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The oldest articulated raniid from Europe: a Pelophylax specimen from the lowest Oligocene of Chartres-de-Bretagne (N.W. France)

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3 1 ARTICLE

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5 2 The oldest articulated ranid from Europe: A *Pelophylax* specimen from the earliest Oligocene
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7 3 of Chartres-de -Bretagne (NW France)

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58 25 RH: LEMIERRE ET AL.—OLIGOCENE *PELOPHYLAX* FROM France
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3 27 ABSTRACT—Ranids represent an important part of the extant anuran diversity of Europe.
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5 28 One of the best-known genera is *Pelophylax* (green-water frog). This genus is considered to
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7 29 have arrived in Europe during the Eocene/Oligocene transition, with numerous occurrences of
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9 30 the genus throughout European Oligocene sites. Unfortunately, most of the specimens are
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11 31 isolated bones, hampering our understanding of the diversity and evolution of the genus during
12
13 32 this time. We here present the description of an incomplete but articulated anuran skeleton
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15 33 from the earliest Oligocene of Chartres-de-Bretagne (Western France). This specimen, missing
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17 34 its head, preserves almost all postcranial bones articulated and skin impressions. The
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19 35 osteological description allows to assign this specimen to *Pelophylax* kl. *esculentus*, making it
20
21 36 one of the oldest known occurrences of the genus. We also suggest that specimens assigned to
22
23 37 the late Oligocene “*Rana*” *aquensis* should be referred to the genus *Pelophylax*. The presence
24
25 38 of a *Pelophylax* in Western Europe during the early Oligocene indicates that the genus had
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27 39 already spread throughout Europe, no later than 5 Ma after its emergence in the eastern part of
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29 40 the continent. It suggests that *Pelophylax* benefitted from the extinction of ranoids during the
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31 41 “Grande Coupure.”
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43 SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at
44 www.tandfonline.com/UJVP
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INTRODUCTION

Anurans have been recovered from numerous Cenozoic sites in Europe, documenting a rich and diverse history of the clade during this period. In peculiar, the Quercy Phosphorites (mostly Eocene/Oligocene deposits; Péliissié et al., 2021) have yielded hundreds of anurans bones, representing most extant anuran clades present in Europe (Rage, 2016). The Phosphorites also document the turnover within neobatrachians anurans during the “Grande Coupure,” with the establishment of “true” ranid taxa during the Oligocene (Rage, 2016; Vasilyan, 2018). Among them, the genus *Pelophylax* (green-water frogs) is thought to have appeared and diversified during the early-middle Oligocene (Chan & Brown, 2017). Unfortunately, the genus is represented only by isolated bones from a single site during the early Oligocene (Sanchíz et al., 1993). Two taxa from the late Oligocene/Early Miocene, “*Rana*” *aquensis* Coquand, 1845 (southern France) and “*Rana*” *meriani* Meyer, 1852 (southern Germany), known by several complete specimens, have been informally assigned to the genus, but several uncertainties remain regarding their attribution (Sanchíz, 1998). Thus, the evolution of the geographical range of *Pelophylax* is almost unknown during a crucial phase of its spread across Western Europe, as the genus is present in most of Western Europe during the Miocene (Roček, 2013). Discovery and identification of specimens of *Pelophylax* from this region would help our understanding of the dispersal and evolutionary history of the genus during the Oligocene.

Our study is focused on the description and identification of a specimen from this geographical area (Fig. 1A, B). The specimen was discovered on July 7, 1922, by the geologist Yves Milon in the Grands-Fours quarry near the city of Rennes (Brittany, western France, Fig. 1C, D). Two days later, the specimen was presented at a session of the Société Géologique et Minéralogique de Bretagne (Dangeard & Milon, 1922). Unfortunately, Milon never described the specimen, and it was considered lost for several decades. One of us (D. Gendry) recently

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3 75 rediscovered this specimen, along with Milon's identification (an anuran) in the collection of
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5 76 the geological museum of the University of Rennes 1. We took this opportunity to describe the
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7 77 osteology of the fossil and propose a taxonomic attribution. We also discuss its implication for
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9 78 the Oligocene occurrence of ranid taxa in Europe.
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14 80 GEOLOGICAL CONTEXT

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19 82 Chartres-de-Bretagne is an ancient complex of quarries located 5 km south of the city
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21 83 of Rennes, within the Cenozoic Basin of Rennes (Fig. 1A). The quarry produced limestone,
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23 84 with numerous open pits present (Vasseur, 1881; Trautmann et al., 2000; Lebrun et al., 2017).
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25 85 The sites are unfortunately backfilled today, and no further investigations are possible.
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27
28 86 The Oligocene beds of Chartres-de-Bretagne are thick (380 m thick) and have been well-
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30 87 known since the end of the nineteenth century (Vasseur, 1881; Lebesconte, 1879; Allix, 1922;
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32 88 Dangeard & Milon, 1926; Lebrun et al., 2017). The Lower Sapropels Formation is the most
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34 89 basal formation. It forms the majority of the Oligocene deposits (around 280 m) and represents
35
36 90 a major regression during the early Rupelian. This bed is overlain by the *Natica crassatina*
37
38 91 marls and "*Archiacina*" limestone formations (52 m thick). These two formations were
39
40 92 deposited during a transgressive event that lasted throughout the early Rupelian (Fig. 1B). The
41
42 93 uppermost Oligocene formation within the region is the Upper Sapropels Formation (Rupelian;
43
44 94 around 6.5 m thick). Within this formation, the foraminiferans *Arenagula kerfornei* and
45
46 95 *Archiacina armorica* (*Peneroplis armorica* in Bauer et al., 2016) have been recovered (Bauer
47
48 96 et al., 2016; Lebrun et al., 2017). In a previous study (Bauer et al., 2016), the foraminiferan
49
50 97 *Archiacina globula* was also mentioned. However, it is a subjective junior synonym of
51
52 98 *Arenagula kerfornei* (World Register of Marine Species: <https://www.marinespecies.org>). Both
53
54 99 *Arenagula kerfornei* and *Archiacina armorica* are early Rupelian markers for the SBZ 21
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56 100 biozone (Cahuzac & Poignant, 1997; Bauer et al., 2016). Notably, they are not present in the

1
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3 101 following SBZ 22 biozone (*Arenagula* is only present in the SBZ 22A of the Aquitaine Basin;
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5 102 Cahuzac & Poignant, 1997), to which a recent study (Bauer et al., 2016) attributed the Upper
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7 103 Sapropels Formation (at least part of it). Thus, we do not agree with this attribution, and
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9 104 consider the entire Upper Sapropels Formation early Rupelian in age (SBZ 21 biozone; MP21-
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11 105 22; Speijer et al., 2020).

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14 106 Within the formation, its lower part is composed of greenish interbedded claystones,
15
16 107 marlstones, and limestones. The flora is rich and made up of hydrophilous taxa while the fauna
17
18 108 is composed of lacustrine taxa (fishes and mollusks; Depape, 1926; Gaudant, 1989; Kerforne,
19
20 109 1915; Milon & Dangeard, 1920; Milon, 1930, 1935, 1936; Bauer et al., 2016; Lebrun et al.,
21
22 110 2017). A small fragment of a crocodylian osteoderm was also collected. All these
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24 111 sedimentological and paleontological elements are consistent with a restricted and quiet
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26 112 lacustrine environment. The blackish color of the Upper Sapropels Formation is also an
27
28 113 indication that the depositional environments was rich in humic materials, and the lake bottom
29
30 114 was likely anoxic (Milon, 1930, 1935; Fig. 1C). Roots, rhizomes, and leaves are exceptionally
31
32 115 well-preserved (Lebrun et al., 2017: pl. B, C). In addition, all known vertebrate specimens
33
34 116 (except the osteoderm) are preserved as articulated skeletons with soft tissues (skin
35
36 117 impressions) preserved (Lebrun et al., 2017: pl. B, C). Therefore, these laminated deposits
37
38 118 likely represent a Konservat-Lagerstätte owing to the exquisite preservation of the fossils. The
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40 119 single anuran specimen was discovered within the Grand-Fours quarry (La Chaussairie) from
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42 120 the Upper Sapropels Formation (around 30 cm below the top of the bed).
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51 122 MATERIALS AND METHODS

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55 124 **Institutional Abbreviations**—**IGR**, Institut de Géologie de Rennes; **MNHN**, Muséum
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57 125 National d'Histoire Naturelle (Paris, France). The specimen is stored within the collection of
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126 the geological museum of the University of Rennes under the following number: IGR 144547.

127 Both main slab (M1) and counterpart slab (M2) are catalogued under the same number.

128 **Reflectance Transformation Imaging (RTI)**—Most bones are crushed or preserved as
 129 partial imprint and thus difficult to identify. RTI is a method that computes an “interactive
 130 specimen” in which illumination can be oriented at will (Hammer et al., 2002). This method
 131 was used with a custom-made portable light dome (same as used in Cui et al., 2022). Sets of 54
 132 photographs under different LED sources were compiled using the RTIBuilder software. The
 133 results RTI files (see supplemental data: 10.5281/zenodo.7223828) can be opened using the
 134 RTIViewer software. Both RTIBuilder and RTIViewer are freely available at
 135 www.culturalheritageimaging.org. This study is one of the few using RTI to study fossil
 136 vertebrate specimens.

137 **Anatomical Comparison**—Comparisons were made with the neotype of “*Rana*”
 138 *aquensis* (Piveteau, 1927), MNHN.F.AIX355 (“*Rana*” *aquensis*). Comparisons were also made
 139 with an unnumbered specimen of *Pelophylax* kl. *esculentus* from the MNHN.

140 **Anatomical Nomenclature**—The anatomical nomenclature used is that by Sanchíz
 141 (1998) for postcranial features, Roček et al (2022) for carpals, and Gómez and Turazzini
 142 (2016) for iliac features.

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144 SYSTEMATIC PALEONTOLOGY

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146 ANURA Duméril, 1805

147 NEOBATRACHIA Reig, 1958

148 RANOIDEA Rafinesque, 1814

149 RANIDAE Batsch, 1796

150 *PELOPHYLAX* Fitzinger, 1843

151 *PELOPHYLAX* KL. *ESCULENTUS* (Linnaeus, 1758)

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153 Position of the Specimen on the Slabs

154 The preserved portion of the specimen is 56 mm long (anterior end of ?omosternum to
155 distal end of femora) on a 101x107 mm slab (M1) with its 69x63 mm partial counterpart (M2).
156 The slab (M1) preserves a majority of the fossil, from base of the cranium to the femora (Fig.
157 2A, B). The partial counterpart (M2) preserves only the posterior region of the body and the
158 hands (Fig. 2C, D). A majority of the bones are surrounded by a thin black veil interpreted as a
159 skin impression, (see below; Fig. 2A, C). The bones of the specimen are preserved as (1)
160 slightly crushed bony elements, (2) crushed and fragmentary bony elements; (3) imprint of the
161 bone and (4) a mix of crushed bony element and imprint on both plates. As M1 is the main
162 plate, the position and lateralization of the anuran skeleton are based on this slab. The imprint
163 left by the humerus on the right side of M1 (see Fig. 2) preserves some detail distally (Fig. 2).
164 Compared to the humeral imprint made from an extant *Pelophylax* (see Fig. S1), the fossa
165 cubitalis and eminentia capitata are preserved as an imprint. Thus, we interpret the humeral
166 imprint on IGR 144547 as visible in ventral view on M1. Hence, when the bone is preserved on
167 M1, it is visible in dorsal view. Thus, IGR 144547 present an anuran specimen in dorsal view
168 on M1, and in ventral view on M2. When only the imprint of the bone is preserved, it is visible
169 in ventral view (on M1, opposite for M2). Hence, on M1, the left side of the specimen is
170 visible on the left region of the plate, while it is preserved on the right region of the plate on
171 M2.

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173 Soft Tissues

174 The soft tissues surround most of the bones, except for the skull and part of the
175 tibiofibula on both M1 and M2 (Fig. 2A, C). Although it is not well defined in most region, the
176 preservation around the hands, femora, and cloacal region allows interpretation of this feature

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3 177 as skin impressions. The body shape is hard to define on the torso, although it seems to widen
4
5 178 at midlength (Fig. 2A). The body outline then narrows towards the cloacal region.

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7 179 The skin around the shoulder and forelimb is poorly preserved. Skin around the hands is
8
9 180 well preserved on both M1 and M2 (Fig. 2A, C). The left hand preserves the shape of the flesh
10
11 181 around the digits, and the skin narrows towards the last phalanx of the digits. Around the
12
13 182 femora, the skin is wider near its proximal margin, and progressively narrows distally until the
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15 183 end of both femora. On M2, small patches of skin imprints seem preserved around the left
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17 184 tibiofibula (Fig. 2C, D).
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23 186 **Osteological Description**

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26 187 IGR 144547 is an anuran skeleton missing its skull, its anterior vertebrae, most of the
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28 188 left elements of its pectoral girdle and most of its hindlimbs (Fig. 3). The skeleton is mostly
29
30 189 articulated, but poorly preserved, in particular in the main body region (Figs. 2, 3).
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35 191 **Vertebral Column**

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37 192 **General Comments**—All vertebrae are badly preserved. Most of them are hollowed
38
39 193 out, with only faint traces of centra and transverse processes preserved. Where bone is still
40
41 194 present, the vertebrae are exposed in dorsal view, but the neural region has been crushed or
42
43 195 eroded on all vertebrae, leaving the centrum exposed (Fig. 4). Presacral and sacral vertebrae
44
45 196 are only preserved on M1. A single sacral vertebra is identified, while five presacral vertebrae
46
47 197 are preserved. The atlas, second and third vertebrae are not preserved, due to a missing piece
48
49 198 on M1 (Fig. 2A). IGR 144547 likely possessed eight presacral vertebrae.
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53 199 **Vertebra IV**—The centrum and transverse processes of the fourth vertebra are
54
55 200 preserved as crushed bone in dorsal view. The centrum is broken anteriorly. It connects
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57 201 posteriorly with the fifth vertebra and on its right lateral side with the sternum (Fig. 4A, B).
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3 202 The base of the left transverse process shows that the processes extend slightly posteriorly.
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5 203 They seem to expand distally (Fig. 4B).

7 204 **Vertebra V**—The centrum of the fifth vertebra is preserved as crushed bone in dorsal
8
9 205 view. It bears an anterior cotyle and a posterior condyle. It connects anteriorly to the fourth
10
11 206 vertebra and posteriorly to the sixth vertebra. A broken transverse process might be preserved
12
13 207 on the left lateral side of the centrum (Fig. 4B). It seems posteriorly oriented, like the
14
15 208 transverse processes of the seventh vertebra (see below), but it is broken from the centrum and
16
17 209 we cannot assess if it is its in-situ orientation.

21 210 **Vertebra VI**—Only the procoelous centrum of the sixth vertebra is preserved as
22
23 211 crushed bone in dorsal view. It connects anteriorly to the fifth vertebra and posteriorly to the
24
25 212 seventh vertebra. No transverse processes are preserved.

28 213 **Vertebra VII**— This vertebra has the longest preserved centrum (2.2 mm). It bears
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30 214 anterior cotyle and a posterior condyle and is connected anteriorly to the sixth vertebra and
31
32 215 posteriorly to the eighth vertebra. The transverse processes are partially preserved. They are
33
34 216 crushed and are separated from the centrum. They are rather long and seem slightly posteriorly
35
36 217 oriented. However, the base of the left transverse process appears to be preserved (Fig. 4A, B)
37
38 218 and is laterally oriented.

42 219 **Vertebra VIII**—The last presacral is preserved throughout its centrum. Its centrum is
43
44 220 short (1.4 mm). It bears an anterior and a posterior cotyle. An amphicoelous posterior presacral
45
46 221 vertebra, with the remaining presacrals procoelous is diagnostic for a diplasiocoelous vertebral
47
48 222 column. A small remnant of the left transverse process is preserved on M1 (Fig. 4A, B). It
49
50 223 shows that the processes were straight and extended laterally.

53 224 **Sacral vertebra**—The sacral vertebra is only preserved on M1. Its centrum is
54
55 225 preserved as a hollow structure exposed dorsally (Fig. 4A, B). Nevertheless, its shows that an
56
57 226 anterior condyle and two posterior condyles are present. The centrum is short (2mm) and wider
58
59 227 than longer (2.6 mm width). The centrum seems to widen posteriorly (Fig. 4B). Both sacral

228 transverse processes are preserved on M1 as imprints (in ventral view) with bone fragments.

229 The right sacral transverse process is incomplete. The processes are oriented posterolaterally.

230 They barely extend distally and instead are slender rod-like structures. Thus, we interpret that

231 IGR 144547 as possessing a “Type IIA” sacrum (Emerson, 1979; Reilly & Jorgensen, 2011).

232 The sacral vertebra possesses a small diapophyseal expansion. Both sacral processes connect

233 distally with the ilium.

234 **Urostyle**—The urostyle is preserved on both M1 and M2. The proximal portion of the
235 urostyle is preserved on M1 as crushed bone exposed in dorsal view on M1 and in ventral view
236 on M2. The urostyle shaft is covered by sediment for most of its length on M1. On M2, the
237 shaft is preserved as crushed bone (Fig. 2C). The urostyle is long (17 mm). It connects
238 anteriorly to the sacral vertebra. Although poorly preserved, it is clear that two cotyles were
239 present on its anterior surface. Most of the urostyle shaft is hollowed. The urostyle narrows
240 progressively distally (Fig. 4C, D). Its distal end is crushed and covered by sediment on both
241 M1 and M2. The urostyle seems to end slightly anterior to the acetabular region of both ilia
242 (Fig. 2B, D). On M2, the anterior region of the urostyle is preserved as an imprint exposed
243 dorsally, with a thin lamina of bone present medially (Fig. 4C). It suggests that a dorsal crest is
244 present on the urostyle of IGR 144547 and extended for at least half of its length. However, we
245 cannot assess the height of the dorsal crest, nor its total extension on the length of the urostyle.

246

247 **Pectoral Girdle**

248 **Scapulae**—The right scapula is preserved on M1 as an imprint with crushed bone. The
249 left scapula is not preserved on M1. Scapulae are not preserved on M2. The scapula is elongate
250 (7.81 mm length), with a shaft extended laterally (Fig. 5A, B). The shaft scapula expands
251 distally, reaching its widest point at the suprascapular margin (Fig. 5B; 4.42 mm width). The
252 latter is straight. The anterior and posterior margins are concave. Both margins lack laminae.
253 The pars acromialis is mostly preserved as an imprint exposed in ventral view (Fig. 5A, B),

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2
3 254 expect near the glenoid fossa. The pars acromialis is wide (3.3 mm), and part of this processus
4
5 255 is preserved as bone exposed in dorsal view in the glenoid region (see Fig. 5B). The glenoid
6
7 256 region is poorly preserved, with undefined crushed bony elements visible (Fig. 5B). As the
8
9 257 specimen is exposed dorsally, it suggests that most of the bony elements form the base of the
10
11 258 pars glenoidalis, distinct from the crushed pars acromialis (Fig. 5B). Thus, it is not possible to
12
13 259 assess the size of the pars glenoidalis and if the latter and the pars acromialis were separated by
14
15 260 a sinus glenoidalis.

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19 261 **Clavicles**—Clavicles are only preserved on M1. The clavicle articulates with the
20
21 262 scapula and humerus (forming a part of the glenoid fossa). The right clavicle is partially
22
23 263 preserved as an imprint (exposed in ventral view; Fig. 5A), while the left clavicle is not
24
25 264 preserved. The extremitas medialis is not preserved. Thus, it is not possible to assess if the
26
27 265 latter articulated with the medial margin of the coracoid. The clavicle is slender and moderately
28
29 266 developed (5.89 mm preserved). Its shaft slightly arched. The glenoid region is partially
30
31 267 obscured by fragments of unidentified bone (Fig. 5A, B).

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33
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35 268 **Coracoids**—Both coracoids are preserved on M1 as imprints exposed in ventral view
36
37 269 (Fig. 2A). The right coracoid is almost complete. It forms part of the glenoid fossa laterally,
38
39 270 thus articulating with the clavicle and humerus. It also articulates medially with the left
40
41 271 coracoid. The coracoid is shorter (6.64 mm) than the scapula. The processus glenoidalis widens
42
43 272 laterally. It bears two distinct articular facets on its proximal surface. The anterior facet
44
45 273 articulates with the clavicle and the posterior facet received the humerus. The shaft is elongated
46
47 274 transversely and narrow. The processus epicoracoidalis is anteroposteriorly elongated. It is the
48
49 275 widest region of the coracoid (5.3 mm). The processus is flat and bears a convex medial margin
50
51 276 (Fig. 5B). It slightly extends anteriorly, but does not seem to form an anterior hook (as seen in
52
53 277 *Thaumastosaurus*; Laloy et al., 2013; Lemierre et al., 2021).

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3 278 Both coracoids were likely in contact medially when accounting for the connecting
4
5 279 cartilage of the coracoids (Ecker, 1889). This is characteristic of the firmsternal condition for
6
7 280 the pectoral girdle (sensu Cope, 1864; Boulenger, 1886).

9
10 281 **Sternum**—The sternum is preserved as a crushed bone (exposed in dorsal view) within
11
12 282 the space left by the vertebral column on M1 (Fig. 5B). The reconstruction shows that the bone
13
14 283 is fully ossified (Fig. 5C). The bone is elongated anteroposteriorly (4.5 mm) and hourglass-
15
16 284 shaped. Both anterior and posterior regions are wider than the shaft and the anterior region is
17
18 285 wider than the posterior.

20
21 286 **Omosternum?**—A small, poorly preserved element is preserved anterior to the
22
23 287 preserved medial region of the right clavicle on M1. It is very small (2.24 mm length) and
24
25 288 crescentic (Fig. 5A, B). It likely represents around half of a bony element. A putative
26
27 289 reconstruction indicates the element had an inverted Y-shape (Fig. 5C). The posterior end
28
29 290 seems connected to the extremitas medialis of the clavicle. The remaining part of the bone is a
30
31 291 slender stylet (Fig. 5B). The position and shape of this element is incompatible with a vertebral
32
33 292 element. Thus, we tentatively interpreted this element as an incomplete omosternum. As for the
34
35 293 non-overlapping coracoids, the presence of an ossified omosternum is diagnostic for a
36
37 294 firmsternal pectoral girdle (sensu Boulenger, 1886).

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43 44 296 **Pelvic Girdle**

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46 297 **Ilia**—Both ilia are preserved on M1 and M2. M1 preserves most of the distal region
47
48 298 and shaft of the ilia as flattened bones, exposed in medial view (Fig. 2A). Both distal ends are
49
50 299 in contact with the posterior region of the sacral apophyses. The acetabular region is only
51
52 300 preserved as an imprint exposed in lateral view of the left ilium on M1 (Fig. 2A). On M2, the
53
54 301 left ilium is preserved in its acetabular region with most of the bone intact and exposed in
55
56 302 lateral view (Fig. 2B, 6B). The right ilium has been broken in two. Its distal region on M1 is
57
58 303 crushed and separated into two halves (Fig. 2A). The shape of the displaced sediment suggests

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2
3 304 it could have been the result of damage during the splitting of M1 and M2 by the collector. The
4
5 305 acetabular region is displaced and covers part of the right femur and the dorsal acetabular
6
7 306 expansion of the right ilium on M2 (Fig. 2C). This part of the right ilium is preserved as a bone
8
9
10 307 exposed in medial view. The distal region of both ilia is preserved on M2 as imprints exposed
11
12 308 in medial view. The ilium is around 19.5 mm long. It is slightly longer than the urostyle. The
13
14 309 iliac shaft is slightly compressed laterally. The shaft bears a high dorsal crest (same height as
15
16 310 the iliac shaft) on its whole length (Fig. 2A), as seen on M1. The dorsal protuberance ('tuber
17
18 311 superior' in Bailon, 1999) is a large pyriform structure protruding laterally posterior to the
19
20
21 312 dorsal crest (Fig. 6B, C). The supracetabular fossa is well-developed (Fig. 6B, C). The dorsal
22
23 313 acetabular expansion is not fully preserved but seems short and oriented posteriorly (Fig. 6C).
24
25
26 314 The ventral acetabular expansion has a large ventral vector (Fig; 6B, C). Its preacetabular angle
27
28 315 is clearly acute (Fig. 6C). In medial view, there is no interiliac tubercle.
29
30
31 316

317 **Forelimbs**

318 **Humeri**—Both humeri are preserved only on M1. The proximal regions of both humeri
319 are preserved as both crushed bone and imprint, while the remaining of the diaphysis and distal
320 region is preserved only as an imprint exposed in ventral view. The right humerus is around 11
321 mm long. The proximal head of the right humerus is hard to identify, as the glenoid region is
322 poorly preserved (Figs. 5, 7D). The proximal region of the left humerus is preserved mostly as
323 crushed bone (exposed in dorsal view) but its outline is difficult to determine (Fig. 7A, B). No
324 crista ventralis is preserved. If present, the crista did not extend past the mid-diaphysis (region
325 preserved as a ventral imprint; Fig. 7C). The distal region of the right humerus is preserved as
326 an imprint exposed ventrally. The fossa cubitalis is shallow and slightly triangular shaped (Fig.
327 7C, D). The fossa does not extend on the diaphysis. The eminentia capitata (humeral ball in
328 Gómez & Turazzini, 2021) is wide and large (Fig. 7C, D). This structure is partially preserved
329 on the left humerus as eroded bone (thus visible in dorsal view; Fig. 7A) and on the right

1
2
3 330 humerus as an imprint (visible in ventral view; Fig. 7C). The eminentia capitata is not shifted
4
5 331 laterally from the central axis of the diaphysis. The epicondylus radialis (lateral epicondyle) is
6
7 332 partially preserved on the right humeral imprint (Fig. 7D). It is distinct from the eminentia
8
9 333 capitata but does not extend distally past the humeral ball (Fig. 7C, D). The epicondylus ulnaris
10
11 334 (medial epicondyle) is not preserved, hidden by the imprint of the radioulna (Fig. 7C).

12
13
14 335 **Radioulnae**—Only the right radioulna is preserved for its entire length on M1. Most of
15
16 336 it is preserved as a ventrally exposed imprint (Fig. 7C). Only the distal region of the left
17
18 337 radioulna is preserved on M1 as a ventrally exposed imprint. The distalmost portion of the left
19
20 338 radioulna is preserved mostly as crushed bone on M2. The right radioulna (around 9 mm) is
21
22 339 slightly shorter than the humerus (around 80% of total humeral length). The proximal region is
23
24 340 articulated with the distal region of the humerus (Fig. 7C). The remaining imprint of the
25
26 341 articulation did not preserve the shape of the proximal region. The diaphysis widens distally
27
28 342 (Fig. 7D). It reaches its widest point at the level of the distal margin. Although badly crushed
29
30 343 on M2, the presence of a shallow groove at mid-width is discernible (Fig. 7D). This groove
31
32 344 allowed to discern both radial and ulnar articulation facets with the carpals (Fig. 7D).

33
34
35 345 **Hands**—Both hands are not fully preserved. The left hand preserves most elements,
36
37 346 except for one phalanx on both M1 and M2 (Fig. 2A, C). Four digits are visible, with the
38
39 347 following phalanx formula : 2–2–3–3. The right hand is poorly preserved on M1 (Fig. 2A)

40
41
42 348 **Carpals**—All carpals are preserved on both hands (Fig. 2A). Unfortunately, they are
43
44 349 poorly preserved as crushed bones exposed in dorsal view. However, most of their shape has
45
46 350 been preserved as imprint. Left and right carpals are preserved on M1 (Fig. 2A). Only the left
47
48 351 carpals are preserved on M2 (Fig. 2C). The description is based on carpals from the left hand,
49
50 352 preserved in dorsal view (see Fig. 8A). The carpals of the left hand seem preserved in
51
52 353 anatomical position. Two rows are preserved.

53
54
55
56 354 The proximal row preserves three bones (left to right): the ulnare, radiale, and distal
57
58 355 radiale (Fig. 8B). The ulnare (left lateral imprint) is roughly ellipsoid, slightly elongated

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2
3 356 transversely (Fig. 8B). It articulates with the ulnare part of the articular surface of the
4
5 357 radioulna, the radiale, and the distal ulnare (Fig. 8B). Three distinct articular facets are present
6
7 358 on the ulnare. The posteromedial region of this element is slight protruding towards the radiale
8
9 359 (Fig. 8B). This protrusion is interpreted as the fused intermedium (following Fabrezi and
10
11
12 360 Alberch, 1996).

13
14 361 The radiale is the largest (both in width and length) of the proximal carpals. Its shape is
15
16 362 difficult to discern but seems circular (Fig. 8). It articulates with the radial part of the articular
17
18 363 surface of the radioulna, the ulnare, the distal radial element, and the distal carpalia III and IV
19
20
21 364 (Fig. 8B). All four articular facets are concave (Fig. 8B).

22
23 365 The distal radial element is free. It articulates with the radiale, the distal carpale II, and
24
25 366 the prepollex (Fig. 8B). The distal radial element is crescent-shaped, and its lateral margin is
26
27 367 concave (Fig. 8B). Its proximal margin seems close to the radial (Fig. 8B). This is likely an
28
29 368 artefact of preservation, as this region is difficult to visualize (Fig. 8A).

30
31 369 The distal row has three bones preserved: the distal carpal element (fused distal carpalia
32
33 370 III, IV and ulnare element), the distal carpal II, and the prepollex (Fig. 8A). Distal carpalia III,
34
35 371 IV and ulnare element (distal carpale V of Fabrezi & Alberch, 1996) are all fused into a single
36
37 372 large bone (Fig. 8B). It contacts the ulnare, radiale, metacarpals III-V and the distal carpale II
38
39 373 (Fig. 8B). The anterior margin bears two distinct articular surfaces for the ulnare and radiale
40
41 374 (Fig. 8B). There is no indication that distinct articular facets are present on the posterior margin
42
43 375 (Fig. 8B). The bone is crescentic, with a convex posterior margin (Fig. 8B).

44
45 376 Distal carpale II is a small circular element (Fig. 8B). It contacts the distal radial
46
47 377 element, the prepollex, the distal carpal element, and the metacarpal II (Fig. 8B).

48
49 378 The prepollex is barely evident. Most, if not all, neobatrachians possess a prepollex
50
51 379 composed of two distinct bones (Fabrezi & Barg, 2001). Unfortunately, only a single imprint is
52
53 380 visible on the left hand of IGR 144547 (Fig. 8A). On its right hand this region is not preserved
54
55 381 (Fig. 2B). As the two bones of the prepollex are often in contact (see Roček et al., 2022:fig.

1
2
3 382 2L) it is possible that they left a single imprint. The prepollex is small and triangular (Fig. 8B).
4
5 383 It contacts the distal radial element, the distal carpale II, and the metacarpal II (Fig. 8B).
6

7
8 384 **Metacarpals**—Metacarpals II-V are all preserved on both hands on M1 (Fig. 2A, C).
9
10 385 Shallow imprints of the left metacarpals are preserved on M2 (Fig. 2B). The right metacarpals
11
12 386 are poorly preserved and poorly defined (Fig. 2A). Metacarpal II contacts the distal carpale II,
13
14 387 and prepollex proximally and the phalanx I of II distally (Fig. 8B). It is one of the longest
15
16 388 metacarpals (4,7 mm). Its proximal head is wider than its distal head. Both proximal and distal
17
18 389 articular facet seems flat and straight (Fig. 8B). The bone is elongated, with a rather narrow
19
20 390 diaphysis (Fig. 8B). Metacarpal III is shorter (4.5 mm) than metacarpal II. It contacts the distal
21
22 391 carpale III proximally and the phalanx I of digit III distally. It is preserved with bone, with both
23
24 392 proximal and distal heads are broken, while the diaphysis seems complete (Fig. 8A). As for
25
26 393 metacarpal II, the diaphysis is elongated and narrow. The proximal head is wider than the distal
27
28 394 head (Fig. 8B). The proximal and distal articular facets are flat and straight (Fig. 8B).
29
30 395 Metacarpal IV is as long as metacarpal III (4.5 mm). It contacts the distal carpale IV
31
32 396 proximally and the phalanx I of digit IV distally. As for metacarpal III, its distal and proximal
33
34 397 heads are broken, and most of the diaphysis is broken as well (Fig. 8A). The proximal end
35
36 398 bears a flat articular surface (Fig. 8B). The distal head is too damaged to assess the shape of its
37
38 399 articular facet (Fig. 8B).
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44 400 Metacarpal V is as long as metacarpal II (4.8 mm). It contacts the distal ulnare element
45
46 401 proximally and the phalanx I of digit V distally. It is complete (Fig. 8B) . Its proximal head is
47
48 402 wider than its distal head. The articular facet of the proximal head is concave (Fig. 8B). The
49
50 403 articular facet of the distal head is flat.
51
52

53 404 **Phalanges**—Phalanges are only preserved on the left hand, on both M1 and M2.
54
55 405 Phalanx I is preserved on all digits (Fig. 8A). It is preserved as an imprint on digits II and V,
56
57 406 and as a complete bone on digits III and IV. On digits II and IV, the phalanx is elongate (3.3
58
59 407 and 3.4 mm). On digit II, it is only preserved as a poorly defined imprint (Fig. 8A). On digit
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1
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3 408 IV, the preservation shows that the proximal head is wider than its distal head (Fig. 8B). Both
4
5 409 articular facets are flat. On digits III and V, phalanx I is shorter (2.8 and 2.4 mm), and the
6
7 410 proximal and distal heads are of the same width (Fig. 8B).

9
10 411 Phalanx II is also preserved on all digits. It is preserved as an imprint on digits II and V,
11
12 412 and as a complete bone on digits III and IV. For digits II and III, it is the terminal phalanx. It is
13
14 413 very short (1.5 mm). The phalanx narrows distally, before ending into a knob (Fig. 8B). On
15
16 414 digits IV and V, the phalanx II is connected distally to the phalanx III (Fig. 9B). It is shorter
17
18 415 than the phalanx I (2.6 and 2.2 respectively mm). Both proximal and distal heads are not
19
20 416 distinct from the diaphysis.

21
22
23 417 Phalanx III is preserved on digit IV only as an imprint (Fig. 8A). It is the terminal
24
25 418 phalanx for digits IV and V (missing on IGR 144547). It is identical to the terminal phalanx of
26
27 419 digits II and III. It is short (1.5 mm) and bears a knob on its distal end (Fig. 8B).

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32 421 **Hindlimbs**

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35 422 **Femora**—Both femora are preserved on M1 and M2. The left femur is incomplete on
36
37 423 M2. Both femora are preserved as a well-delimited imprints (exposed in ventral view) with
38
39 424 remnants of bone (Figs. 2A, C; 11A). Femora are long (22.1 mm) and slender. The proximal
40
41 425 head of the femur is badly preserved and mostly crushed near the acetabulum (Fig. 9B). No
42
43 426 crest nor flange is visible on its lateral and medial margins (Fig. 9B). The femur is slightly
44
45 427 sigmoid (S-shaped). No crest is visible on the femur shaft.

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48 428 **Tibiofibulae**—Only the left tibiofibula is incompletely preserved on both M1 and M2.
49
50 429 The proximal region is preserved as an uncrushed bone, while the diaphysis is mostly
51
52 430 preserved as an imprint (exposed in ventral view). The distal region is not preserved (Fig. 9A,
53
54 431 B). The proximal head bears a shallow groove mid-width. This groove marks the separation
55
56 432 between the fused tibia and fibula (Fig. 9A, B). The tibiofibula is long (14 mm in length) and
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3 433 straight. Slightly more than half of the tibiofibula appears to be preserved. Thus, the complete
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5 434 tibiofibula is probably slightly longer than the femur.
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7 435

10 436 DISCUSSION

11 437

14 438 **Taxonomic Attribution**

16 439 **Comparison to Extant European Anurans**—The presence of a bicondylar sacro-
18 440 urostylar articulation, a firmsternal pectoral girdle and a diplasiocoelous vertebral column are
20 441 diagnostic for ranoid (Frost et al., 2006). Within Ranoidea, only natatanuran taxa are known in
22 442 Europe in the Cenozoic (Roček, 2013). Furthermore, an ossified omosternum, if present, is
24 443 considered a natatanuran synapomorphy (Frost et al., 2006; Lemierre et al., 2021). Within this
26 444 clade, only Ranidae are known in Europe from the Oligocene (Sanchíz, 1998; Roček, 2013;
28 445 Rage, 2016; Vasilyan, 2018). IGR144547 is similar to Ranidae in the following features:
30 446 slender rod-like sacral apophyses, the eminentia capitata of the humerus is not shifted from the
32 447 central axis of the humeral diaphysis and there is no crest on the femur.

34 448 Cenozoic and extant ranids from Western Europe have been only referred to two
36 449 genera, *Rana* and *Pelophylax* (Duellman & Trueb, 1994; Sanchíz, 1998; Roček, 2013; Rage,
38 450 2016). During the twentieth and early twenty-first centuries, most authors considered the two
40 451 genera synonymous (with *Pelophylax* sometimes considered a subgenus of *Rana*; Frost et al.,
42 452 2006). In consequence, almost all known Cenozoic ranid from Europe were described as
44 453 “*Rana*” (Sanchíz, 1998), regardless of their affinity towards the green water frogs (*Pelophylax*
46 454 spp.) or brown water frogs (*Rana* spp.). In addition, osteological differences between extant
48 455 European ranid and their Cenozoic counterpart are sometimes hard to find (Sanchíz, 1998). In
50 456 addition, most of the European *Pelophylax* are grouped into the *Pelophylax* kl. *esculentus*, as
52 457 hybridization is possible between species included into this complex (Lymberakis et al., 2007),
54 458 and few (if any) osteological differences exists (Crochet et al., 1995). Thus, most of the taxa

erected since the nineteenth century are considered dubious (Sanchíz, 1998; Roček, 2013; Blain et al., 2023).

Osteological differences between *Pelophylax* and *Rana* are known for their postcranial elements (Sanchíz et al., 1993; Bailon, 1999) and cranial elements (Böhme, 1977; Bailon, 1999). The only element that allows a comparison is the ilium of IGR 144547, on which several character can be used to differentiate *Rana* and *Pelophylax* (Sanchiz et al., 1993; Bailon, 1999). IGR 144547 shares with *Pelophylax* kl. *Esculentus*: a large pyriform-shaped dorsal protuberance (Sanchíz et al., 1993; Bailon, 1999), a well-developed supracetabular fossa (‘dorsal preacetabular fossa’ in Sanchíz et al., 1993), a high dorsal crest anterior to the dorsal protuberance (Sanchíz et al., 1993); a high angle between the dorsal protuberance and the iliac shaft (~52° in IGR 144547; Sanchíz et al., 1993), and a small preacetabular zone (Sanchíz et al., 1993). Thus, we assign IGR 144547 to the genus *Pelophylax*, as a member of the complex *Pelophylax* kl. *esculentus*. Unfortunately, there is no current diagnostic apomorphies on the ilium between the different European species *Pelophylax* that would allow a more precise taxonomic assignment (Blain et al., 2015).

***Pelophylax* in the Oligocene of France**—As mentioned above, all extinct ranids from the Oligocene of Europe were described as *Rana* until recently. Thus, the most complete Oligocene ranid, “*Rana*” *aquensis* Coquand, 1845 has been referred to *Pelophylax* in the last decades (Sanchíz, 1998) on the basis of a similar osteology to *Pelophylax esculentus* (Sanchíz, 1998). However, there has not been any formal assignment to the genus, and the taxonomic validity of the taxon (i.e, as distinct from extant *Pelophylax* species placed under the *Pelophylax* kl. *esculentus*) has yet to be established (Sanchíz, 1998).

“*Rana*” *aquensis* is known by several subcomplete articulated specimens (Fig. 12A; Piveteau, 1927: fig. 4) from the late Oligocene of Southern France (Coquand, 1845; Piveteau, 1927; Sanchíz, 1998; Gaudant et al., 2018). The neotype (MNHN.F.AIX355) of “*Rana*” *aquensis* should be referred to the genus *Pelophylax* on the following features: a high and well-

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3 485 developed dorsal crest on the ilium (Sanchiz et al., 1993; Bailon, 1999), a dorsal protuberance
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5 486 pyriform well-developed (Sanchiz et al., 1993), and a high angle ($\sim 42^\circ$) between the dorsal
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7 487 protuberance and the iliac shaft (Sanchiz et al., 1993; Bailon, 1999). Thus, we consider that all
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9 488 specimens assigned to “*Rana*” *aquensis* should be referred to the genus *Pelophylax*. However,
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11 489 we refrain from assessing the validity of *Pelophylax aquensis*, as this is beyond the scope of
12
13 490 the study. *Pelophylax aquensis* has been considered closely related to the Miocene “*Rana*”
14
15 491 *meriani* (Piveteau, 1927). Furthermore, a recent redescription of *Pelophylax pueyoi* (Blain et
16
17 492 al., 2023) mentioned that the latter taxon (*P. pueyoi*) could be a subjective junior synonym of
18
19 493 the Lower Miocene “*Rana*” *meriani* Meyer, 1852 (Meyer, 1860). Thus, a complete revision of
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21 494 the Oligo-Miocene *Pelophylax* is needed to assess if they represent distinct taxa, and if they
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23 495 could be differentiated from extant *Pelophylax* taxa.

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28 496 **Comparison of IGR 144547 to *Pelophylax aquensis***— IGR 144547 resembles
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30 497 *Pelophylax aquensis* in features of the ilium, that are diagnostic for *Pelophylax* kl. *esculentus*.
31
32 498 The pectoral girdle of *Pelophylax aquensis* is poorly preserved (Piveteau, 1927), with only the
33
34 499 cleithrum (“omoplate” in Piveteau, 1927) mentioned. Other specimens assigned to *P. aquensis*
35
36 500 are known but have not been described (A.L. pers. obs). Thus, IGR 144547 does not differ from
37
38 501 *Pelophylax aquensis*, but it cannot be distinguished from extant European *Pelophylax*. Hence,
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40 502 we refrain from any generic assignment for *Pelophylax aquensis*.
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46 503 47 504 **Paleobiogeography**

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49 505 The palearctic water frog *Pelophylax* ranges throughout Europe and Asia today
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51 506 (Duellman & Trueb, 1994; Chan & Brown, 2017). The divergence between the western
52
53 507 (Europe) and eastern (Asia) lineages of *Pelophylax* has been estimated to have occurred around
54
55 508 35 Ma (Chan & Brown, 2017). The genus then spread throughout Europe and underwent a
56
57 509 diversification event during the last 15 Ma (Lymberakis et al., 2007). However, the early
58
59 510 diversification of the genus is almost unknown, as a single occurrence has been reported from
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3 511 the early Oligocene of Germany (MP22; Sanchíz et al., 1993) and the genus is currently absent
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5 512 from the early Oligocene sites of the Quercy Phosphorites (Rage, 2016). The attribution of IGR
6
7 513 144547 to *Pelophylax* and its geographical location, in northwestern France is very interesting.
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9
10 514 It implies that the genus was present in northwestern Europe (from southern Germany to
11
12 515 northwestern France) no later than 5 Ma after its arrival in Europe. Thus, *Pelophylax*
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14 516 apparently underwent a rapid dispersal throughout Europe during the early Oligocene. During
15
16 517 the late Oligocene, the genus is known throughout western Europe (Roček, 2013). This wide
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18 518 and rapid dispersal was likely facilitated by the “Grande Coupure” extinction event. It is linked
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21 519 to the Eocene/Oligocene transition (33.9 Ma) when a large turnover of the amphibian fauna
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23 520 took place (Rage, 2016; Vasilyan, 2018), with the rise of “true” ranid (*Pelophylax*, *Rana*) in the
24
25 521 Oligocene (Roček, 2013; Rage, 2016). Thus, *Pelophylax* benefitted of the presence of
26
27 522 unoccupied ecological niches, and easily spread in Europe. It should be noted that this rapid
28
29 523 and vast dispersal might also reflect a sampling bias, in particular within the Quercy
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31 524 Phosphorites (that represent most of anuran occurrences from western Europe during the early
32
33 525 Oligocene; Rage, 1984, 2016). Several possible ranids have been identified (Rage, 1984, 2016)
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35 526 in the Quercy (MP22-23; Rage, 2016), but have not been studied since *Rana* and *Pelophylax*
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37 527 became accepted as separated genera.
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44 529 CONCLUSION

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49 531 In conclusion, IGR 144547 represents one of the oldest known members of the
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51 532 European *Pelophylax* kl. *esculentus*, and the oldest articulated specimen of *Pelophylax*
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53 533 identified. We also suggest that ‘*Rana*’ *aquensis* should be included within *Pelophylax* kl.
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55 534 *esculentus*. IGR 144547 resembles the holotype of *Pelophylax aquensis*, but a complete
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57 535 revision of this taxon must be made before any assignment can be proposed. Our specimen
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59
60 536 represents the first occurrence of *Pelophylax* in the early Oligocene of France. This occurrence

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3 537 suggests a rapid dispersal of *Pelophylax* throughout western Europe during the Oligocene. This
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5 538 opportunistic frog genus likely benefited from unoccupied ecological niches and the decrease
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7 539 in anuran diversity following the “Grande Coupure”.

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11 541

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21 697 SUPPLEMENTARY INFORMATION

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26 699 Supplementary Data 1.docx: supplementary figure.

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35 703 The data underlying this article are available in zenodo at [10.5281/zenodo.7223828](https://zenodo.org/doi/10.5281/zenodo.7223828).

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39 705 FIGURE CAPTIONS

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44 707 FIGURE 1. Location of the discovery in the Grand Four quarry (Chartres-de-Bretagne). **A**,
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46 708 Geological map of the Chartres-de-Bretagne basin with location of the quarry (black circle;
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48 709 modified from Bauer et al., 2016); **B**, Stratigraphic section of the quarry (modified from Bauer
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50 710 et al., 2016) with **C**, photography of the outcrop taken by Yves Milon in march 1922, note the
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52 711 black clay with quarrymen in the Upper Sapropels that yielded the anuran remains just above
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54 712 paleosols; **D**, close-up on the black clay with Yves Milon and two quarrymens, position of
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56 713 hammers indicates first fish remains discovered the 17th March 1922, the anuran comes from
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58 714 the left hammer level (photography Dangeard). Labels at the bottom are for the geological map

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3 715 of **A** and black star (red in online version) represents the position of IGR 144547 within the
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5 716 stratigraphic log. [page width]

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10 718 FIGURE 2. IGR 144547 main slab (M1) and its counterpart (M2). **A**, IGR 144547 M1, **B**,
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12 719 interpretative drawing of the same specimen; **C**, IGR 144547 M2 and **D**, interpretative drawing
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14 720 of the same specimen. Light gray areas represent regions on the specimen where bony elements
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16 721 could not be delimited, dark gray areas represent skin impressions, scale bars represent 10 mm.
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18 722 **Abbreviations:** **ca**, carpals; **cl**, clavicle; **co**, coracoid; **f**, femur; **hu**, humerus; **il**, ilium; **mtc**,
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20 723 metacarpal; **omst?**, putative omosternum; **phx I, II, III**, phalanx I, II, III; **rdul**, radioulna; **sc**,
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22 724 scapula; **tf**, tibiofibula; **ur**, urostyle. [page width]

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28 726 FIGURE 3. Reconstruction of IGR 144547 in ventral view. Non-preserved elements are
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30 727 inferred from *Pelophylax esculentus*, gray areas represent non-preserved elements, scale bar
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32 728 represents 10 mm. [column width]

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37 730 FIGURE 4. Vertebral elements of IGR 144547. **A**, close-up on the vertebral region of IGR
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39 731 144547 on M1, **B**, interpretative drawing of the same region, **C**, close-up on the urostyle of
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41 732 IGR 144547 on M2 and **D**, interpretative drawing of the same region. Scale bars represent 5
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43 733 mm and light gray areas represent unidentified bony elements. **Abbreviations:** **IV**, fourth
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45 734 vertebra; **V**, fifth vertebra; **VI**, sixth vertebra; **VII**, seventh vertebra; **VIII**, eighth vertebra; **il**,
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47 735 ilium; **stp**, sacral transverse process; **sv**, sacral vertebra; **tp**, transverse process; **ur**, urostyle.
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49 736 [column width]

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55 738 FIGURE 5. Pectoral elements of IGR 144547. **A**, close-up on the right pectoral region of IGR
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57 739 144547 on M1, **B**, interpretative drawing of the same region and **C**, reconstruction of the
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59 740 pectoral girdle in ventral view. Light gray area represents the glenoid region. **Abbreviations:**

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3 741 **cl**, clavicle; **co**, coracoid; **glf**, glenoid fossa ?; **hu**, humerus; **omst?**, putative omosternum; **par**,
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5 742 pars acromialis; **pecd**, processus epicoracoidalis; **pgl**, pars glenoidalis; **prgl**, processus
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7 743 glenoidalis; **sc**, scapula; **st**, sternum. Scale bar is 5 mm. [2/3 page width]
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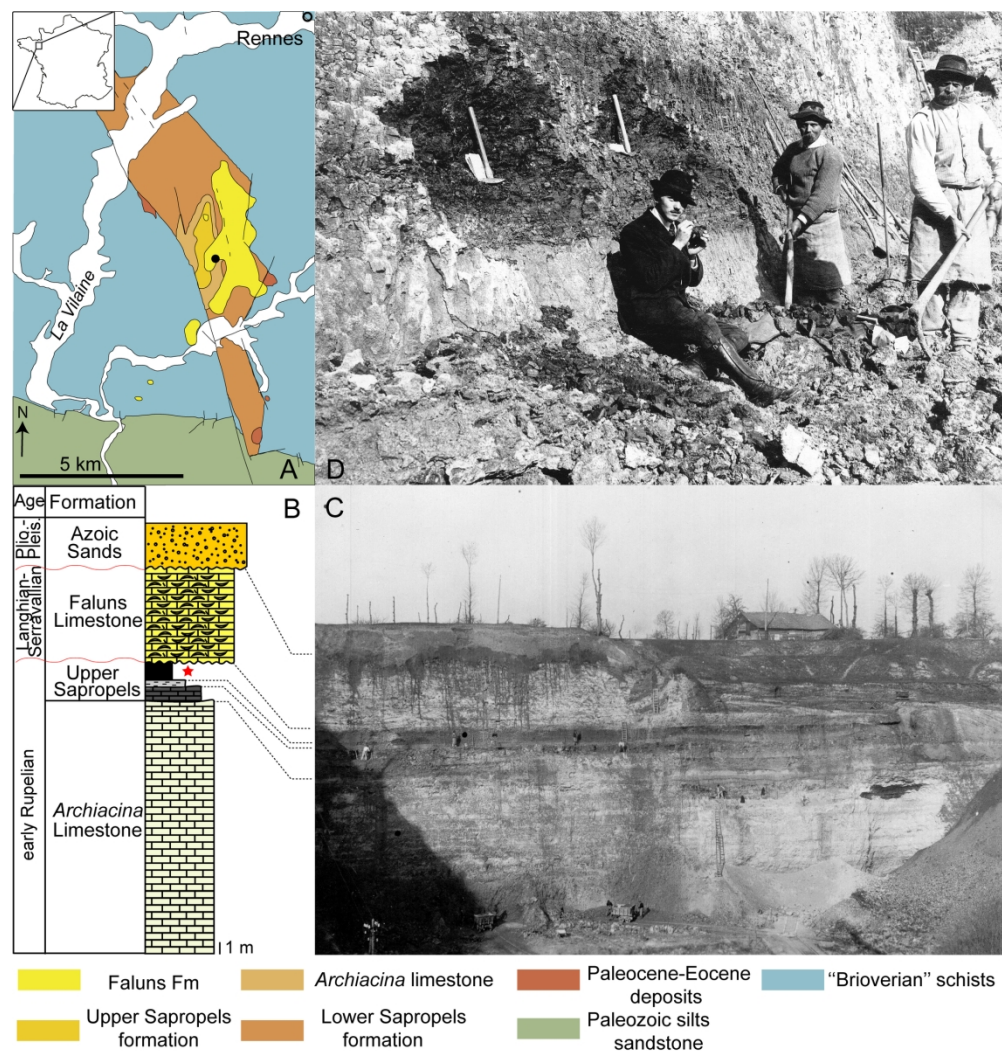
10 744
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12 745 FIGURE 6. Ilium of IGR144547. **A**, acetabular region of the left ilium exposed in lateral view
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14 746 on M2, **B**, proposed reconstruction of the acetabular region of the left ilium in lateral view and
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16 747 **C**, right ilium in exposed in medial view on M2. Scale bars represent 2 mm. **Abbreviations:**
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18 748 **acf**, acetabular fossa; **acr**, acetabular rim; **dae**, dorsal acetabular expansion; **dc**, dorsal crest;
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20 749 **dpt**, dorsal protuberance; **ish**, iliac shaft; **pz**, preacetabular zone; **saf**, supraacetabular fossa;
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22 750 **vae**, ventral acetabular expansion. [full page width]
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28 752 FIGURE 7. Forelimbs of IG144547. **A**, left humerus on M1, **B**, interpretative drawing of the
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30 753 same humerus, **C**, right forelimb on M1 and **D**, interpretive drawing of the same forelimb.
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32 754 Light gray area represents skin impressions, scale bars represent 5 mm. **Abbreviations:** **ec**,
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34 755 eminentia capitata; **dia**, diaphysis; **fc**, fossa cubitalis; **recd**, epicondylus radialis.[column
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44 759 same hand. Light gray areas represent skin impressions of the digits, scale bar represents 2
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46 760 mm. **Abbreviations:** **dis rd**, distal radiale; **dist ul**, distal ulnare; **dist II**, distal carpale II; **dist**
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48 761 **III**, distal carpale III; **dist IV**, distal carpale IV; **mtc**, metacarpal; **phx I, II, III**, phalanx I, II,
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50 762 III; **pp**, prepollex; **rd**, radiale; **rdul**, radioulna; **ul**, ulnare. [column width]
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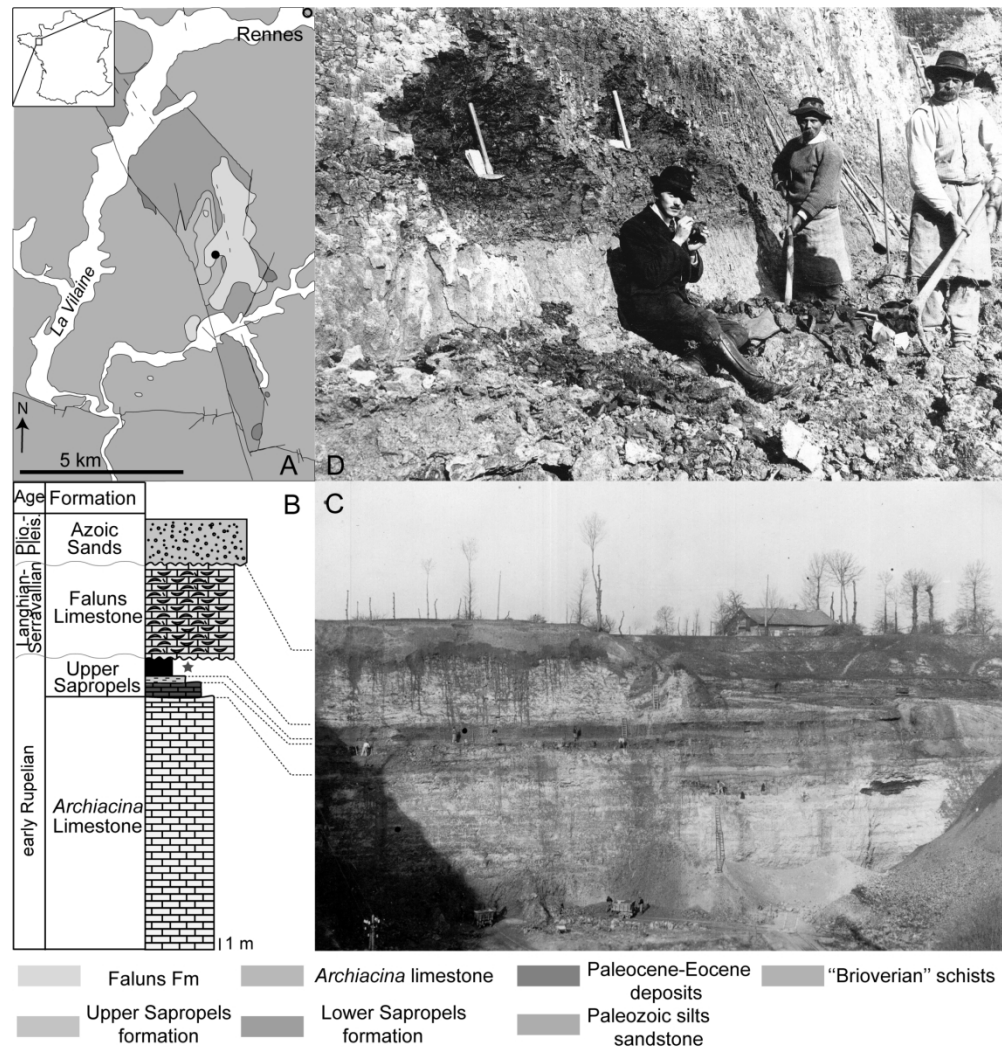
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56 764 FIGURE 9. Hindlimb of IGR 144547. **A**, right hindlimb on M1 and **B**, interpretative drawing
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58 765 of the same hindlimb. **Abbreviations:** **f**, femur; **tf**, tibiofibula. Dotted lines delimit skin
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60 766 impressions, scale bar represents 5 mm. [column width]

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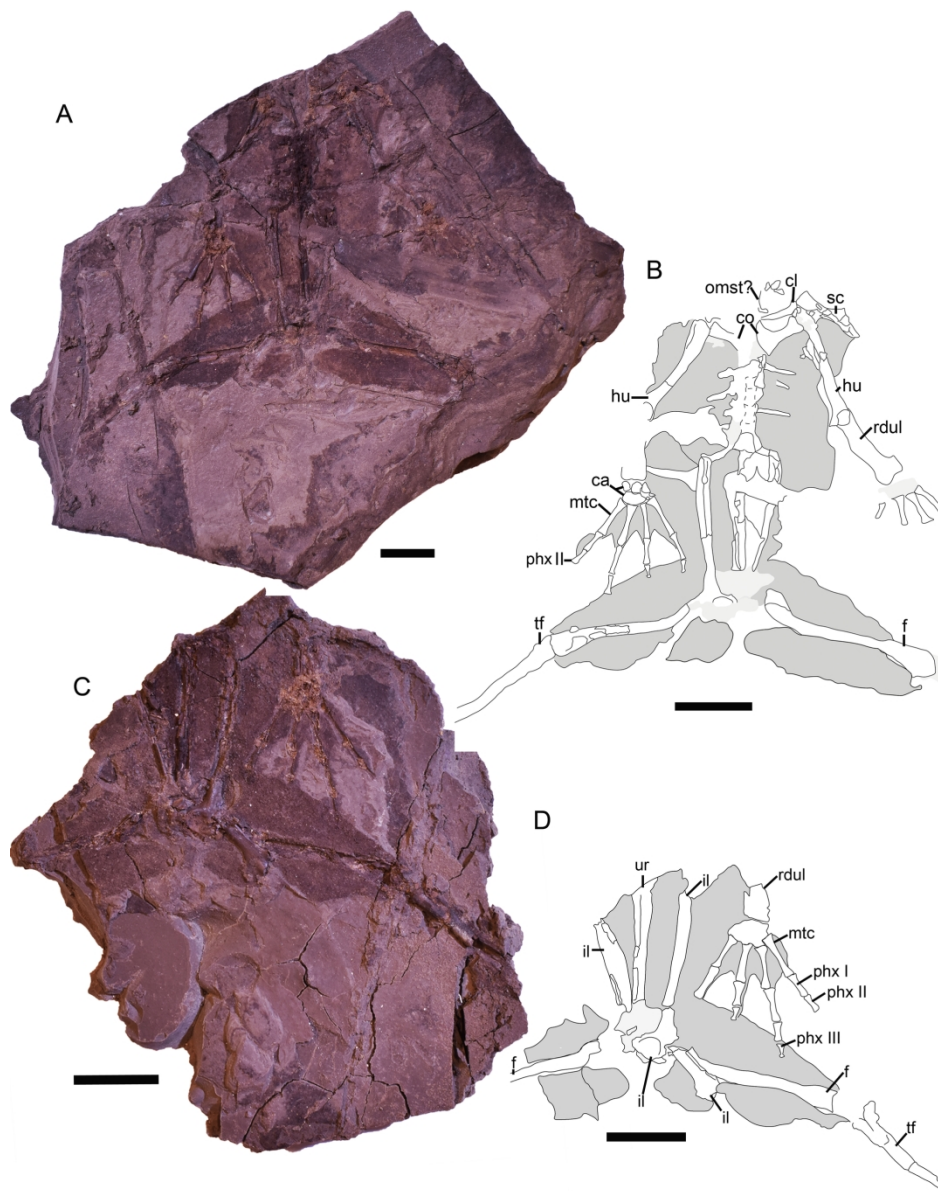
Location of the discovery in the Grand Four quarry (Chartres-de-Bretagne). **A**, Geological map of the Chartres-de-Bretagne basin with location of the quarry (black circle; modified from Bauer et al., 2016); **B**, Stratigraphic section of the quarry (modified from Bauer et al., 2016) with **C**, photography of the outcrop taken by Yves Milon in March 1922, note the black clay with quarrymen in the Upper Spropels that yielded the anuran remains just above paleosols; **D**, close-up on the black clay with Yves Milon and two quarrymen, position of hammers indicates first fish remains discovered the 17th March 1922, the anuran comes from the left hammer level (photography Dangeard). Labels at the bottom are for the geological map of **A** and black star (red in online version) in **B** represents the position of IGR 144547 within the stratigraphic log.

182x190mm (300 x 300 DPI)



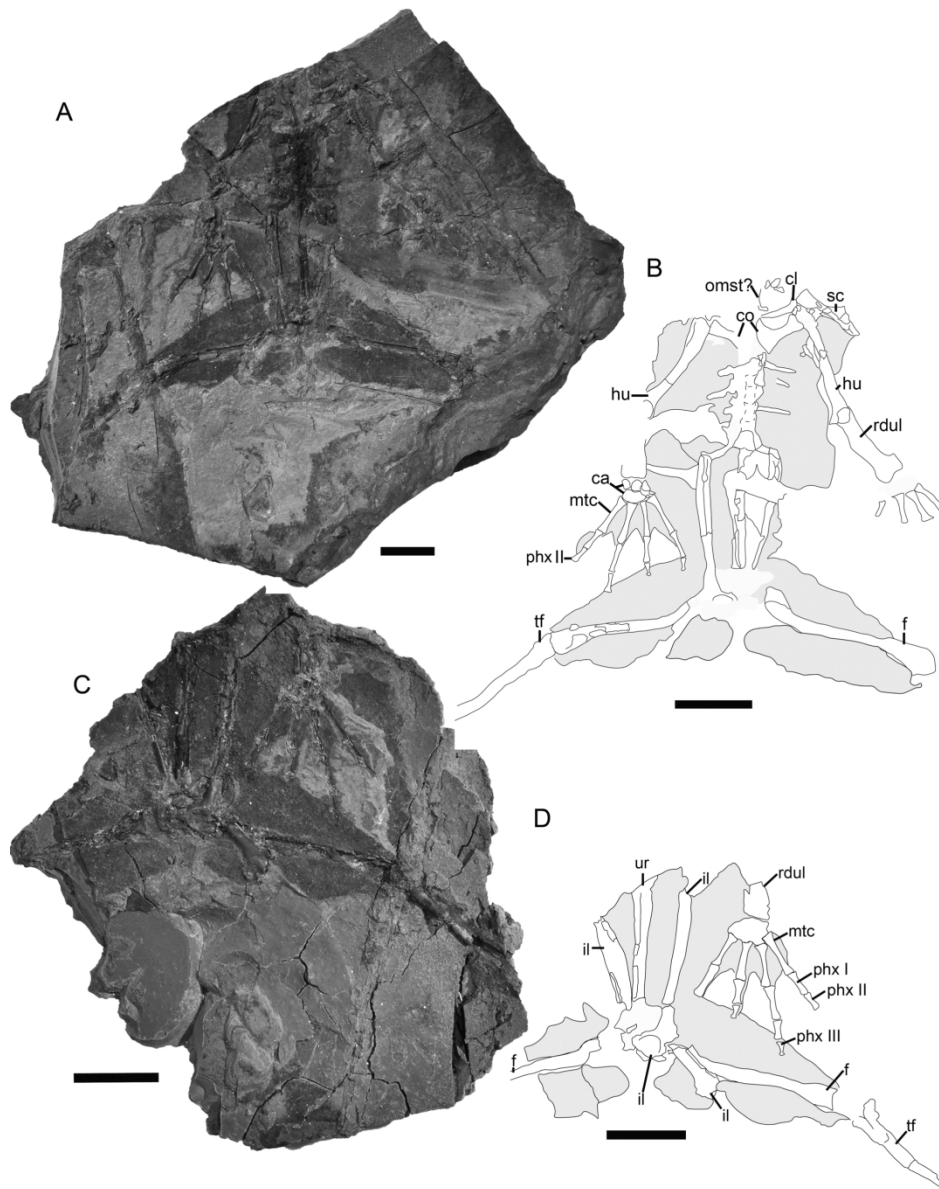
Location of the discovery in the Grand Four quarry (Chartres-de-Bretagne). **A**, Geological map of the Chartres-de-Bretagne basin with location of the quarry (black circle; modified from Bauer et al., 2016); **B**, Stratigraphic section of the quarry (modified from Bauer et al., 2016) with **C**, photography of the outcrop taken by Yves Milon in march 1922, note the black clay with quarrymen in the Upper Sapropels that yielded the anuran remains just above paleosols; **D**, close-up on the black clay with Yves Milon and two quarrymens, position of hammers indicates first fish remains discovered the 17th March 1922, the anuran comes from the left hammer level (photography Dangeard). Labels at the bottom are for the geological map of **A** and black star (red in online version) in **B** represents the position of IGR 144547 within the stratigraphic log.

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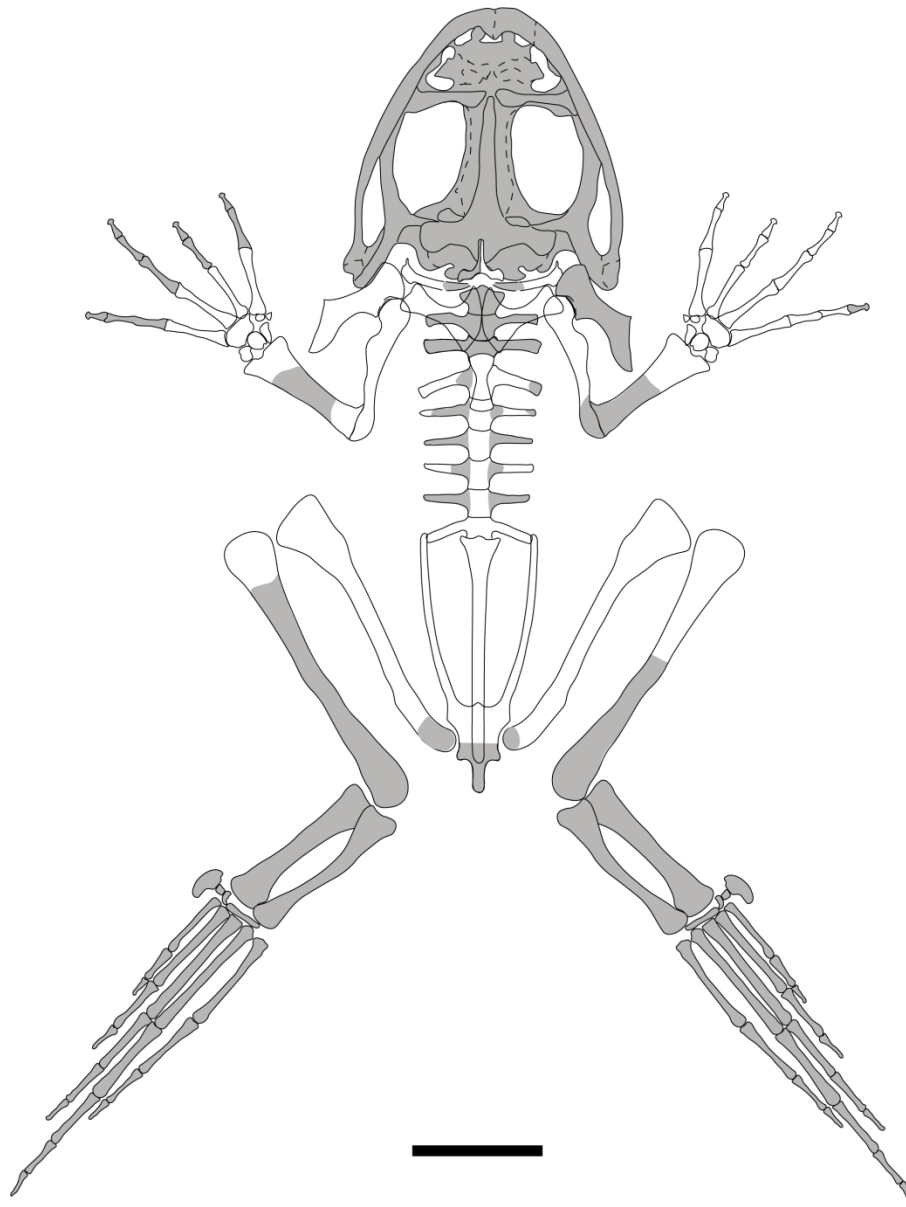
45 IGR 144547 and its counterpart. **A**, IGR 144547 M1, **B**, interpretative drawing of the same specimen; **C**, IGR
46 144547 M2 and **D**, interpretative drawing of the same specimen. Light gray areas represent regions on the
47 specimen where bony elements could not be delimited, dark gray areas represent skin impressions regions,
48 scale bars represent 10 mm. **Abbreviations:** **ca**, carpals; **cl**, clavicle; **co**, coracoid; **f**, femur; **hu**, humerus;
49 **il**, ilium; **mtc**, metacarpal; **omst?**, putative omosternum; **phx I, II, III**, phalanx I, II, III; **rdul**, radioulina;
50 **sc**, scapula; **tf**, tibiofibula; **ur**, urostyle.

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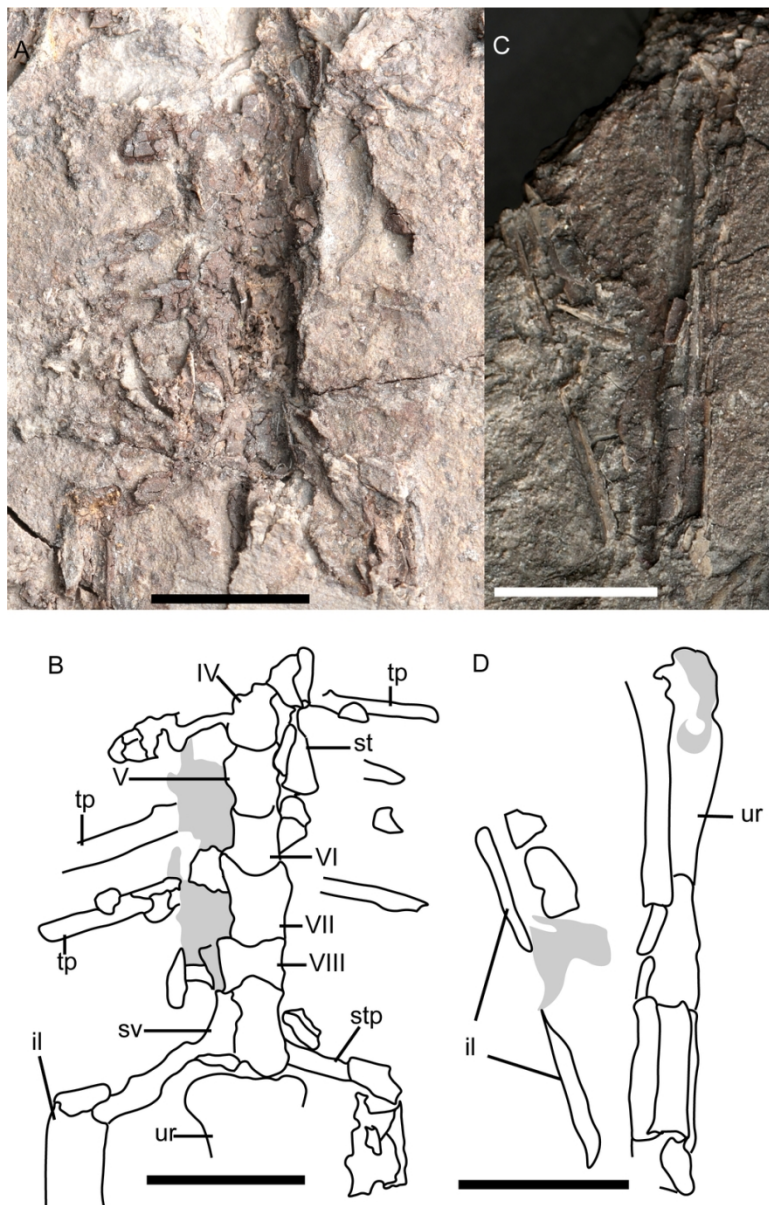
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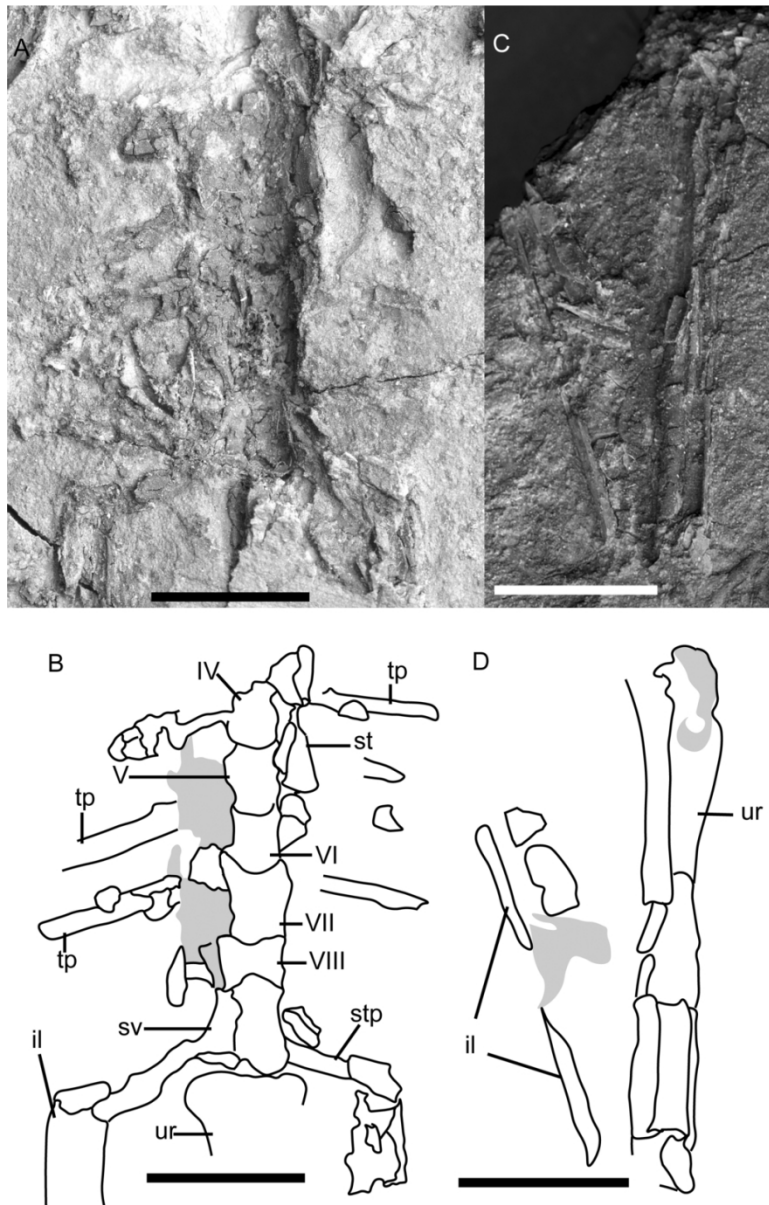
Reconstruction of IGR 144547 in ventral view. Non-preserved elements are inferred from *Pelophylax esculentus*, gray areas represent non-preserved elements, scale bar represents 10 mm.

88x116mm (600 x 600 DPI)



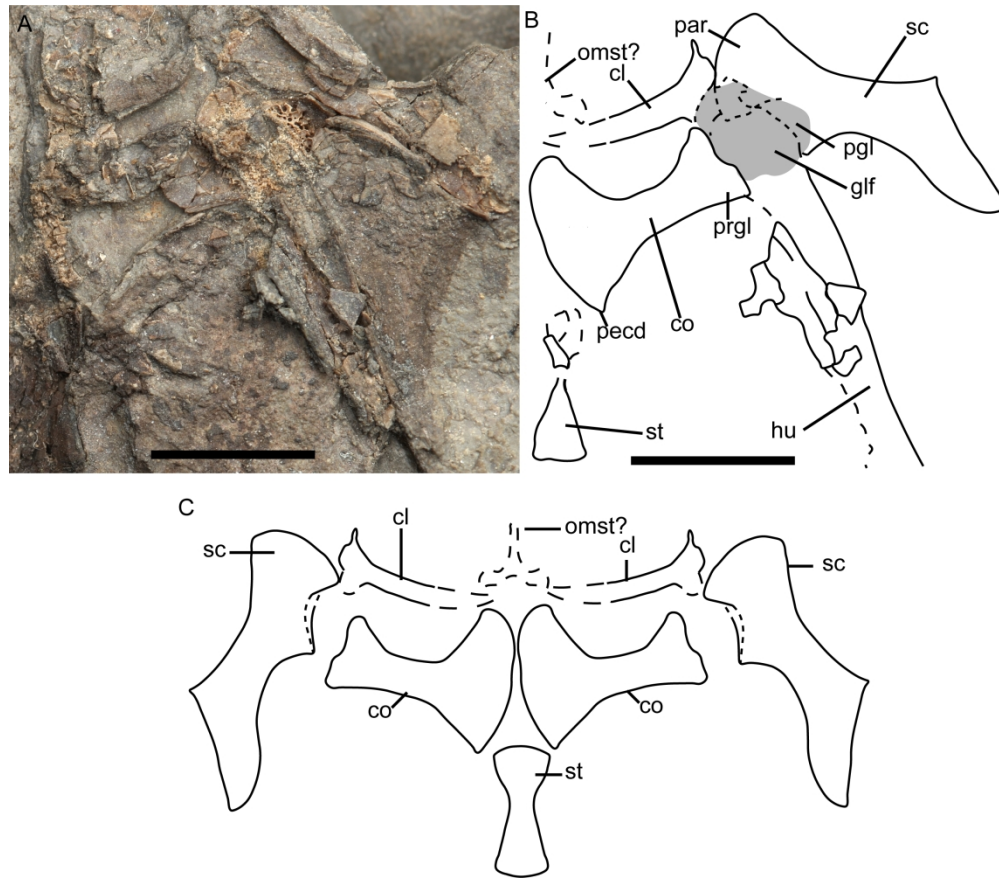
Vertebral elements of IGR 144547. **A**, close-up on the vertebral region of IGR 144547 on M1, **B**, interpretative drawing of the same region, **C**, close-up on the urostyle of IGR 144547 on M2 and **D**, interpretative drawing of the same region. Scale bars represent 5 mm and light grey areas represent unidentified bony elements. **Abbreviations:** **IV**, fourth vertebra; **V**, fifth vertebra; **VI**, sixth vertebra; **VII**, seventh vertebra; **VIII**, eighth vertebra; **il**, ilium; **stp**, sacral transverse process; **sv**, sacral vertebra; **tp**, transverse process; **ur**, urostyle.

88x136mm (300 x 300 DPI)



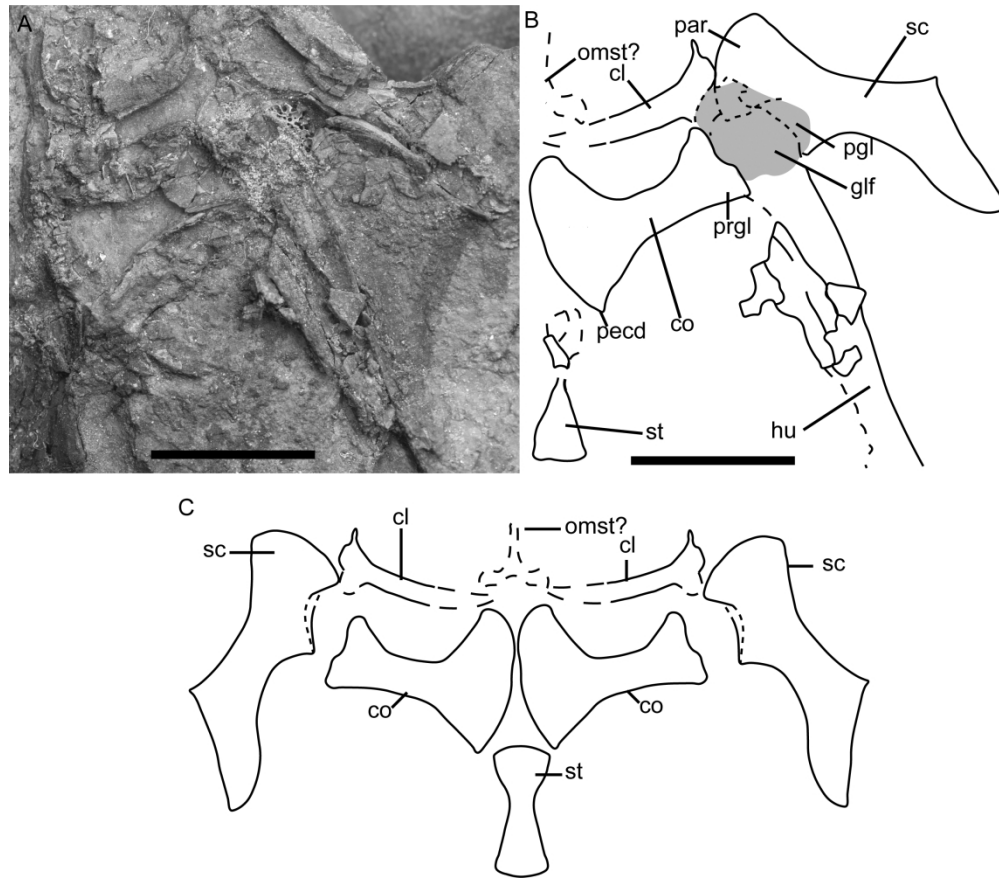
Vertebral elements of IGR 144547. **A**, close-up on the vertebral region of IGR 144547 on M1, **B**, interpretative drawing of the same region, **C**, close-up on the urostyle of IGR 144547 on M2 and **D**, interpretative drawing of the same region. Scale bars represent 5 mm and light grey areas represent unidentified bony elements. **Abbreviations:** **IV**, fourth vertebra; **V**, fifth vertebra; **VI**, sixth vertebra; **VII**, seventh vertebra; **VIII**, eighth vertebra; **il**, ilium; **stp**, sacral transverse process; **sv**, sacral vertebra; **tp**, transverse process; **ur**, urostyle.

88x136mm (300 x 300 DPI)



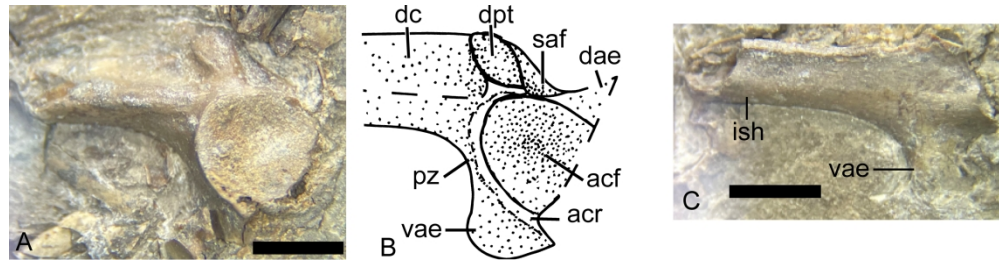
Pectoral elements of IGR 144547. **A**, close-up on the right pectoral region of IGR 144547 on M1, **B**, interpretative drawing of the same region and **C**, reconstruction of the pectoral girdle in ventral view. Light gray area represents the glenoid region. . **Abbreviations:** **cl**, clavicle; **co**, coracoid; **glf**, glenoid fossa?; **hu**, humerus; **omst?**, putative omosternum; **par**, pars acromialis; **pecd**, processus epicoracoidalis; **pgl**, pars glenoidalis; **prgl**, processus glenoidalis; **sc**, scapula; **st**, sternum. Scale bar is 5 mm.

122x106mm (600 x 600 DPI)



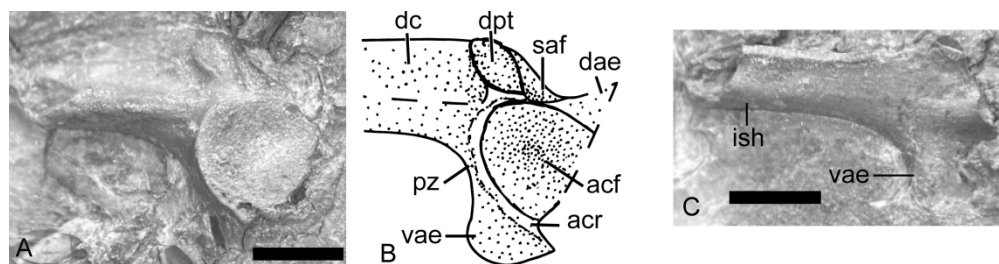
Pectoral elements of IGR 144547. **A**, close-up on the right pectoral region of IGR 144547 on M1, **B**, interpretative drawing of the same region and **C**, reconstruction of the pectoral girdle in ventral view. Light gray area represents the glenoid region. . **Abbreviations:** **cl**, clavicle; **co**, coracoid; **glf**, glenoid fossa?; **hu**, humerus; **omst?**, putative omosternum; **par**, pars acromialis; **pecd**, processus epicoracoidalis; **pgl**, pars glenoidalis; **prgl**, processus glenoidalis; **sc**, scapula; **st**, sternum. Scale bar is 5 mm.

122x106mm (600 x 600 DPI)



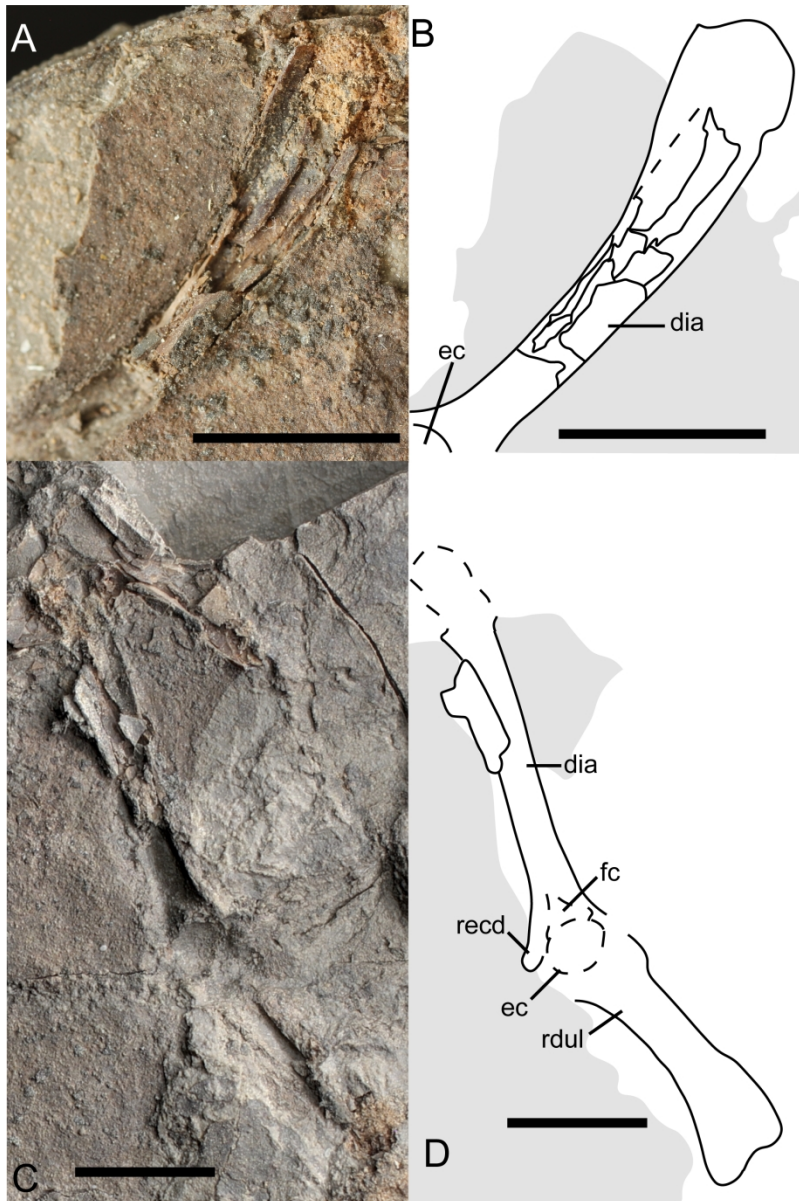
Ilium of IGR144547. **A**, acetabular region of the left ilium exposed in lateral view on M2, **B**, proposed reconstruction of the acetabular region of the left ilium in lateral view and **C**, right ilium in exposed in medial view on M2. Scale bars represent 2 mm. **Abbreviations:** **acf**, acetabular fossa; **acr**, acetabular rim; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **ish**, ilial shaft; **pzf**, preacetabular zone; **saf**, supraacetabular fossa; **vae**, ventral acetabular expansion.

181x46mm (600 x 600 DPI)



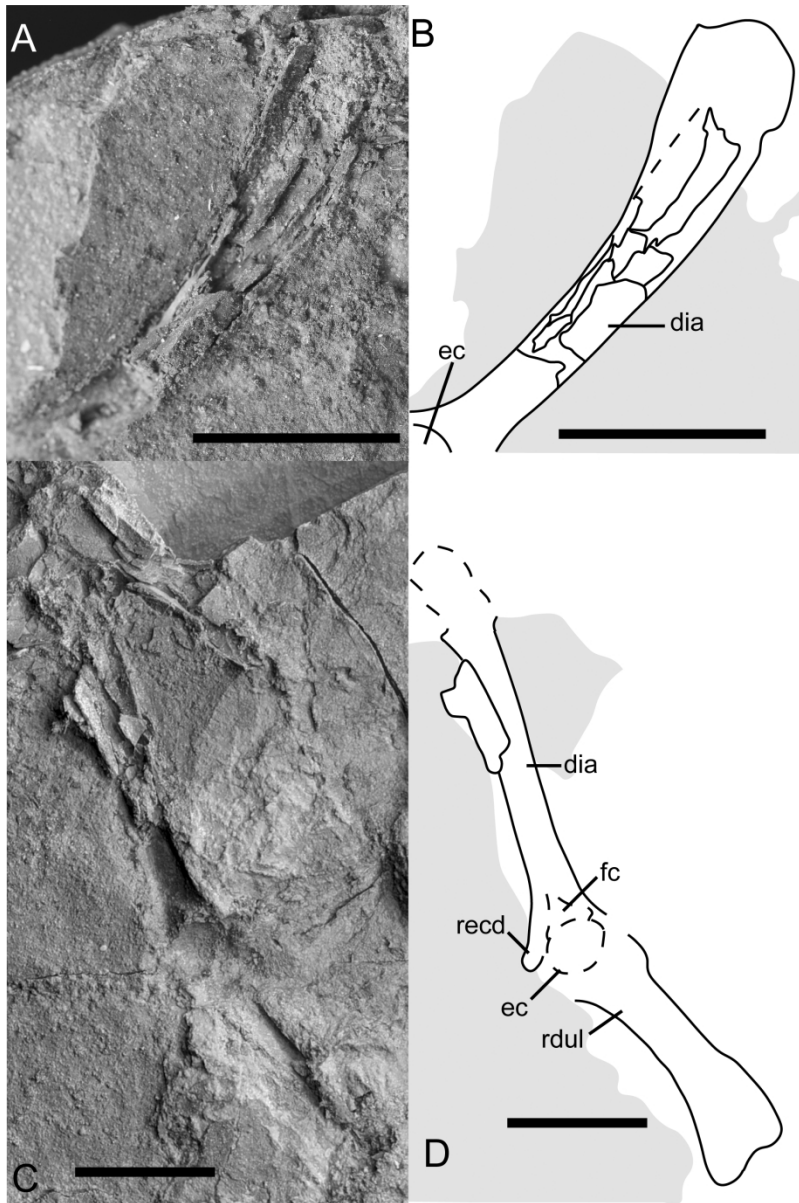
Ilium of IGR144547. **A**, acetabular region of the left ilium exposed in lateral view on M2, **B**, proposed reconstruction of the acetabular region of the left ilium in lateral view and **C**, right ilium in exposed in medial view on M2. Scale bars represent 2 mm. **Abbreviations:** **acf**, acetabular fossa; **acr**, acetabular rim; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **ish**, ilial shaft; **pzt**, preacetabular zone; **saf**, supraacetabular fossa; **vae**, ventral acetabular expansion.

181x46mm (600 x 600 DPI)



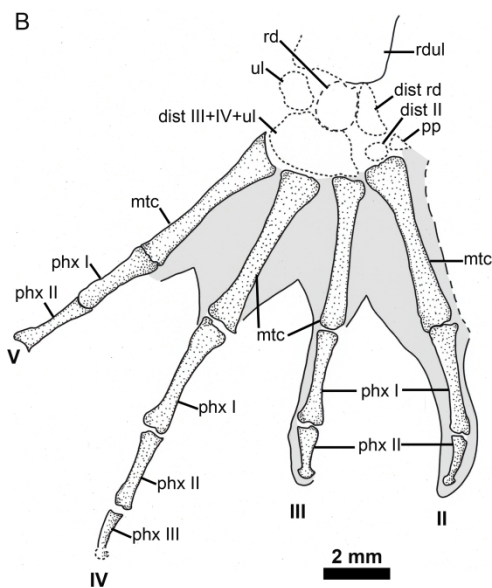
45 Forelimbs of IG144547. **A**, left humerus on M1, **B**, interpretative drawing of the same humerus, **C**, right
46 forelimb on M1 and **D**, interpretive drawing of the same forelimb. Light gray area represents skin
47 impressions, scale bars represent 5 mm. **Abbreviations:** **ec**, eminetia capitata; **dia**, diaphysis; **fc**, fossa
48 cubitalis; **hb**, humeral ball; **raf**, radiale articular facet ; **recd**, epicondylus radialis.

49 88x132mm (600 x 600 DPI)



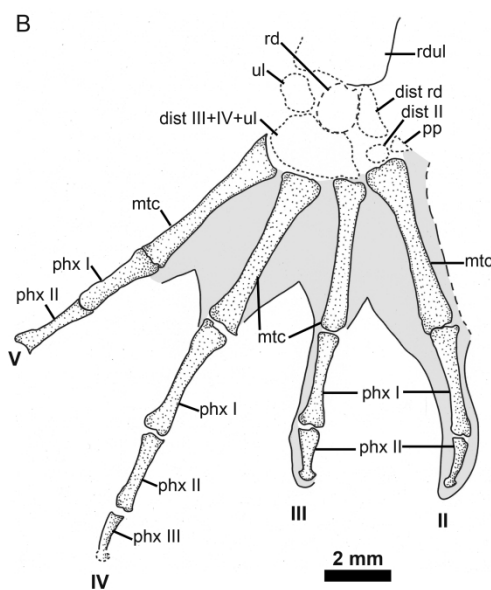
45 Forelimbs of IG144547. **A**, left humerus on M1, **B**, interpretative drawing of the same humerus, **C**, right
46 forelimb on M1 and **D**, interpretive drawing of the same forelimb. Light gray area represents skin
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48 cubitalis; **hb**, humeral ball; **raf**, radiale articular facet ; **recd**, epicondylus radialis.

49 88x132mm (600 x 600 DPI)



45 Hand of IGR 144547. **A**, left hand on M1 and **B**, interpretative drawing of the same hand. Light gray areas
46 represent skin impressions of the digits, scale bar represents 2 mm. **Abbreviations:** **dis rd**, distal radiale;
47 **dist ul**, distal ulnare; **dist II**, distal carpale II; **dist III**, distal carpale III; **dist IV**, distal carpale IV; **mtc**,
48 metacarpal; **phx I, II, III**, phalanx I, II, III; **pp**, prepollex; **rd**, radiale; **rdul**, radioulna; **ul**, ulnare.

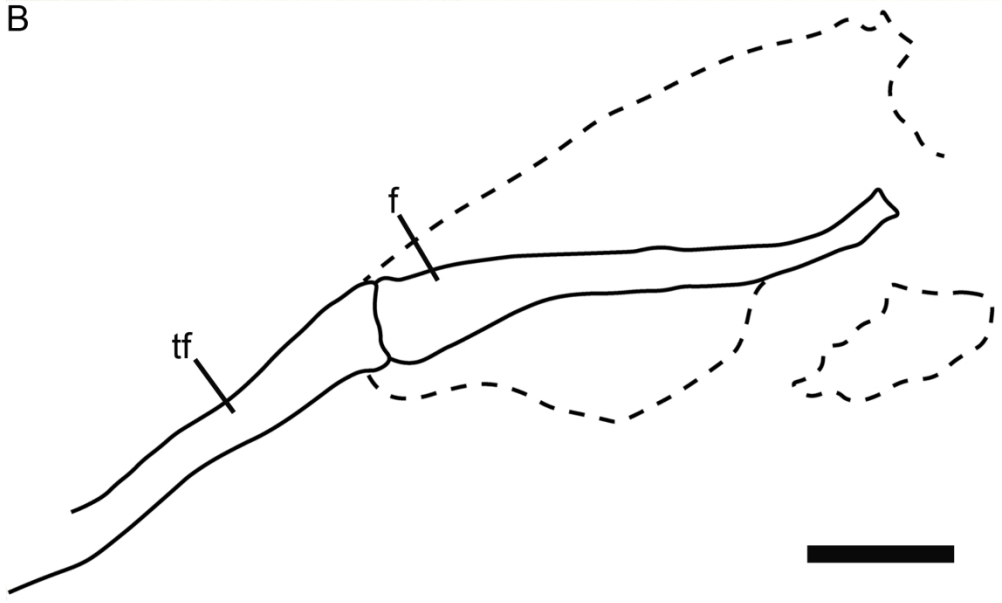
49 88x216mm (600 x 600 DPI)



44
45 Hand of IGR 144547. **A**, left hand on M1 and **B**, interpretative drawing of the same hand. Light gray areas
46 represent skin impressions of the digits, scale bar represents 2 mm. **Abbreviations:** **dis rd**, distal radiale;
47 **dist ul**, distal ulnare; **dist II**, distal carpale II; **dist III**, distal carpale III; **dist IV**, distal carpale IV; **mtc**,
48 metacarpal; **phx I, II, III**, phalanx I, II, III; **pp**, prepollex; **rd**, radiale; **rdul**, radioulna; **ul**, ulnare.

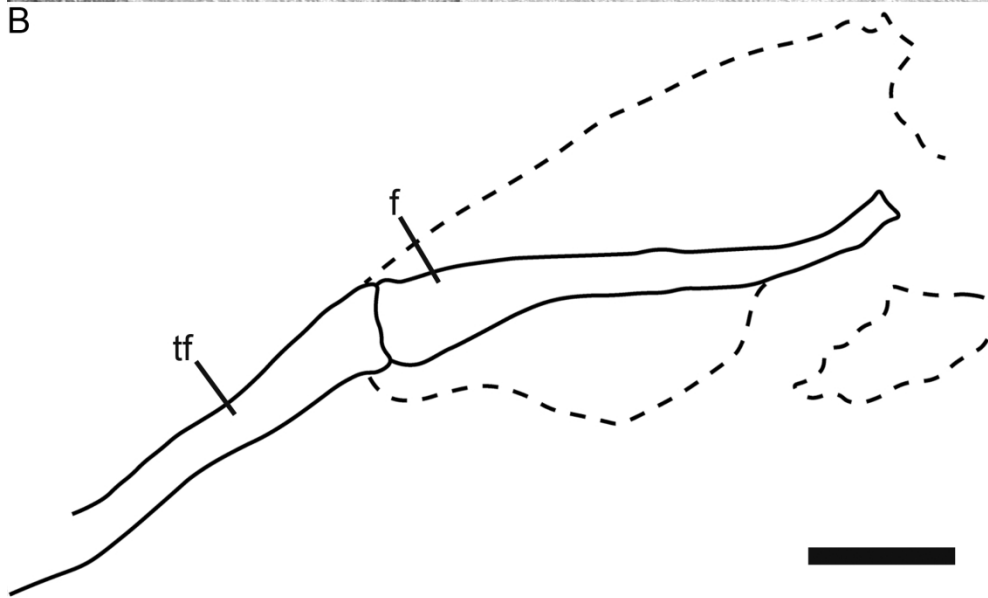
49 88x216mm (600 x 600 DPI)

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Hindlimb of IGR 144547. **A**, right hindlimb on M1 and **B**, interpretative drawing of the same hindlimb. **Abbreviations:** **f**, femur; **tf**, tibiofibula. Dotted lines delimit skin impressions, scale bar is 5 mm.

88x107mm (600 x 600 DPI)

**B**

Hindlimb of IGR 144547. **A**, right hindlimb on M1 and **B**, interpretative drawing of the same hindlimb. **Abbreviations:** **f**, femur; **tf**, tibiofibula. Dotted lines delimit skin impressions, scale bar is 5 mm.

88x107mm (600 x 600 DPI)

Journal of Vertebrate Paleontology

Supplementary Data 1

The oldest articulated ranid from Europe: A *Pelophylax* specimen from the earliest Oligocene
of Chartres-de -Bretagne (NW France)

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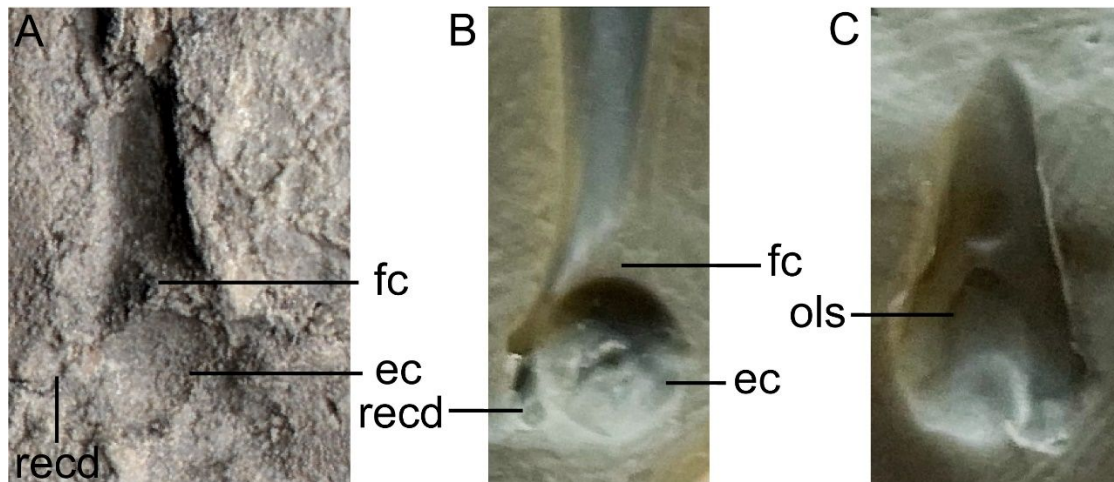


FIGURE S1. Comparison between the imprint of the humerus of IGR 144547 and the humerus of *Pelophylax kl. esculentus*. **A**, imprint of a humerus of IGR 144547 on M1, **B**, imprint of a humerus of *P. kl. esculentus* in ventral view and **C**, imprint of the same humerus in dorsal view. Abbreviations: **ec**, eminentia capitata; **fc**, fossa cubitalis; **ols**, oleocranon scar; **recd**, epicondylus radialis.