalus
Ichthyosaura alpestris
Cynops ensicauda
Cynops orientalis
Cynops pyrrhogaster
Paramesotriton deloustali
Paramesotriton chinensis
Paramesotriton hongkongensis
Paramesotriton maolanensis
Pachytriton inexpectatus
Pachytriton archospotus
Pachytriton breviceps
Pachytriton labiatus
Lissotriton helveticus
Lissotriton montadoni
Lissotriton vulgaris
Calotriton asper
Triturus dobrogicus
Triturus cristatus
Triturus carnifex
Triturus karelinii
Ommatotriton oephryticus
Ommatotriton vittatus
Neurergus microspilotus
Neurergus crocatus
Neurergus kaiseri

Salamandridae

Proteus anguinis
Necturus lewisi
Necturus beyeri
Necturus maculosus
Rhyacotriton kezeri
Rhyacotriton olympicus
Rhyacotriton variegatus
Amphiuma tridactylum
Amphiuma means
Amphiuma pholeter

Proteidae

Rhyacotritonidae

Amphiumidae

Plethodon elongatus
Plethodon vandykei
Plethodon serratus
Plethodon hubrichti
Plethodon cinereus
Plethodon dorsalis
Plethodon wehrlei
Plethodon yonahlossee
Plethodon cheoah
Plethodon fourchensis
Plethodon ouachitae
Plethodon jordani
Plethodon albagula
Plethodon glutinosus
Hydromantes platycephalus
Karsenia koreana
Ensatina eschscholtzi
Aneides flavipunctatus
Aneides lugubris
Aneides aeneus
Aneides ferreus
Aneides hardii
Desmognathus auriculatus
Desmognathus marmoratus
Desmognathus monticola
Desmognathus ocoee
Desmognathus quadramaculatus
Desmognathus wrighti
Desmognathus ochrophaeus
Desmognathus aeneus
Desmognathus apachicolae
Gyrinophilus porphyriticus
Stereochilus marginatus
Pseudotriton ruber
Pseudotriton montanus
Eurycea spelaea
Eurycea rathbuni
Eurycea waterlooensis
Eurycea neotenes
Eurycea sosorum
Eurycea lucifuga
Eurycea guttolineata
Eurycea longicauda
Eurycea bislineata
Eurycea cirrigera
Eurycea wilderae
Hemidactylium scutatum
Batrachoseps attenuatus
Nyctanolis pernix
Bradytriton silus
Oedipina complex
Cryptotriton adelos
Dendrotriton bromeliaceus
Thorius dubius
Thorius longicaudus
Thorius pinicola
Thorius flaxiacus
Thorius pulmonaris
Thorius aureus
Thorius minutissimus
Thorius narisovalis
Chiropterotriton dimidiatus
Chiropterotriton lavae
Chiropterotriton magnipes
Chiropterotriton multidentatus
Chiropterotriton priscus
Aquiloeurycea cephalica
Parvimolge townsendi
Pseudoeurycea smithi
Pseudoeurycea robertsi
Pseudoeurycea gadovii
Pseudoeurycea unguidentis
Pseudoeurycea leprosa
Pseudoeurycea lineola
Bolitoglossa subpalmata
Bolitoglossa epimela
Bolitoglossa marmorea
Bolitoglossa colonnea
Bolitoglossa schizodactyla
Bolitoglossa adspersa
Bolitoglossa altamazonica
Bolitoglossa rostrata
Bolitoglossa franklini
Bolitoglossa porrasorum
Bolitoglossa alvaradoi
Bolitoglossa deficni
Bolitoglossa occidentalis
Bolitoglossa rufescens
Bolitoglossa flaviventris
Bolitoglossa platydactyla
Bolitoglossa mexicana
Bolitoglossa lignicolor
Bolitoglossa striatula

Plethodontidae

■ Absent
■ Present
■ Ambiguous

Figure 6

Examples of joints in salamanders and frogs showing the difference in the complexity of the joint surfaces.

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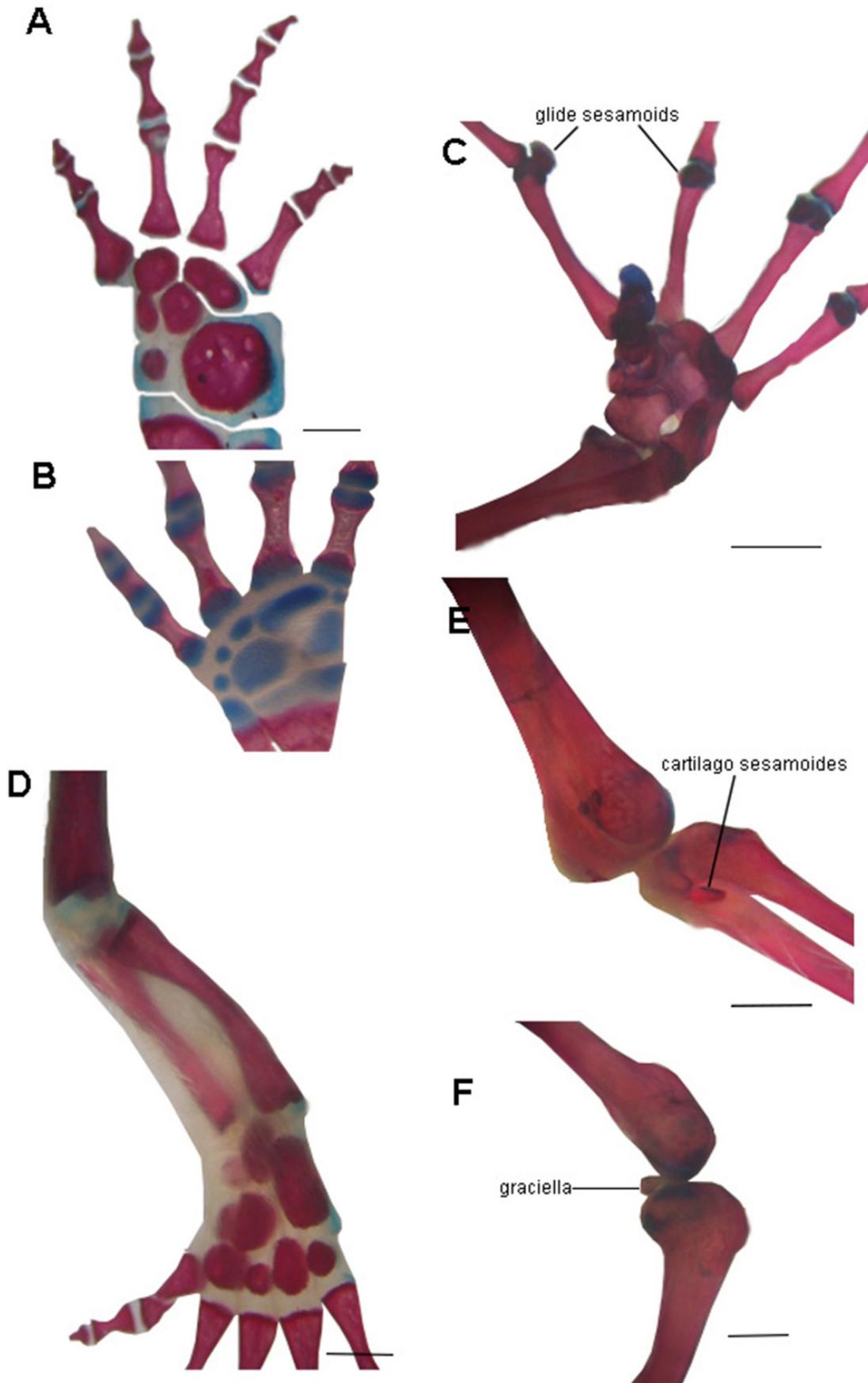
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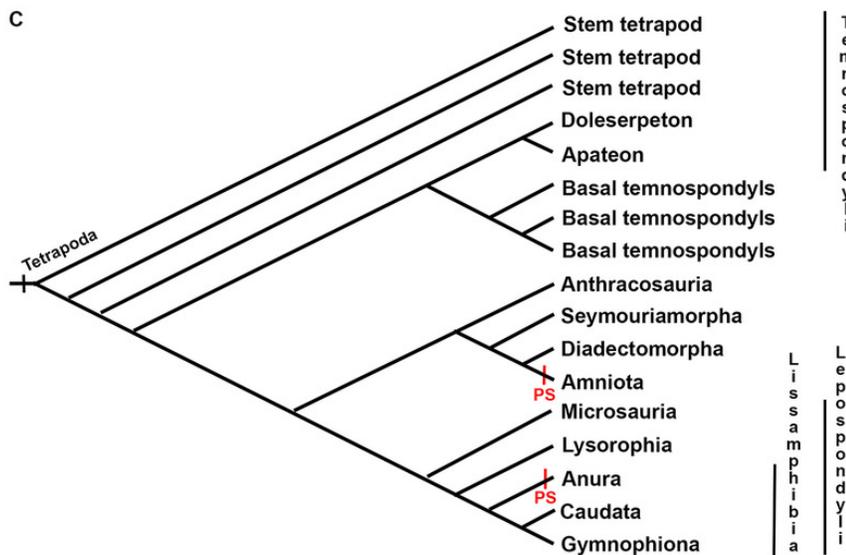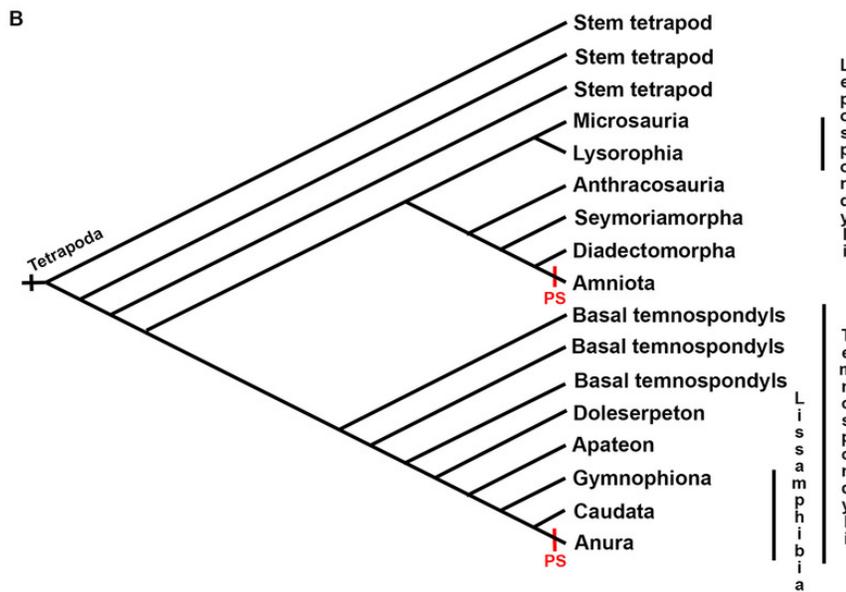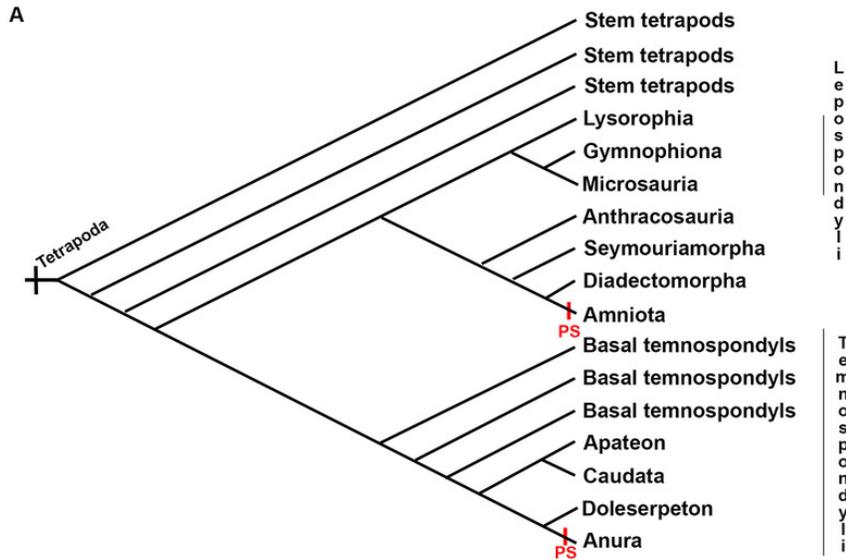
Table 1(on next page)

Comparison of probabilities of occurrence of bony or cartilaginous sesamoids considering the described extant species to date in Caudata and Gymnophiona. *Data were taken from Frost (2020)

1   Table 1: Comparison of probabilities of occurrence of bony or cartilaginous sesamoids considering the
2   described extant species to date in Caudata and Gymnophiona. *Data were taken from Frost (2020)

	Species described	Species reviewed		Species with sesamoids		Probability of occurrence	
		Skull	Poscranium	Skull	Poscranium	Skull	Poscranium
Caudata	757*	200	147	16	0	2%	0%
Gymnophiona	214*		42	0	0	0%	0%

3