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Acynodon adriaticus from Villaggio del Pescatore (Campanian of Italy): anatomical
and chronostratigraphic integration improves phylogenetic resolution in
Hylaeochampsidae (Eusuchia)

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Crocodylomorpha; Systematics; Bayesian; Maximum Parsimony; Cretaceous; Tethys;

ABSTRACT

The hylaeochampsid crocodylomorph *Acynodon adriaticus*, from the uppermost Cretaceous ‘Villaggio del Pescatore’ site, belongs to an early diverging lineage in Eusuchia. Here an additional specimen, MCSNT 57031, is osteologically and osteohistologically described in detail. After integrating this morphological information together with the recent chronostratigraphic recalibration of the site to the lower–middle Campanian, the tip-dated Bayesian phylogenetic analysis recovers this taxon in a monophyletic clade with the Spanish *Acynodon iberoccitanus*. Conflicting results from the maximum parsimony analyses and discussion on the intraspecific variability between the specimens assigned to *A. adriaticus* highlights the need for a detailed morphological description and integration with an updated phylogenetic scaffold, in order to resolve the monophyly of the genus *Acynodon* and the relationships of these branch of early diverging eusuchians. The curious discrepancy between morpho- and osteo-skeletal maturity suggest unique ecomorphological adaptations in this Campanian crocodylomorph.

1. Introduction

The Villaggio del Pescatore Lagerstätte (VdP hereafter), located in the municipality of Duino-Aurisina, Trieste (NE Italy), is a world-renown paleontological site due to its well-preserved Cretaceous vertebrate remains, standing out in the European palaeontological landscape (Chiarenza et al., 2021). In addition to the famous hadrosauroid *Tethyshadros insularis* (Dalla Vecchia, 2009; Chiarenza et al., 2021), remains of the small hylaeochampsid crocodylomorph *Acynodon adriaticus* were described from this site (Delfino et al., 2008a). *Acynodon* exhibits an overall bizarre morphology in comparison to other eusuchians, including a brevirostrine cranial condition: the skull is broadly similar to that of small alligatoroids (Brochu, 2010) although with larger and ‘molariform’ dentition. Given the bizarre morphology, fully reflective with the peak ecomorphological variation recently reported for Cretaceous crocodylomorphs by Stubbs et al. (2021), a stable phylogenetic placement of *Acynodon* in Eusuchia has been problematic (Rio and Mannion, 2021). *Acynodon* was previously considered as an example of ‘archaic’ alligatoroid, one of the oldest and most primitive representatives of the entire Globidonta (Santonian–Campanian) (Buscalioni et al., 1997; Brochu, 2003; Martin, 2007; Brochu, 1999, 2001, 2003; Delfino et al., 2008a; Delfino et al., 2008b). However, recent phylogenetic analyses place this group outside Crocodylia in the clade Hylaeochampsidae, with conflicting results regarding the monophyly of the genus (Brochu, 2011, 2012; Brochu et al., 2012; Jouve et al., 2019; Martin et al., 2014, 2016; Ristevski et al., 2020; Blanco, 2021). *Acynodon* includes three known species: *A. adriaticus*, only known from the VdP site in Italy, *A. iberoccitanus*, with referred material from Spain, southern France and Romania (with remains from these latter two countries represented by multiple, fairly complete crania), and *A. lopezi* based on isolated teeth found in Spain (Buscalioni et al. 1997). Other occurrences of this genus come from several European locations (Blanco et al., 2020; Delfino et al., 2008a; Puértolas-Pascual et al., 2020): Muthmannsdorf (Austria), La Cabaña in Asturias (Spain), Chera (Spain), Els Nerets (Spain), Quintanilla del Coco (Spain), Laño (Spain), Arén (Spain), Massecaps (France), Quarante (France), Fox-Ampoux (France), Hațeg Basin (Romania) and VdP (Italy). Only *A. adriaticus* and *A. iberoccitanus* have been analysed

65 in a phylogenetic context (being the material referred to *A. lopezi* not informative enough). In a
66 context of phylogenetic uncertainty (among others, Blanco, 2021; Martin et al., 2020; Narváez et al.,
67 2016; Rio and Mannion, 2021), the revised chronostratigraphy of the VdP site (Chiarenza et al.,
68 2021), type and only locality of *A. adriaticus*, offers a unique opportunity to test the phylogenetic
69 implications of the temporal recalibration of this fossil bearing site.

70 This study focuses on *Acynodon adriaticus* with a comprehensive analysis of all skeletal
71 remains ascribed to this taxon from the VdP site, discussing its age and taphonomy. Specifically, a
72 nicely preserved individual, MCSNT 57031 (Fig. 1), assigned to the genus *Acynodon* by Delfino and
73 Buffetaut (2006), conservatively considered as *Crocodylia* indet. by Delfino et al. (2008) due to the
74 lack of definitive autapomorphies, is herein extensively described. Here we parsimoniously refer
75 MCSNT 57031 to *A. adriaticus* by providing an accurate anatomical description of the specimen,
76 followed by osteohistological analysis and consideration of the palaeobiology of *A. adriaticus*. We
77 furthermore integrate these new anatomical and chronostratigraphic information in a combined
78 framework to improve the resolution of the genus *Acynodon* (the less inclusive clade including
79 *Acynodon adriaticus* and *A. iberoccitanus*).

80

81 **2. Institutional abbreviations**

82 MCSNT, Museo Civico di Storia Naturale in Trieste, Italy

83 MGGC, Museo Geologico Giovanni Capellini in Bologna, Italy

84

85 **3. Methods**

86 *3.1 Specimens*

87 All crocodilian remains from the VdP were collected between 1996 and 1999 (*see* Table 1)
88 and are currently housed at the Museo Civico di Storia Naturale in Trieste (MCSNT). Specimens
89 were prepared with a chemical dissolution technique consisting in selective matrix removal with

multiple formic acid baths. For this study, measurements and photographs were obtained *ex-novo* and compared with available prior measurements used in other publications (e.g. Delfino et al., 2008). The anatomical illustrations were preliminarily made using a microscope with integrated *camera lucida* (Leica DM 2500 P petrographic microscope with a ProgRes CFscan camera adapter), subsequently assembled with Adobe Photoshop 2020. Thin sections of rib fragments and dorsal osteoderms from MCSNT 57031 were prepared for osteohistological study and are housed in Bologna (access number MGGC 22304, 22305, 22306).

3.1.1 New specimens assigned to Acynodon adriaticus and discussed in this study

MCSNT 57031: ventrally exposed, articulated, sub-complete specimen (main focus of this study; Fig. 1); Initially described by Delfino and Buffetaut, 2006.

MCSNT 21.S239-1.0.22 (57248a): six well-preserved osteoderms, three of them in partial overlap (Fig. 2A). The larger ones, measured at their longer axis, are 22.8 mm, 24.5 mm, and 27 mm long respectively. These osteoderms show two low keels, one straight and the other concave and larger, comparable to the condition described in the paratype by Delfino et al. (2008).

MCSNT 57245: an isolated, well-preserved robust crocodilian rib laying on the flat surface of a larger matrix slab with other unidentified bone fragments. The tuberculum is shorter than the capitulum and has a larger articular surface. The rib progressively thickens distally and has a wide costal cartilage articular surface (Fig. 2B).

MCSNT 21.S239-1.0.22 (57248b): three small osteoderms and two robust ribs in association, both showing shorter and stouter tubercula than capitula, with wider articular surfaces (Fig. 2C). The shorter rib measures 46.7 mm in length and lacks its distalmost portion; the longer one measures 57.2 mm, appears to be complete and gradually thickens at its distal end, revealing a large costal articular surface.

115 3.1.2 *Specimens assigned to Crocodylomorpha indet.*

116 **MCSNT 57033**: a ~4 cm long unidentified small reptile bone, possibly a rib, exposing its sagittal
117 section on the surface of a small laminite fragment (Fig. S1A).

118 **MCSNT 57035**: a ~5 cm long bone element exposed on a calcareous slab with an ornamented surface,
119 here identified as a ventrally exposed crocodilian mandibular symphysis (Fig. S1B).

120 **MCSNT 57036**: a ~2 cm anteroposteriorly long vertebra, possibly a fragmented cervical, three-
121 dimensionally prepared out of the matrix (Fig. S1C).

122 **MCSNT 57037**: an almost unrecognizable smooth bone fragment hardly visible on a small matrix
123 slab associated with other indeterminate vertebrate fossil material, previously tentatively identified
124 as a fragmented ventral osteodermal surface (Fig. S1D).

125

126 3.2 *Stratigraphy and age*

127 The VdP site is located near a dismissed quarry in the municipality of Duino Aurisina, Trieste,
128 Italy (Fig. 3). The overall geological setting of the site and surrounding areas, including key
129 information on facies analysis, sedimentology, paleontology, and isotope-based stratigraphy, has
130 been described in detail in the literature (Tarlao et al., 1993, 1995; Attura, 1999; Palci, 2003; Dalla
131 Vecchia, 2008, 2009; Chiarenza et al., 2021; Consorti et al., 2021), with a recent redescription and
132 re-evaluation documented in Chiarenza et al. (2021). The VdP deposits originated at the northern
133 margin of the Adriatic Carbonate Platform system (AdCP): in the area, the Upper Cretaceous to
134 lowermost Paleocene interval is represented by two informal units, the Aurisina formation and the
135 Cretaceous/Palaeogene (K/Pg) bearing Liburnian formation (or by their equivalent synonyms along
136 the adjacent Slovenian units [see Jurkovšek et al., 2016]). From a sedimentological perspective, the
137 site is included in the Aurisina formation and is represented by sharp *facies* variations from open
138 marine, shallow-water limestones to organic-rich rhythmites, which interbed with breccias that
139 accumulated as underwater bodies by subaqueous, density-driven, sedimentary flows. Each
140 identifiable lamina consists of micro-couplets made by a millimetric-thick, dark colored, organic-rich

141 lamina superimposed to a light lamina made of carbonate mud. Given an overall thickness of ~10 m
142 and a thickness of each couplet ranging from 1 to 2.5 cm, the '*laminites*' lens was estimated to
143 represent a time interval of 4–10 kyrs (Arbulla et al., 2006). However, recent surveys at the site have
144 documented how rhythmites and breccia bodies are folded by syn-depositional slumping and
145 deformed by wet-sediment normal faults, thus largely reducing the estimated depositional length to
146 few thousand kyrs (Chiarenza et al., 2021). Relevant to our comprehension of the genus *Acynodon*, a
147 recent revision of the fossil content of the site has restricted the dating of the fossil interval to the
148 lower-middle Campanian (81.5–80.5 Ma) based on the vertical distribution of the benthic
149 foraminifera assemblage and calibrated with strontium isotopes stratigraphy (Frijia et al., 2015;
150 Chiarenza et al., 2021). From a stratigraphic perspective, specimen MCSNT 57031 represents the
151 lowermost occurrence of *A. adriaticus* at the site, being collected at the onset of the organic-rich
152 rhythmites. All other elements discussed in this paper are confined in a very restricted interval made
153 of a single, syn-depositional, slumped set of rhythmites. Remarkably, this interval also includes
154 crustaceans, fish, coprolites, and the fully articulated specimens of the hadrosauroid dinosaur
155 *Tethyshadros insularis* (see Chiarenza et al., 2021). Taphonomic and sedimentological parameters
156 support a rapid genetic process for this interval, thus hinting to the presence of a single eusuchian
157 taxon at the site.

158

159 3.3 Taphonomy

160 Slumped rhythmites at the VdP raise crucial questions concerning the taphonomy of the site,
161 including the preservation of vertebrate remains (i.e.: dinosaurs, pterosaurs, crocodiles, fish) in
162 dysoxic-anoxic bottom waters in marginal-marine settings. Prior to this study, a complete survey of
163 crocodylomorph material from the VdP site was never addressed, and very little was known on the
164 precise stratigraphic occurrence of crocodilian remains within the relatively small fossil-bearing area.

165 Therefore, for this study, a comprehensive survey of fossil material housed at the MCSNT was
166 undertaken, coupled with a detailed analysis of all available quarry reports and associated
167 photographic material of extractive campaigns between 1996 and 2020 (Dalla Vecchia, 1999; F.
168 Bacchia, pers. comm. 2022). In addition, we used Unmanned Aerial Systems (UAS) and Vehicles
169 (UAV) and related processing technologies to produce the most accurate and up-to-date quarry map
170 (Fig. 3A-C) for the VdP site, a framework into which geological and paleontological data could be
171 precisely included (Fig. 3D). Using these elements we produced an up-to-date list of crocodilian
172 specimens (*see 3.1*) and were able to relocate each specimen into the stratigraphic setting of the main
173 quarry area. Our data indicate that the occurrence of crocodilian remains is limited to very precise
174 stratigraphic intervals, each represented by a single, slumped, approximately 1.5 meter thick, set of
175 laminae (Fig. 3D). These intervals contain the vast majority of fossil remains from the site. Specimen
176 MCSNT 57031 is the lowermost occurrence of crocodilians at the site, found in the proximity of an
177 articulated but poorly preserved individual of *Tethyshadros insularis* (SC 57026). The type specimen
178 of *A. adriaticus* (MCSNT 57248) and most isolated crocodilian elements were collected from the
179 same slump that preserved the type specimen of *T. insularis* (SC 57021) and other nicely preserved
180 and articulated dinosaur remains (SC 57022). Finally, a single isolated bone assigned to an
181 undetermined crocodilian was collected from a third slump in the proximity of a fully articulated
182 skeleton of *T. insularis* (SC 57247) and to other, still *in situ*, articulated dinosaur remains.
183 Remarkably, at the VdP site, large and fully articulated vertebrates are found in association with
184 recurrent fish and crustacean remains: this, coupled with the documented sharp facies variation (open
185 marine limestone to slumped, organic-rich rhythmites interbedded with breccias), rise questions on
186 the depositional processes that led large terrestrial taxa and minute, both freshwater and marine
187 species, to be rapidly buried into anoxic, shallow marine settings.

188

189 3.4 Osteohistological sampling

190 We sampled the 6th dorsal rib and a loose osteoderm fragment (presumably cervical) for
191 osteohistological analyses, in order to investigate the ontogenetic stage of MCSNT 57031. Although
192 long bones have been shown to have a better-preserved growth record, and, therefore, to be more
193 appropriate for quantitative extrapolation of growth strategies and life history, these elements were
194 inaccessible in our sample for curatorial reasons. Furthermore, dorsal ribs and osteoderms have been
195 demonstrated to be excellent skeletal elements for an effective and reliable ontogenetic assessment
196 across tetrapods, and, more specifically, for non-avian archosaurs (Erickson and Brochu, 1999; de
197 Ricqlès et al., 2003, 2003; Parker et al., 2008; Scheyer and Sander, 2009; Witzmann, 2009; Witzmann
198 and Soler-Gijón, 2010; Scheyer and Desojo, 2011; Woodward Ballard et al., 2011; Cerda and Desojo,
199 2011; Taborda et al., 2013; Woodward et al., 2014; Ponce et al., 2017; von Baczko et al., 2019). The
200 thin sections were prepared following the protocol by Chinsamy and Rath (1992), reaching a final
201 thickness of 50–70 microns in the samples that were then analyzed with a Leica DM 2500 P
202 petrographic microscope. Photographs of the thin sections were taken with a ProgRes Cfscan camera.
203 Inference of skeletal maturity follows recently proposed nomenclature by Griffin et al. (2021)

204

205 3.5 Phylogenetic analyses

206 We scored the holotype of *Acynodon adriaticus* (MCSNT 57248) and MCSNT 57031 as
207 independent Operational Taxonomic Units (OTUs) performing a maximum parsimony and time-
208 calibrated Bayesian phylogenetic analyses. We used the phylogenetic data matrix published by
209 Blanco (2021), an update of the dataset from Narváez et al. (2016) and originally published by Brochu
210 and Storrs (2012). This matrix does not include the Spanish hylaechampsid *Unasuchus* (Brinkmann,
211 1992), since the limited amount of material referred to the taxon (and the interpretative drawings
212 reported in the literature) allows a minimal amount of scoring in the Blanco's (2021) matrix.
213 Similarly, the Turkish taxon *Turcosuchus* (Jouve et al., 2019) is based on fragmentary material with
214 limited characters scorable in Blanco (2021). A total of 85 out of 189 characters and 31 out of 189

215 characters were scored for MCSNT 57248 and MCSNT 57031 respectively in Mesquite 3.70
216 (www.mesquiteproject.org), for a total of 109 OTUs (Data S1).

217 Characters were treated as unordered and equally weighted. Maximum Parsimony analyses
218 were computed in TNT 1.5 beta (Goloboff et al., 2008), using a ‘New Technology’ search, with Sect
219 Search, Ratchet, Drift, and Tree Fusing algorithms, and 10 random addition sequences (Chiarenza et
220 al., 2020). A thorough exploration of tree space for obtaining strict consensus and majority rule trees
221 was computed on the trees held in RAM via a ‘Traditional Tree Bisection-Reconstruction (TBR)
222 Branch-Swapping’ method and both Bootstrap and Bremer support was calculated using standard
223 absolute frequencies for 1000 replicates. The analysis recovered 9 trees with best step length score of
224 807. Notably, the use of TBR after the ‘New Technology’ search further explores the tree space
225 ([Barrett et al., 2014](#); [Raven and Maidment, 2018](#)). Notably, while this procedure differs from those
226 described in [Blanco \(2021\)](#), [Brochu \(2011\)](#), [Narváez et al. \(2016\)](#) and [Puértolas-Pascual et al. \(2020\)](#),
227 it generated similar general tree topologies, although with different steps and support values.

228 For the Bayesian analysis, the same nexus file used for the Maximum Parsimony analyses was
229 expanded following the optimization criteria for ‘Morphological Clock Analyses’ (Lee et al., 2014)
230 in MrBayes 3.2.7. OTUs’ age was matched using midpoint age constraints available in Mannion et
231 al., (2019) and updated following recent chronostratigraphic updates on fossil crocodilian bearing
232 formations (e.g. Chiarenza et al., 2021). Age values and tips in tree were paired using the function
233 ‘phylo_check’ from the package ‘palaeoverse’ (Jones et al., 2023) in R version 4.1.3. The MrBayes
234 script encoded the use of a gamma parameter for modelling uniform rate variation across traits, an
235 uncorrelated relaxed clock for modelling rate variation across branches was used instead (igr) of
236 autocorrelated, relaxed clock or a strict clock following Lee et al., (2014). The convergence of all
237 independent runs, together with stationarity were assessed using TRACER v.1.7.1, assuming
238 significance of effective sample size (ESS) for each parameter when ≥ 200 (Rambaut et al., 2018).
239 MrBayes script is included as Data S2. Tree topologies were explored in FigTree v1.4.4. Time-
240 calibrated Bayesian tree was plotted for showing stratigraphic ranges of the tips using the R package

241 ‘strap’ by Bell and Lloyd (2015), which was also used to calculate values of stratigraphic congruence
242 of different tree outputs compared to randomly generated trees using the Stratigraphic Consistency
243 Index (SCI).

244

245 **4. Results**

246 *4.1. Systematic Paleontology*

247 **Crocodylomorpha** Hay, 1930 *sensu* Nesbitt, 2011

248 **Neosuchia** Benton and Clark, 1988

249 **Eusuchia** Huxley, 1875 *sensu* Brochu, 2003

250 **Hylaeochampsidae** Andrews, 1913

251 *Acynodon* Buscalioni *et al.* 1997

252 *Acynodon adriaticus* Delfino *et al.* 2008

253

254 *4.2 Description of MCSNT 57031*

255 **Skull**

256 The ventrally exposed cranium (Fig. 4) is roughly 15 cm long, only partially preserved, and
257 obliterated by the slab matrix on its dorsal margin. Based on visible elements (Fig. 4B) it appears to
258 be roughly 80% of the holotype in anteroposterior size (Fig. 5). No maxillary nor premaxillary teeth
259 are visible. Part of the rostral region, although fragmentary, is preserved and corresponds to the palatal
260 portion of the right maxilla (Fig. 4). Very little is preserved of the posterior region of the skull: a
261 wide, subrectangular articular surface (Fig. 4) may represents the ventral portion of the quadrate
262 condyle. However, given the fragmentary preservation, such element may also be the articular glenoid
263 fossa, exposed dorsally due to a rotation of 180°.

264 The distal section of the right dentary is three-dimensionally preserved, exhibiting clear
265 ornamentations on the labial surface arranged as longitudinal grooves (Fig. 6). The suture with the

splénial is located on a deep groove on the ventromedial surface of this distal portion of the mandibular ramus (Fig. 4B). The splénial is well preserved, showing three aligned foramina (Fig. 6). The slab margin is obscured by a protective layer of resin, thus precluding additional observations on the mandible and skull elements. The angular, surangular and articular bones are heavily fragmented and hardly distinguishable. The right retroarticular process is partially damaged but better preserved than the left one, at least in its general outline (Fig. 4). From the posterior end of the retroarticular process to the preserved distal end of the dentary, the right mandibular ramus is 132 mm long and around 10 mm thick dorsoventrally in its distal, less deformed section. The left mandible is represented only by small, hardly identifiable proximal fragments, most likely the angular and articular. One fragment preserves the ornamented surface texture (Fig. 6), with the relatively large pits morphologically similar to those observed on the angular and surangular surfaces of the holotype.

Axial skeleton

The preserved cervical vertebrae are lateroventrally exposed on their left side (Fig. 7): centra show a markedly procoelic condition. Five articulated middle cervical vertebrae, complete with centra, neural arches and cervical ribs are identified and tentatively interpreted as cervicals 3–7, with an anterior neural spine and a few overlapping or nearby fragments corresponding to cervical c2 or c1+c2, and a posteriorly disarticulated tall neural spine probably referable to c8. Given the estimated number of eight total cervical vertebrae in the holotype (Delfino *et al.* 2008), the series could be partially overlapped with the holotypic cervical one. Centra are twice anteroposteriorly long as dorsoventrally high. Centra are mediolaterally wide with relatively short and lateroventrally directed parapophyses. The putative c2 centrum is partially lateroventrally rotated, exposing either a convex anterior articular facet, a ventral tuberosity or a blunt hypapophysis. At least 7 cervical ribs are exposed on the surface of the slab, with three well preserved left ribs associated with cervicals 3–5. Ribs have short tubercula and capitula, and they are hatchet-shaped in overall morphology, with a smooth surface and with curved and relatively thick inferior margins. Neural arches are apparently

not articulated to each other in cervicals 4–6, and in c5 and c6 they are clearly unfused from their centra, exhibiting open neurocentral sutures (Fig. 7). Both zygapophyses are clearly recognizable in c3, a single c2 postzygapophysis is still articulated to c3 and traces of a prezygapophysis are potentially visible in c4. The c8 neural spine is clearly detached from its arch. Overall, the morphology of the more anterior neural spines is flatter and more anteroposteriorly elongated, gradually becoming proportionally taller and narrower in c5 and c6, with the supposed c8 spine being the tallest of the preserved series, bearing also a distal anteroposterior expansion. An additional vertebral centrum, possibly one of the first dorsal vertebrae, is partially preserved posteriorly to the last cervical neural spine, apparently rotated by almost 180°.

Ribs

Assessing the exact number of preserved ribs is challenging due to the fragmentary nature of the specimen. At least three partial ribs can be recognized on the left side of the animal, located between the bend of the cervical series and the dorsal patch of osteoderms, whereas on the right side, at least nine ribs or partial ribs are preserved (Fig. 8). Their morphology is characterized by a wide anteroposterior expansion along their diaphyses, therefore presumably appearing as a flattened oval shape or eccentrically D-shaped section. The distal epiphysis is preserved in some ribs, appearing to be blunter and more rectangular in their outline in longer posterior ribs than in the anterior ones, consistent with the attachment for cartilage portions connecting the sternal ribs or gastralium. At least three small, elongated structures overlapping with the unidentified clusters of dark bone portions in the abdominal region of the specimen might represent small fragments of gastralium or other sternal ribs (Fig. 8). The dark amorphous mass that partially engulfs them, already described by Delfino (2008) as a “uniformly vermicular surface”, most likely is here identifiable as a cluster of small lateral or ventral osteoderms exposed on their visceral surface, heavily overlapped and crushed together.

Pectoral girdle

318 The right coracoid is preserved close to the right humerus and partially overlapped by a
319 narrow-elongated bone, here interpreted as the interclavicle (Fig. 9). The margin of its enlarged distal
320 end appears to be slightly damaged and its proximalmost portion not properly visible. The left
321 coracoid is either not preserved or represented by some fragments located anteriorly to the left
322 humerus. The interclavicle has an enlarged, weakly plate-shaped anterior end. Toward its posterior
323 margin, a short longitudinal keel is visible (Fig. 9). A partially exposed element overlapped by the
324 right coracoid most probably represents the ventrally exposed right scapula. Its shape is consistent
325 with the holotypic right scapula, with subparallel dorsal and ventral margin of the distal portion, but
326 the bad preservation and partial damage in this area prevents a proper description of its morphology
327 at its distalmost process. Given the relevance and direct phylogenetic implication of the scapular
328 blade morphology in crocodilians (*see Brochu and Storrs, 2012*), we prefer not to define (and score)
329 the morphology of this anatomical trait. The heavily damaged bone between the right scapula and the
330 left humerus can be tentatively referred as the left scapula. The more anterior position of the entire
331 pectoral girdle in the fossil, in relation to the ribs and axial skeleton, suggests an anteriorward slippage
332 of the forelimb-girdle complex from their *in vivo* position.

333

334 **Right forelimb**

335 Except for a few elements of the manus, the entire right forelimb is exquisitely preserved,
336 although slightly disarticulated. The humerus is ventrally exposed and displays a prominent concave
337 deltopectoral crest with a well-defined apex (Figs. 10, 11), becoming a low longitudinal crest in its
338 proximoventral portion; the deltopectoral crest runs almost up to the distal epiphysis, with a rough
339 apical surface texture reminiscing of a fibrous surface. The proximal epiphysis is not sharply rotated
340 relatively to the distal epiphysis (as described in character 303 by Rio and Mannion 2021). A
341 relatively large, saddle-like surface lies between the well-developed radial and ulnar condyles, the
342 latter being larger and more laterally prominent. The articular surface of the distal epiphysis exhibits

343 a rough surface, indicating the exact location of the articular cartilage. An interesting detail is the
344 osteoporotic-like bone tissue on the distal condyles (Fig. 12).

345 The right radius and ulna are robust, medially exposed, parallel to each other (slightly offset
346 from their anatomical position) and near to the distal end of the humerus. They appear to be still
347 articulated at their distal end and only slightly disarticulated proximally. The olecranon process of
348 the ulna is approximately round, the proximal epiphysis is the thickest portion of the bone, the
349 diaphysis gradually becomes thinner towards the distal epiphysis, which is probably missing a small
350 portion, or it is not completely ossified. The radius is distally as thick as the ulna, with well developed,
351 wide epiphysis. The epiphyses of both the radius and ulna show a similar osteoporotic bone tissue as
352 in the distal humerus (Fig. 11).

353 The carpus seems to be complete, and all its elements are lying in anatomical position. The
354 large radiale and ulnare are well preserved with the epiphyseal surfaces showing osteoporotic-like
355 conditions as in the humerus, radius, and ulna (Fig. 12). A carpal element distal to the pisiform seem
356 to be partially fragmented into two separate elements. While the fragmentary nature of these –
357 partially still embedded in matrix – elements prevent a confident identification, one of this may
358 represent the central carpal [*centrale sensu Gregorovičová et al., (2018)*; Fig. 12B]. A few bone
359 fragments scattered between the zeugopodium and the carpus may be coming from the anterior
360 proximal portion of the two larger carpals or from the anterior distal end of the radius and/or ulna.
361 The matrix obscures most portions of these elements. Three metacarpals are well preserved,
362 tentatively identifiable as metacarpals I, II and III due to their relative arrangement and position to
363 the carpus. Other two bone elements, possibly the other two metacarpals or phalanges, can be found
364 below these elements. All metacarpals show an even more pronounced epiphyseal bone porosity and
365 irregular surface than every previously mentioned element (Fig. 12). Five phalanges and two closely
366 placed unguals are preserved. The smaller ungual phalanx is found against the metacarpal III, whereas
367 the larger one, relatively big in comparison to the overall forelimb proportions, is characterized by a
368 deep lateral groove, with a short flexor tubercle and pronounced dorsal and ventral process.

369 In adult crocodylians the carpus has a highly reduced number of ossified elements, with living
370 representatives (e.g. Alligatoridae) having four elements [*Alligator mississippiensis*, (Müller and
371 Alberch, 1990), *Caiman yacare* (Lima *et al.*, 2011), *Melanosuchus niger* (Vieira *et al.*, 2018)].
372 *Acynodon* is therefore expected to reflect a similar condition: in this specimen however, although four
373 major elements are clearly identifiable (Figs. 10, 12), a higher number may be present but obscured
374 by and preservation of these elements.

375

376 **Left forelimb**

377 Of the left forelimb, the humerus, radius, ulna, the ulnare, and four (possibly five) manual
378 elements are preserved (Fig. 13). The humerus, radius and ulna are badly fragmented, and the bone
379 surface in all of them is not as well preserved as in the right forelimb. The humerus is broken halfway
380 along its proximodistal length. The radius and ulna are overlapping along their proximodistal length
381 and appear broken at their diaphysis. What seems to be a heavily damaged radiale partially overlaps
382 the distal ulnar epiphysis. Up to five other elements are located distally to the radiale including two
383 possible metacarpals or a metacarpal and a carpal. Given their morphology and size, they are here
384 interpreted here as an ulnar carpal, two metacarpals and two phalanges (Fig. 13).

385

386 **Osteoderms**

387 Many osteoderms are preserved in MCSNT 57031 (Fig. 1). A few oval, cervical osteoderms
388 are preserved in ventral view around the cervical area. The largest and most articulated osteoderm
389 cluster is located dorsally to the rib cage. Despite the overall orientation of the specimen (lying on its
390 ventral side), the entire osteoderm series is dorsally exposed so that the dorsal left rows are visible.
391 Single osteoderms of this area are partially overlapping their neighboring elements on their right and
392 posterior end. This arrangement suggests a 180° rotation of the entire dorsal and lateral osteoderm
393 armor. Ventrally to the anterior elements, however, a smooth surface may in fact represent the
394 somewhat smoother ventral surface of the osteoderms from the row of the right side. Following this

395 interpretation, the whole paravertebral shield would have been affected by a sharp lateral folding
396 along its parasagittal axis. Morphologically, dorsal osteoderms are squared in overall shape,
397 proportionally large mediolaterally and with deep circular pits and grooves surrounded by tall keels
398 on their dorsal surfaces (Fig. 14A). The second anteriormost osteoderm is the best preserved one and
399 displays a radial arrangement of the dorsal ornamentation (Fig. 14B). The majority of other
400 osteoderms exhibit a dorsal tubercular keel running posteriorly and diagonally to the osteoderm
401 quadrangular outline, a feature consistent with the ornamentation of the outer lateral rows of dorsal
402 osteoderms of the paratype MCSNT 57032 described by Delfino *et al.* 2008, although they display a
403 much smoother surface. The previously mentioned dark and smooth mass (Fig. 8) located in the
404 abdominal region of the specimen may represent a second cluster of osteoderms. In this roughly
405 polygonal outline, we recognized two main areas: a dorsal one, characterized by a smooth continuous
406 surface, and a ventral amorphous osteoderm mass, with a rougher pattern vaguely reminiscent of
407 black flakes at its margins.

408

409 4.3 Osteohistology

410 **Dorsal rib (6th)**

411 The cross section of the dorsal rib appears oval in shape (Figure 15A). Trabecular bone is
412 present in the medullary cavity, making the transition from the center of the section to the cortex
413 gradual and characterized by intense remodeling (Figure 15A). The primary bone tissue is composed
414 of lamellar bone (Figure 15B-C). Primary vascularization is very rare and sparse, but present, and is
415 mainly longitudinal in orientation. Large, secondary osteons are present in the inner third of the
416 cortex, obscuring the early growth record. 31 Lines of Arrested Growth (LAGs) are present; annuli
417 are commonly present. An External Fundamental System (EFS) is absent.

418

419 **Osteoderm**

420 The primary bone tissue composing the cortex is constituted by lamellar bone (Figure 15D-
421 E). Primary vascularization is scarce, but present with a longitudinal orientation. Zonation is present
422 in the preserved primary cortex: 15 LAGs can be counted. Cancellous bone, erosional cavities, and
423 haversian systems obscure the majority of the inner cortex, as generally observed in osteoderms
424 among pseudosuchians. The lower number of LAGs recovered in the cortex of the osteoderm in
425 comparison to the count in the dorsal rib is therefore explained by the overprinting of the early growth
426 record by bone remodeling. An EFS is absent, although zonation tends to decrease and the primary
427 vascularization becomes virtually absent towards the outer surface of the osteoderm.

428

429 5. Phylogenetics

430 The phylogenetic relationships of MCSNT 57031 and the holotype of *A. adriaticus* MCSNT
431 57248 were tested with Maximum Parsimony and Bayesian analyses (Fig. 16). The maximum
432 parsimony strict consensus of 9 trees (Fig. 16A, Fig. S2) is 807 steps long, with a Consistency Index
433 of 0.305 and a Retention Index of 0.785. The strict consensus recovers both specimens assigned to *A.*
434 *adriaticus* in a polytomy with *Hylaeochampsia vectiana* and *Iharkutosuchus makadii* [Bremer (decay)
435 Index of DI = 1]. *Acynodon iberoccitanus* is found as sister group of this polytomy (DI = 2).
436 *Shamosuchus djadochtaensis* and *Pietraroiiasuchus ormezzanoi* are found in a polytomy with the
437 *Acynodon* + *Hylaeochampsia* clade (DI = 1). The Majority rule tree (Fig. 16B, Fig. S3) increases
438 resolution in this ‘hylaeochampsid polytomy’ placing both specimens of *A. adriaticus* (bootstrap
439 support of BS = 77%) as sister group of the clade including *H. vectiana* and *I. makadii* (BS = 100%),
440 but breaking the monophyly of the genus *Acynodon*, since the Spanish eponym taxon *A. iberoccitanus*
441 is found as sister taxon of the *Hylaeochampsia* + *A. adriaticus* clade (BS = 100%). According to this
442 result, a synapomorphy of Hylaeochampsidae is the maxilla with a posterior process between the
443 lacrimal and the prefrontal (character 128, state 2 of Brochu and Storrs, 2012). The synapomorphy
444 defining the *Acynodon* + *Hylaeochampsia* clade is the presence of anterodorsally projected anterior

dentary teeth (character 48, state 1 of Brochu and Storrs, 2012). The *Hylaeochampsia* + *A. adriaticus* clade is defined by: a penultimate maxillary alveolus more than twice the diameter of the last maxillary alveolus (character 106, state 1 of Brochu and Storrs, 2012); a prefrontal longer than the lacrimal (character 130, state 1 of Brochu and Storrs, 2012); and a quadrate bearing a prominent, mediolaterally thin crest on its dorsal surface (character 179, state 1 of Brochu and Storrs, 2012). *Acynodon iberoccitanus* is diagnosed in this analysis by the unexposed supraoccipital on the dorsal surface of the skull table (character 160, state 1 of Brochu and Storrs, 2012).

The Bayesian analysis (Fig. 16C; Fig. S4) solves this paraphyletic ambiguity by placing *A. adriaticus* and *A. iberoccitanus* in a monophyletic clade, with a Posterior Probability (PP) value of 80. The genus *Acynodon* is sister taxon of *I. makadii* (PP=60), and both form the sister group of *H. vectiana* (PP=91). This hylaeochampsid clade is sister group (PP=86) of a lineage including *Pietraroiasuchus ormezzanoi* and *Shamosuchus djadochtaensis* (PP=61). The phylogenetic topology found in the Bayesian analysis has as higher stratigraphic congruence ($SCI=0.5-1 > 0.45$; Fig. S5) than the strict consensus ($SCI=0-0.45 > 0.48$; Fig. S6) and the majority rule ($SCI=0.5-1$ vs 0.585; Fig. S7) trees from the maximum parsimony analysis.

460

6. Discussion

6.1 Differences between MCSNT 57031 and *Acynodon adriaticus* holotype MCSNT 57248

Based on overall measurements, MCSNT 57031 is smaller than the holotype MCSNT 57248 (Fig. 17), but single elements show different degree of size disparity between the two specimens. Allometric growth of individual bones is common in crocodylians (Kramer and Medem, 1955; Dodson, 1975; Deeming and Ferguson, 1990), implying that measurements of single bones are inappropriate for precise body size estimations (Brochu, 1996), preventing a further discussion on speculative absolute estimates.

469 From an overall superimposition between the MCSNT 57031 lower jaw outline and the
470 holotype, some differences emerge (Fig. 5). The holotype possesses a ~20% longer mandible
471 compared to MCSNT 57031, suggesting a larger skull in this individual. The right mandibular ramus
472 of MCSNT 57031 measures 123.4 mm in length, although it is distally incomplete. The maximum
473 mediolateral width of the mandible, when considering from the right angular/surangular region to the
474 highly damaged angular fragments of the left hemimandible, measures 98.5 mm. According to
475 Delfino et al. (2008) the holotype skull is 155 mm long from the distal premaxilla to the posterior
476 edge of the quadrate condyles and is 125 mm wide. Unfortunately, no longitudinal measurements of
477 the ventrally exposed mandibular rami are provided in Delfino et al. (2008), but we provide an overall
478 measurement of 165 mm in length. Although incomplete at the symphyseal region, the holotype
479 mandible is roughly 24% longer than in MCSNT 57031. Intraspecific variability in skull proportions
480 was documented in *Acynodon iberoccitanus* specimens ACAP-FX1 and ACAP-FX2 (Martin, 2007).
481 While considering intraspecific variability a possibility, we consider such differences in available
482 *Acynodon adriaticus* specimens as better explained by taphonomical damage and partial bone
483 dislocation.

484 As mentioned above, when compared to the holotype, cervical centra in MCSNT 57031
485 appear proportionally longer and more gracile, most likely due to differential preservation. Delfino
486 et al. (2008) estimated an anteroposterior length of 17 mm for the holotypic c6 centrum. We measured
487 the putative c6 centrum in MCSNT 57031 reporting the same measurement (17.2 mm long), thus
488 comparable in anteroposterior length. In the holotype, the neurocentral sutures of all visible vertebrae
489 are closed (Delfino et al., 2008a), suggesting developmental maturity at the time of death (Brochu,
490 1996). Cervical vertebrae of MCSNT 57031 show detached neural arches from the respective centra
491 along relatively smooth section-like fractures, most probably representing open neurocentral sutures
492 (Fig. 7). Neurocentral sutures in the crocodilian axial skeleton follow a distinct caudal to cranial
493 closure sequence during ontogeny, with the sutures in caudal vertebrae being fully closed in
494 hatchlings, and closure of remaining sutures toward the cranium occurring progressively later.

495 Closure of the cranial-most sutures occurs relatively late in ontogeny and indicates the attainment of
496 morphological maturity (Brochu, 1996). Without histological information, this trait in MCSNT 57031
497 might be interpreted as a signal of developmental immaturity.

498 The bone surface on the epiphysis of long bones and manual elements in MCSNT 57031 is
499 consistently osteoporotic, a condition not documented in the holotype. Similar but not identical traits
500 are often linked to skeletal immaturity in tetrapods. This trait however affects a different region of
501 the bone, and Tumarkin-Deratzian et al. (2006) demonstrated that little to no association was present
502 between bone textures and either body size or skeletal maturity in *Alligator mississippiensis*, possibly
503 due to the extremely plastic environment-induced developmental rates common to most crocodilians.
504 This makes the porosities on MCSNT 57031 a weak immaturity signal if considered alone, although
505 it is still widely used for other archosaurs, particularly of the avian lineage (Bennett, 1993; Carr, 1999;
506 Chiappe and Göhlich, 2010; Chiarenza et al., 2020; Hone et al., 2016; Sampson et al., 1997). In
507 contrast, the osteoarthropathy of unknown etiology reported by Huchzermeyer et al. (2013) in
508 *Crocodylus niloticus* is not correlated to ontogenetic immaturity, and the reported humeral epiphyseal
509 osteolytic lesions are somewhat similar to the condition described for MCSNT 57031. The
510 pathological nature of the epiphyseal porosity discussed here should not be excluded.

511 Although not somatically mature, ontogenetic immaturity (juvenile ontogenetic stage) can be
512 rejected in MCSNT 57031 based on osteohistological results. The amount of remodeling in the inner
513 cortex of the dorsal rib, the high number of LAGs, and the decrease of spacing between them suggest
514 that sexual maturity was probably reached in this individual (Fig. 15). These results contrast with the
515 osteological observations suggesting an immature ontogenetic stage for MCSNT 57031. Although it
516 is currently unclear why such mismatch between these observations is present, previous studies have
517 shown how osteohistological analyses are generally preferable and more reliable than osteological
518 observations (e.g. Griffin et al., 2021). Lack of closure for neurocentral sutures along the axial
519 skeleton and porous epiphyses in the long bones have been previously observed in late ontogenetic
520 stages in aquatic animals, such as marine reptiles: these were described as skeletal paedomorphosis

521 and suggested to be an adaptation to more aquatic ecologies (e.g. Motani et al., 2015; Rieppel, 1989).
522 A paedomorphic overall skeletal morphology due to the potentially bizarre ecomorphology of
523 *Acynodon adriaticus* is a possibility, although more data and observations are necessary to confirm
524 this.

525

526 6.2 Phylogenetic implications of MCSNT 57031 for the phylogeny of *Acynodon*

527 Few morphological characters in MCSNT 57031 improved previous scorings of *A. adriaticus*
528 material in the available character matrix. Character 26 in Brochu and Storrs (2012), related to the
529 scapulocoracoid facet anterior to glenoid fossa and previously unscored in the holotype, is scored
530 here from MCSNT 57031 as broad immediately anterior to glenoid fossa, and tapering anteriorly.
531 Similarly, the olecranon process of the ulna (Character 29 in Brochu and Storrs, 2012) is scored as
532 wide and rounded. The dentary is scored as gently curved in MCSNT 57031 (Character 50 in Brochu
533 and Storrs 2012), a feature previously unscored from the holotype. The strict consensus from
534 maximum parsimony analysis recovers a complete polytomy of the main groups of Eusuchia when
535 the specimen MCSNT 57031 is added to the dataset, while when this OTU is inactive, the topology
536 between the main eusuchian lineages is identical to that reported by Blanco (2021). This is probably
537 due to the low proportion of diagnosable characters in this specimen of *A. adriaticus*.

538 On a purely morphological basis and under a maximum parsimony approach, the phylogenetic
539 integration of the new scoring confirms the paraphyly of *Acynodon* as shown in several previous
540 analyses (Brochu, 2011; Brochu, 2012; Brochu et al., 2012; Blanco, 2021; Martin et al., 2014, 2016;
541 Jouve et al., 2019; Ristevski et al., 2020; Narváez et al., 2016). If confirmed, this may require the
542 erection of a new genus, based exclusively on the material from VdP, but further reconsideration
543 including a redescription of the other species included in *Acynodon*, at the light of several newly
544 described characters of phylogenetic value, is strongly needed. In particular, a better scoring of the
545 poorly preserved hylaeochampsids and the retrieval of new remains (above all *Hylaeochampsia*)

would be also recommended in order to properly reevaluate the phylogeny and therefore taxonomy of *Acynodon* as well as the phylogenetic position of Hylaeochampsidae and closely related taxa within Eusuchia.

We remark that the chronostratigraphic re-evaluation of the age of VdP to the early–middle Campanian improves stratigraphic congruence and sets the specimens of *A. adriaticus* as chronologically older and stratigraphically overlaid by the range of *A. iberoccitanus*. Furthermore, the Bayesian analysis re-establishes the monophyly of *Acynodon*, creating ambiguity between parsimony-based and Bayesian-based topologies. These results shorten the ghost lineage between *Hylaeochampsia* and *A. iberoccitanus* resulting from previous tip-dated Bayesian analyses of crocodylomorph taxa (Lee and Yates, 2018). The question of the monophyly of *Acynodon* is probably key to solve the relationships between hylaeochampsids and may bear some weight on the resolution of this clade inside Eusuchia (and early diverging eusuchian relationships overall). The morphological redescription and chronostrigraphic datum added herein are preliminary steps to increase the resolution at the base of Eusuchia and provide a better understanding of the palaeobiology and evolutionary history of this interesting clade of Mesozoic crocodylomorphs from the Tethyan domain.

561

7. Conclusions

A detailed description of specimen MCSNT 57031 herein referred to *Acynodon adriaticus* offers a new opportunity to evaluate the variation in the fossil eusuchians from Villaggio del Pescatore locality. The uppermost Cretaceous genus *Acynodon* is herein found monophyletic by the Bayesian analysis, with the Italian taxon representing an earlier diverging species from the lower-middle Campanian while the eponym taxon *Acynodon iberoccitanus* occupies a more recent chronostratigraphic range (middle-late Campanian). The Parsimony-based phylogenetic results, though, is in conflict with this interpretation, creating a paraphyletic *Acynodon*, probably also induced by the poorly phylogenetically sampled sister taxa (e.g. *Hylaeochampsia*), for which a redescription

571 and more complete phylogenetic scoring would be recommended (ideally, supplemented by new and
572 more complete material). We highlight the need for a detailed and descriptive phylogenetic work
573 focusing on key taxa at the base of Eusuchia, to resolve the phylogenetic relationships of these taxa
574 (i.e. ‘hylaechampsids’) and resolve the taxonomy of *Acynodon*, with important possible
575 repercussions on the palaeobiology of these remarkable peri-Tethyan crocodylomorphs, highlighted
576 by the interesting asynchrony between histological and morphological maturity-related traits in its
577 skeleton.

578

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844 **Figure captions**

845 **Figure 1.** Specimen of *Acynodon adriaticus* MCSNT 57031. Laminite slab with the specimen embedded in
846 matrix (A) and anatomical elements highlighted in B. Abbreviations: c: cervical vertebrae, icl: interclavicle,
847 lhu: left humerus, lmr: left mandibular ramus, lr: left radius, lu: left ulna, ost: osteoderms, rb: ribs, rca:
848 radiale carpal, rco: right coracoid, rhu: right humerus, rmc: right metacarpals, rmr: right mandibular ramus,
849 rmx: right maxilla, rph: right phalanges, rr: right radius, ru: right ulna. Scale bar: 5 cm.

851 **Figure 2.** Isolated or fragmentary specimens referred to *Acynodon adriaticus*. A: MCSNT21.S239-1.0.22
852 (57248a), B: MCSNT 57245, C: MCSNT21.S239-1.0.22 (57248b). Scale bar: 5 cm.

853 **Figure 3.** Geographic and geological setting of the Villaggio del Pescatore quarry. Geographic location of
854 the site (A); orthophotographic view of the quarry obtained with UAV and photogrammetric processing (B),
855 simplified geological map of the site (C) and location of the specimen in the quarry superimposed to GIS-
856 based orthophoto (D). S, slumped rhythmites, L, laminites. Core S3 is the reference core for biostratigraphic
857 analyses (*see* Chiarenza et al., 2021).

858 **Figure 4.** Skull of MCSNT 57031 (A), with anatomical labels in B. Abbreviations: cs: condylar surface, lrp:
859 left retroarticular process, or: ornamentations, rd: right dentary, rmx: right maxilla, rrp: right retroarticular
860 process. Scale bar: 5 cm.

861 **Figure 5.** Cranial outlines in ventral views of specimens referred to *Acynodon adriaticus*, with MCSNT
862 57031 (A) and the holotype MCSNT 57248 (B). Scale bar: 5 cm.

863 **Figure 6.** Close-up of the dentary of MCSNT 57031 in cranioventral view. Scale bar: 1 cm.

864 **Figure 7.** Cervical series of MCSNT 57031 in lateral view (A) with anatomical labels and outlines
865 highlighted in B. Abbreviations: c: cervical, cr: cervical ribs. Scale bar: 5 cm.

866 **Figure 8.** Ribs of MCSNT 57031 in lateral view with gastralia highlighted in different colours (red) than
867 dorsal ribs (blue). Abbreviations: rb: ribs. Scale bar: 5 cm.

868 **Figure 9.** Pectoral girdle elements of MCSNT 57031 in lateral view. Abbreviations: icl: interclavicle, lco:
869 left coracoid, lsc: left scapula, rco: right coracoid, rsc: right scapula. Scale bar: 5 cm.

870 **Figure 10.** Right forelimb elements of MCSNT 57031. Arrows indicate restoration in the zeugopodium.

871 Abbreviations: dca: distale carpal, dpc: deltopectoral crest, icl: interclavicle, mc: metacarpal, pca: pisiform
872 carpal, ph: phalanges, rca: radiale carpal, rco: right coracoid, rhu: right humerus, rr: right radius, rsc: right
873 scapula, ru: right ulna, uca: ulnare carpal. Scale bar: 5 cm

874 **Figure 11.** Details of right forelimb elements of MCSNT 57031. Arrows indicate osteoporotic surfaces.

875 Abbreviations: dpc: deltopectoral crest, rhu: right humerus, rr: right radius, ru: right ulna. Scale bar: 5 cm.

876 **Figure 12.** Details of right autopodium elements of MCSNT 57031. Arrows indicate osteoporotic articular

877 surfaces. Abbreviations: dca: distale carpal, mc: metacarpal, pca: pisiform carpal, ph: phalanges, rca: radiale
878 carpal, uca: ulnare carpal, ?cca, possible fragments of the central carpal (centrale). Scale bar: 1 cm.

879 **Figure 13.** Left forelimb elements of MCSNT 57031 (A) with anatomical labels reported in B.

880 Abbreviations: lhu: left humerus, lr: left radius, lu: left ulna, mc: metacarpals, ph: phalanges, rca: radiale
881 carpal, uca: ulnare carpal. Scale bar: 5 cm.

882 **Figure 14.** Osteodermal series of MCSNT 57031 sketched and in different light direction (A) and

883 morphological outlines of the best-preserved ones in B. Black triangle points to possible ventrally exposed
884 osteoderms (*see* section 4.2). Arrows points to the direction towards the cranium of the specimen. Scale bars:
885 5 cm.

886 **Figure 15.** Histological thin sections under polarised light of MCSNT 57031 6th dorsal rib. A, overall rib

887 histological section; B, detail of secondary osteons, C, lines of arrested growth (LAGs) and annuli in the
888 outer cortex of the rib section; D, overview of the osteoderm thin section; E, close up of the outer cortex of
889 the osteoderm. Scale bars in: B, 250 nm; C, 500 nm; E, 200 nm. Abbreviations: An: annuli; cb: cancellous
890 bone; ec: erosional cavity; hs: haversian system; pv: primary vascularization. Red arrows indicate LAGs.

891 **Figure 16.** Phylogenetic position of *Acynodon adriaticus*. Results of Maximum Parsimony with strict

892 consensus (A) and majority rule (B) trees. Time calibrated Bayesian tree focused on the base of Eusuchia

893 (C). Yellow box is used to highlight the position of the genus *Acynodon*. Specimens referred to *Acynodon*

894 *adriaticus* highlighted in red. Abbreviation in the chronological y-axis ‘Ma’ refers to Mega annum (million

895 years). Numbers in A indicate Bremer support (Decay index) while bootstrap support values are reported for
896 the Majority rule tree in B.

897 **Figure 17.** Skeletal reconstruction of MCSNT 57031 in A with size comparison between the latter specimen
898 in ventral view and the holotype (more complete in dorsal view) in B.

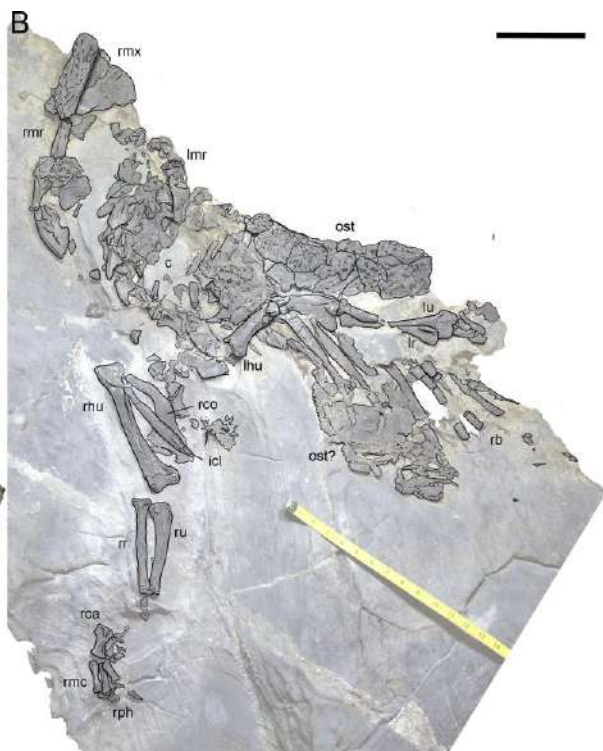
899 **Table 1.** List of crocodilian remains found at the Villaggio del Pescatore site. VP, Villaggio del Pescatore,
900 progressive numbers referring to limestone blocks quarried in order to collect vertebrate remains.

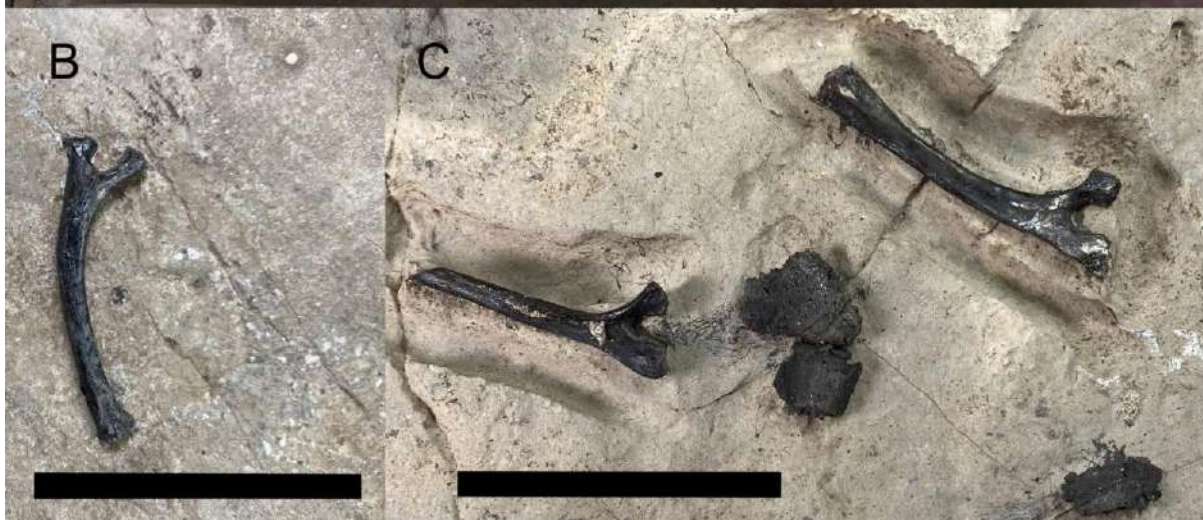
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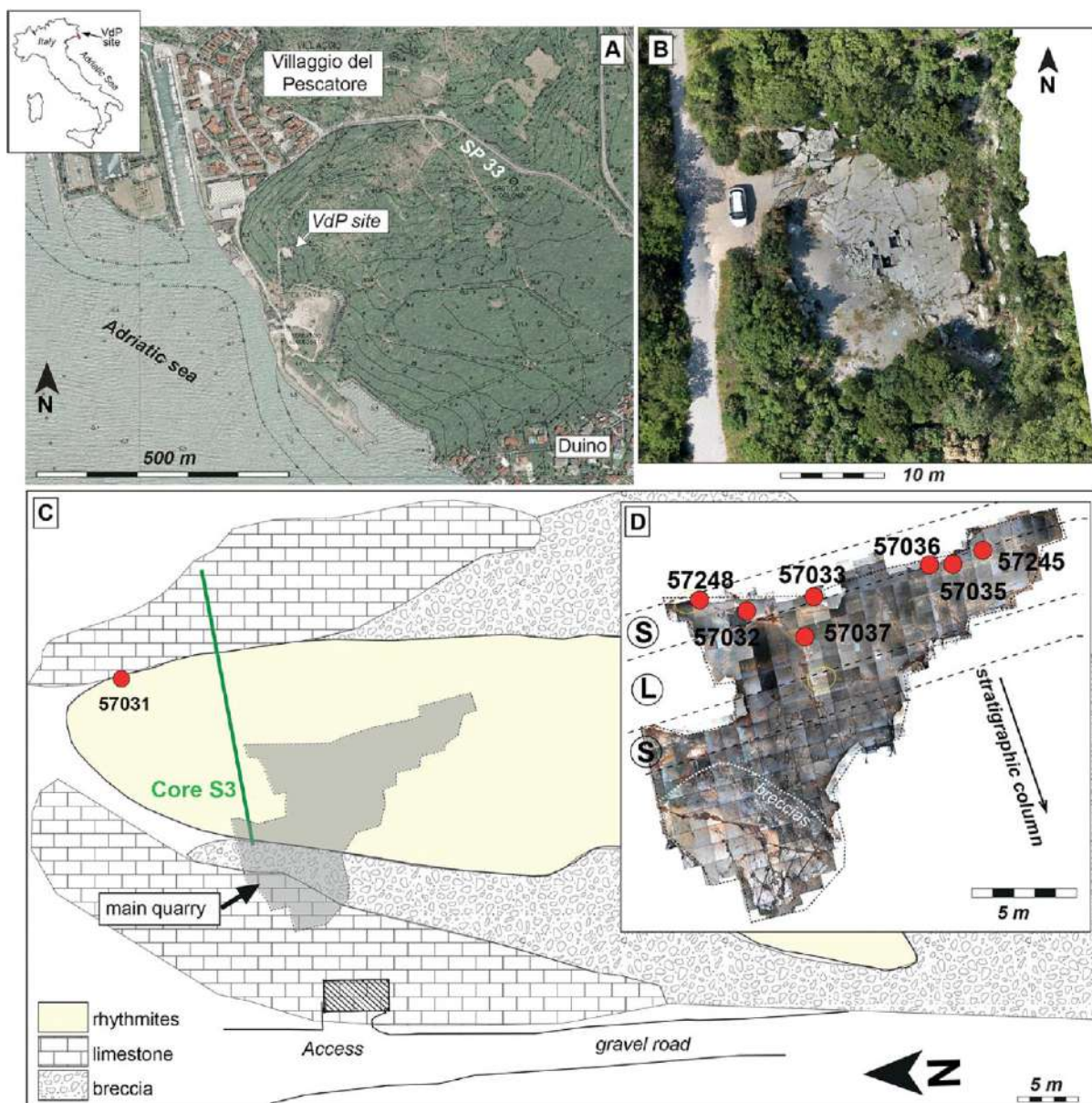
SPECIMENT INVENTORY	SPECIMEN DESCRIPTION	QUARRY INFORMATI ON
<i>Acynodon adriaticus</i>		
MCNST 57248	Holotype, Delfino et al., 2008	Collected near VP12, about 55 cm above VP1 in 1998-1999
MCNST 57032	Paratype, Delfino et al., 2008	Collected in the proximity of the holotype in 1996-1997
New specimens assigned to <i>Acynodon adriaticus</i> and discussed in this study		
MCSNT 57031	ventrally exposed, articulated, sub-complete specimen	Collected in VP4 in the same horizon as VP2 in 1996- 1997
MCSNT 57245	an isolated, well preserved robust crocodilian rib laying on the flat surface of a larger matrix slab with other unidentified bone fragments. The tuberculum is shorter than the capitulum and	Collected from Slab 38 in 1998-1999

	apparently has a larger articular surface. The rib progressively thickens distally and has a wide costal cartilage articular surface	
MCSNT 21.S239-1.0.22 (57248a)	six well preserved osteoderms, three of them in partial overlap. The larger ones, measured at their longer axis, are 22,8 mm, 24,5 mm and 27 mm long respectively. These osteoderms show two low keels, one straight and the other concave and larger, comparable to the condition described in the paratype by Delfino et al., 2008	Collected near the holotype in 1998-1999
MCSNT 21.S239-1.0.22 (57248b)	three small osteoderms and two robust ribs in association, both showing shorter and stouter tubercula than capitula, with wider articular surfaces. The shorter rib measures 46,7 mm in length and lacks its distalmost portion; the longer one measures 57,2 mm, appears to be complete and gradually thickens at its distal end, revealing a large costal cartilage articular surface.	Collected near the holotype in 1998-1999
Specimens assigned to Crocodylomor pha indet.		
MCSNT 57033	a ~4 cm long unidentified small reptile bone, possibly a rib, exposing its sagittal section on the surface of a small laminite fragment.	Collected in the proximity of the holotype in 1998-1999
MCSNT 57035	a ~5 cm long bone element exposed on a calcareous slab with an ornamented surface, here identified as a ventrally exposed crocodilian mandibular symphysis	Collected from Slab 41 in 1998-1999
MCSNT 57036	a ~2 cm anteroposteriorly long vertebra, possibly a fragmented cervical, three-dimensionally prepared out of the matrix	Collected from Slab 41 in 1998-1999

MCSNT 57037	an almost unrecognizable smooth bone fragment hardly visible on a small matrix slab associated with other indeterminate vertebrate fossil material, previously tentatively identified as a fragmented ventral osteodermal surface	Collected from Slab 15 in 1996-1997 and 1998-1999
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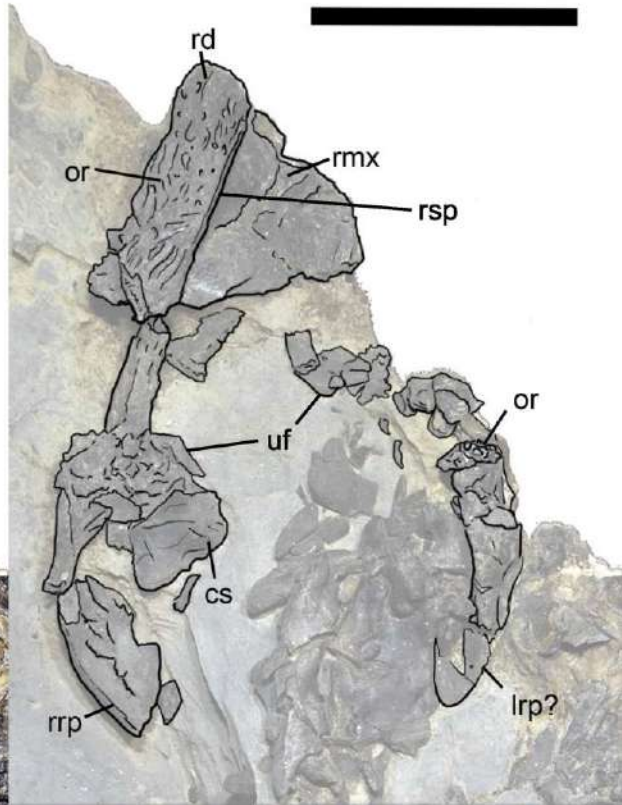




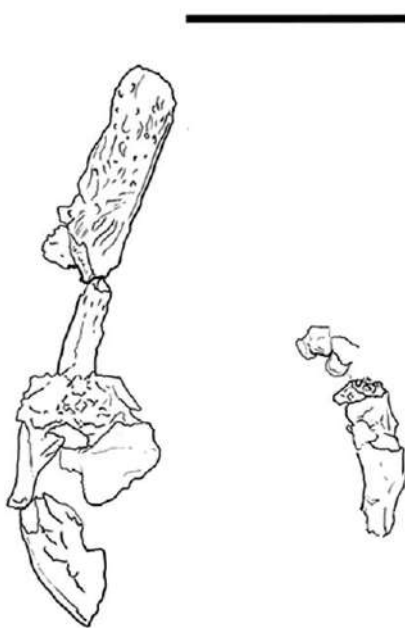
A



B



A

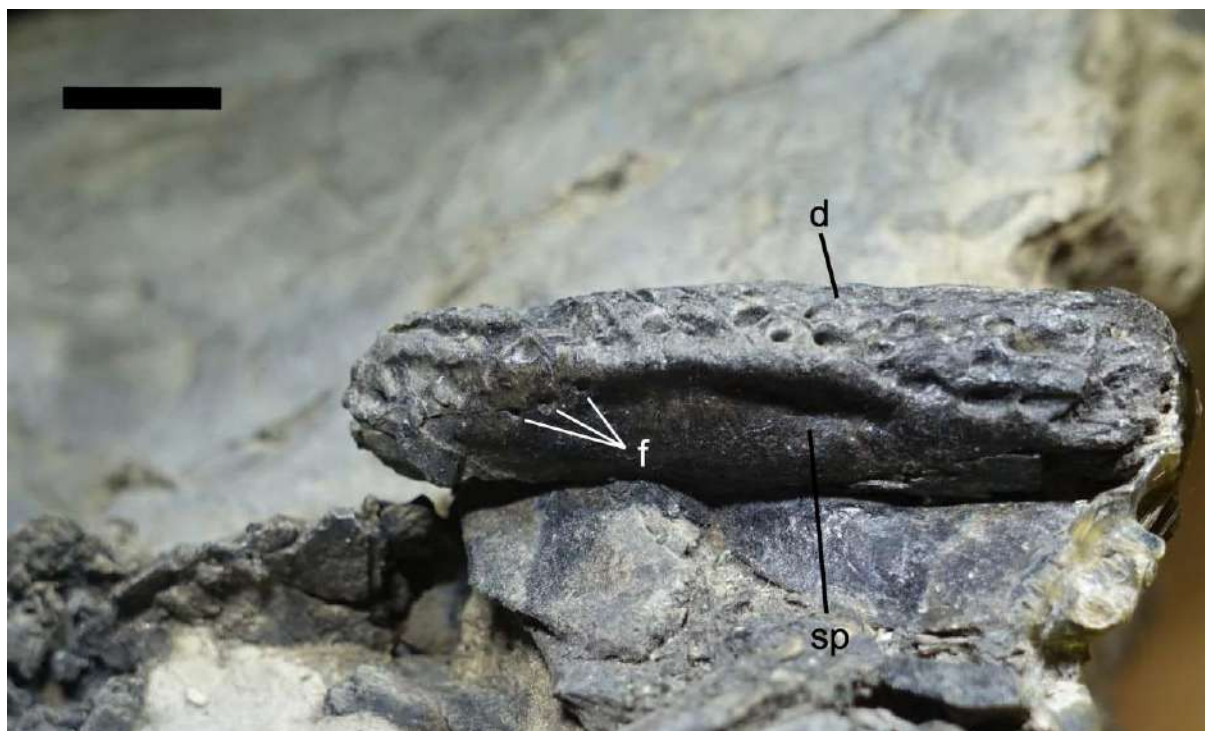


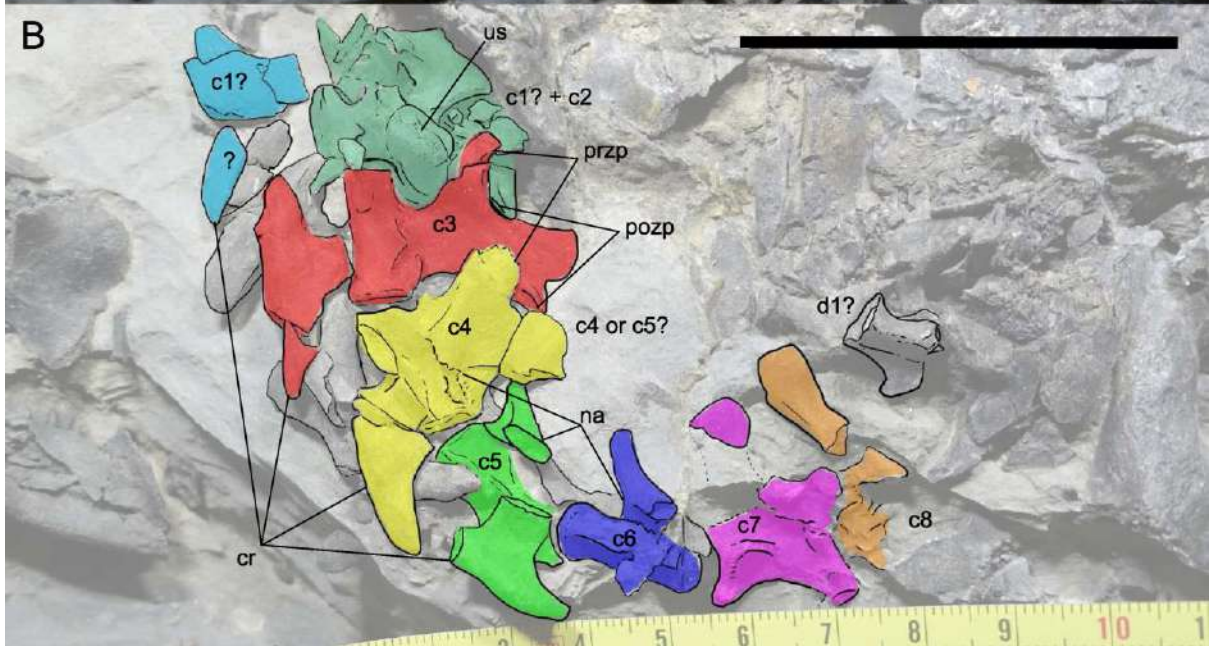
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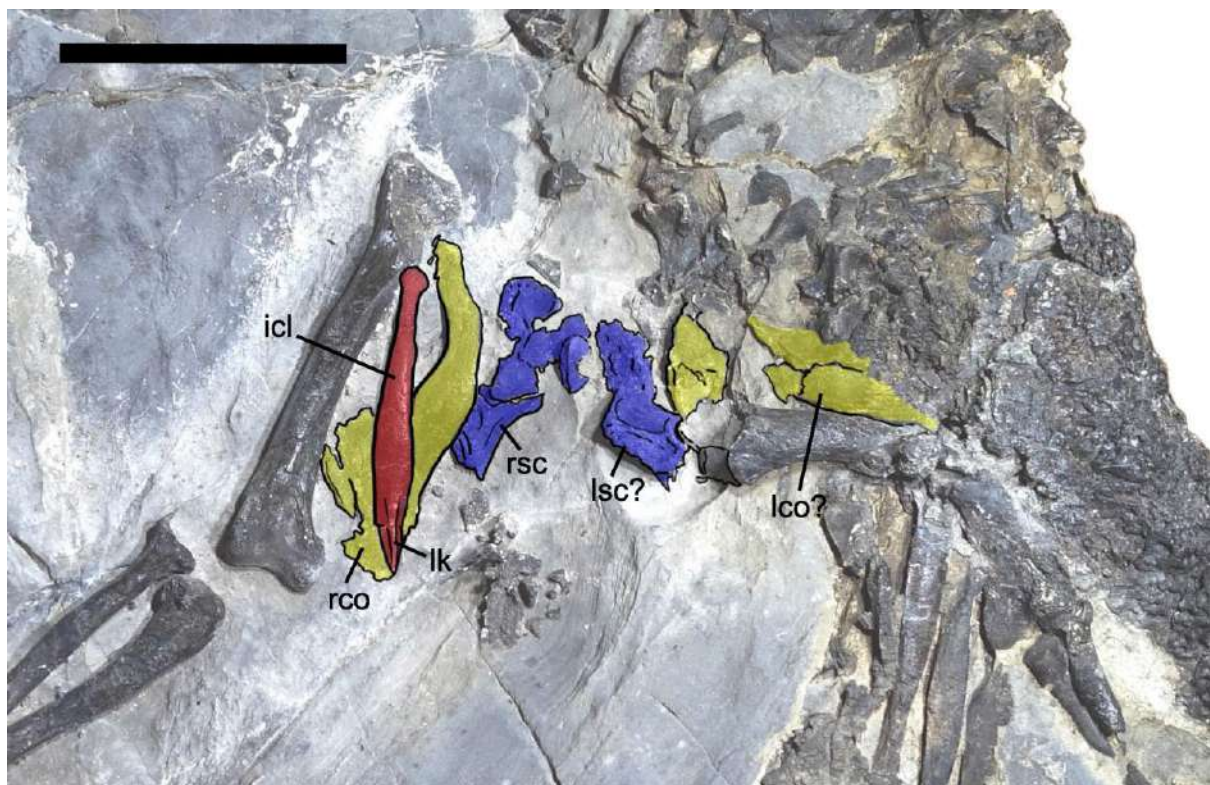
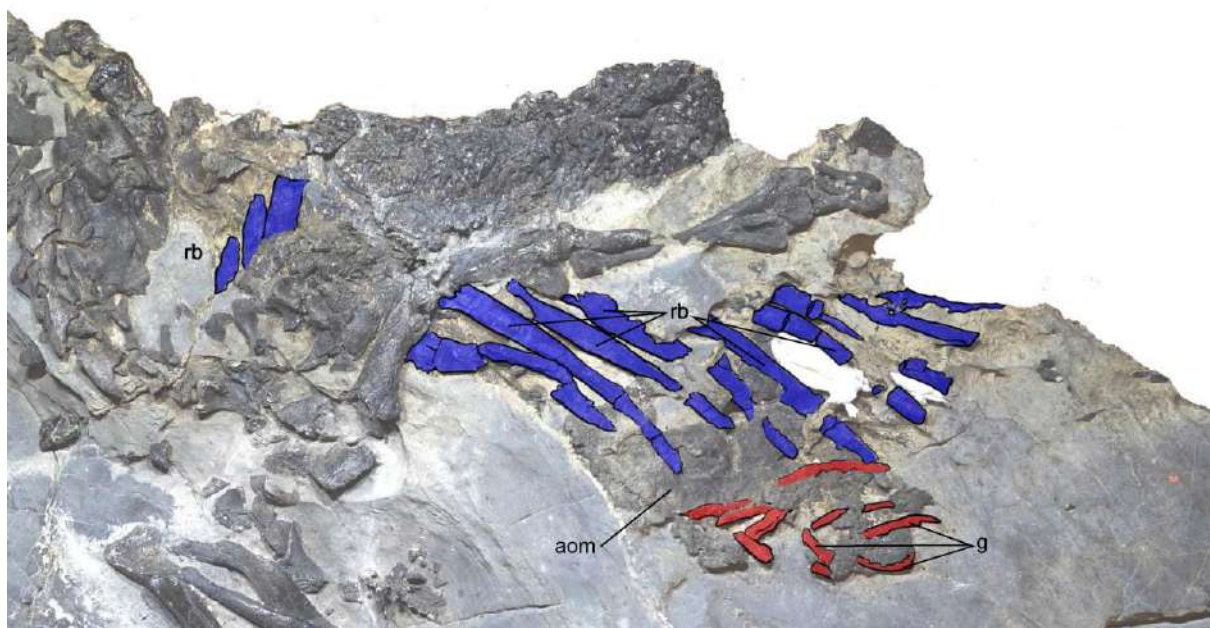


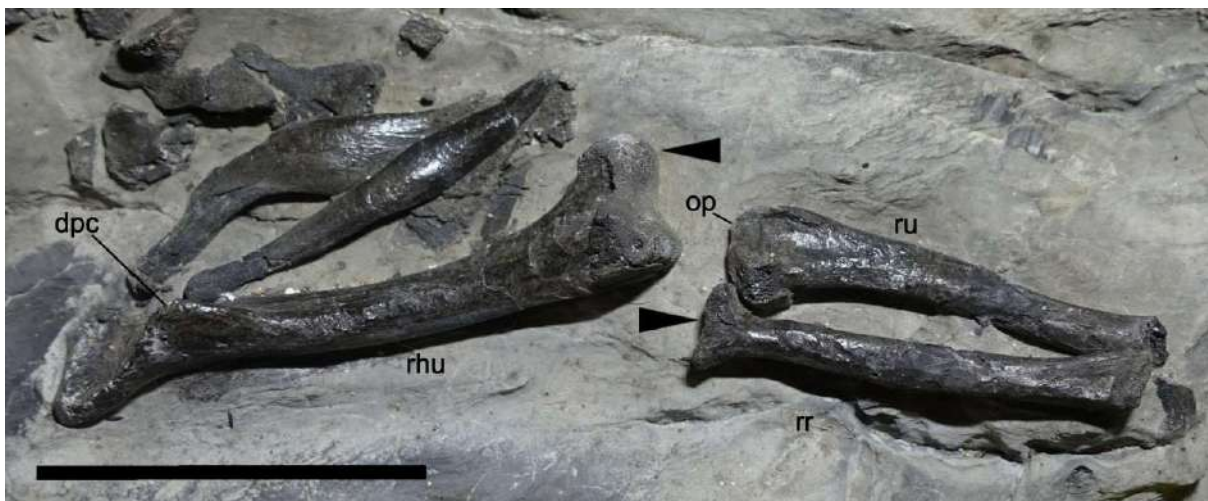
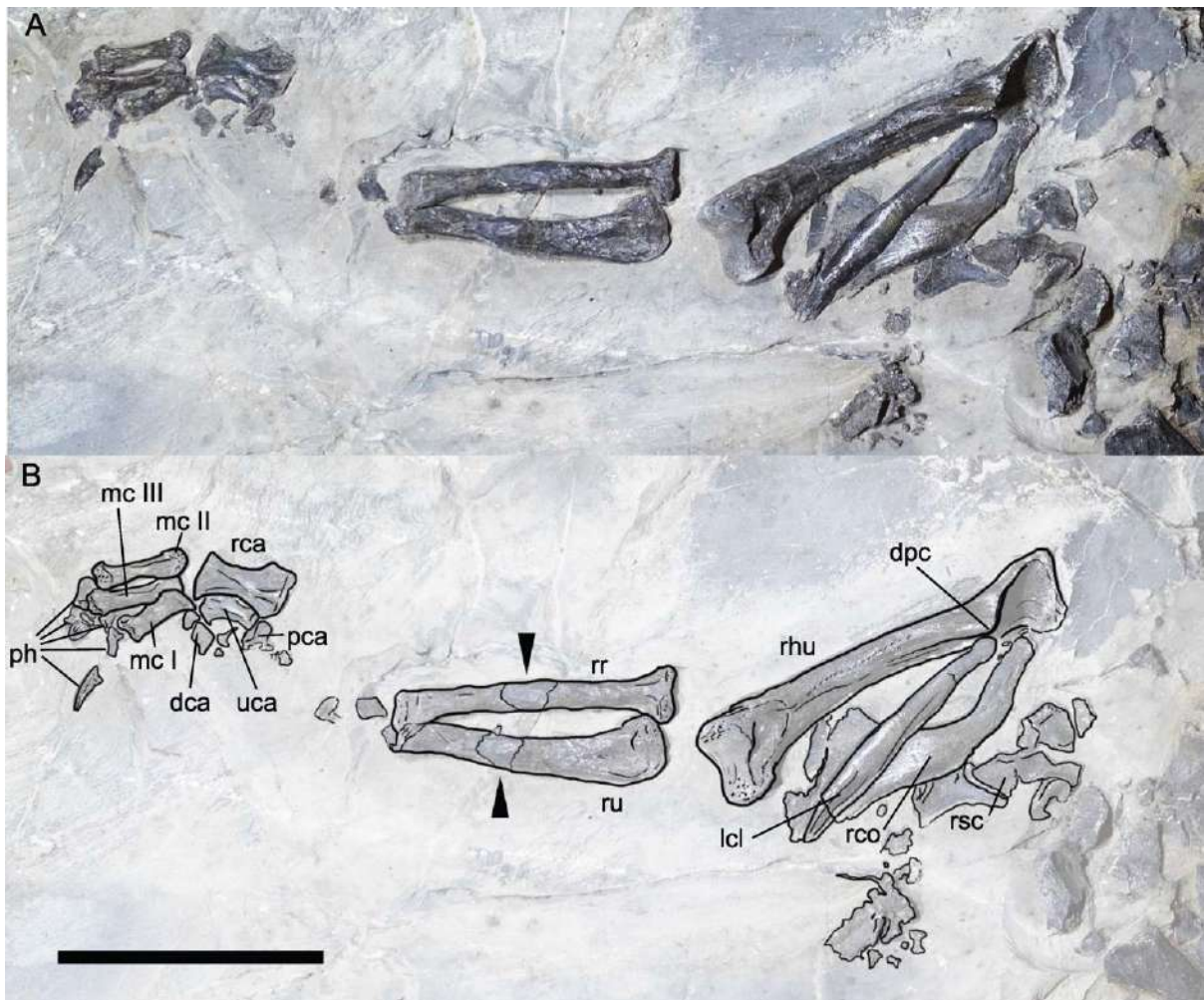
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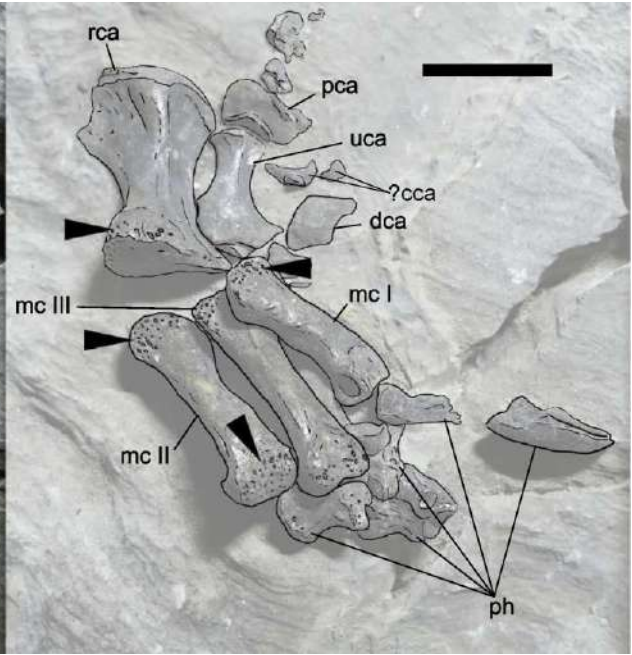
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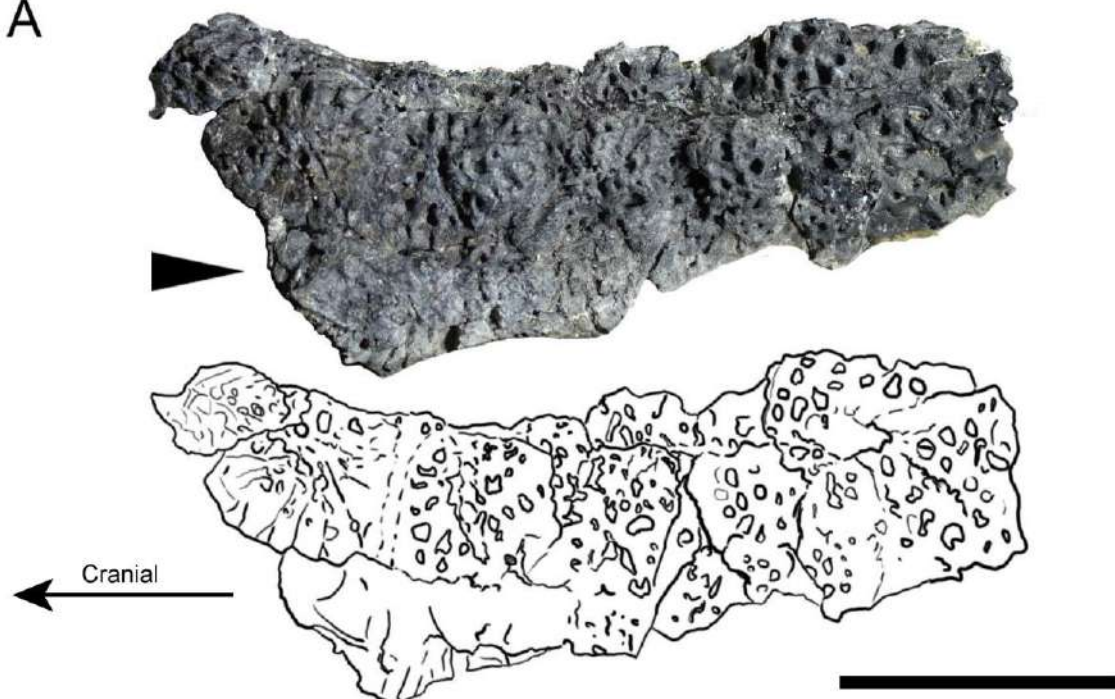




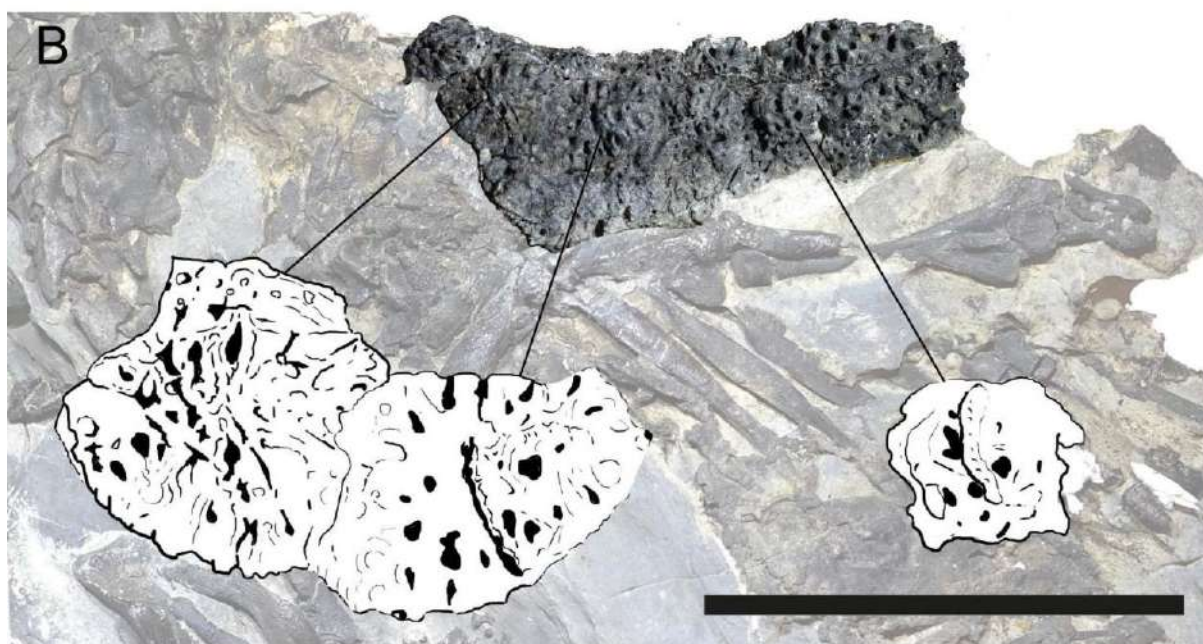


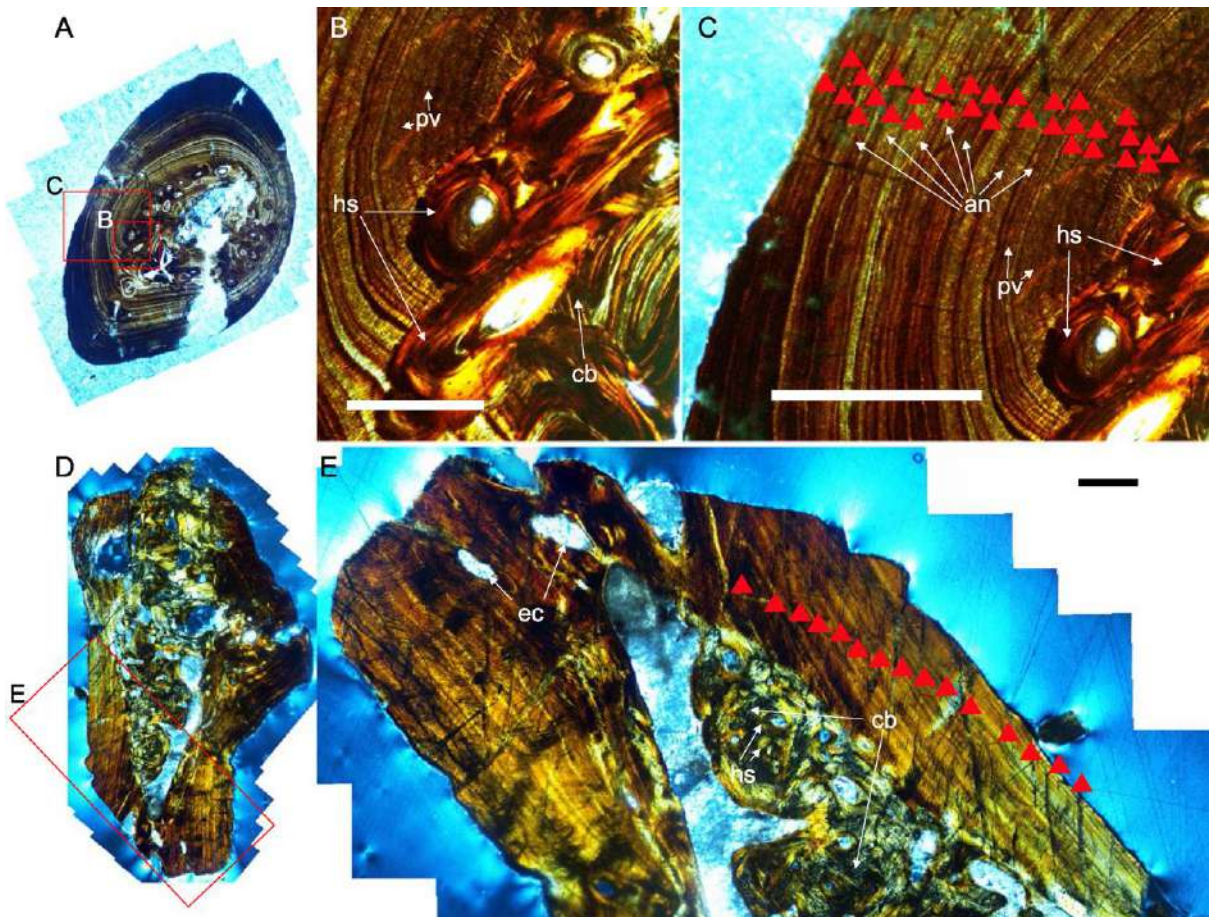
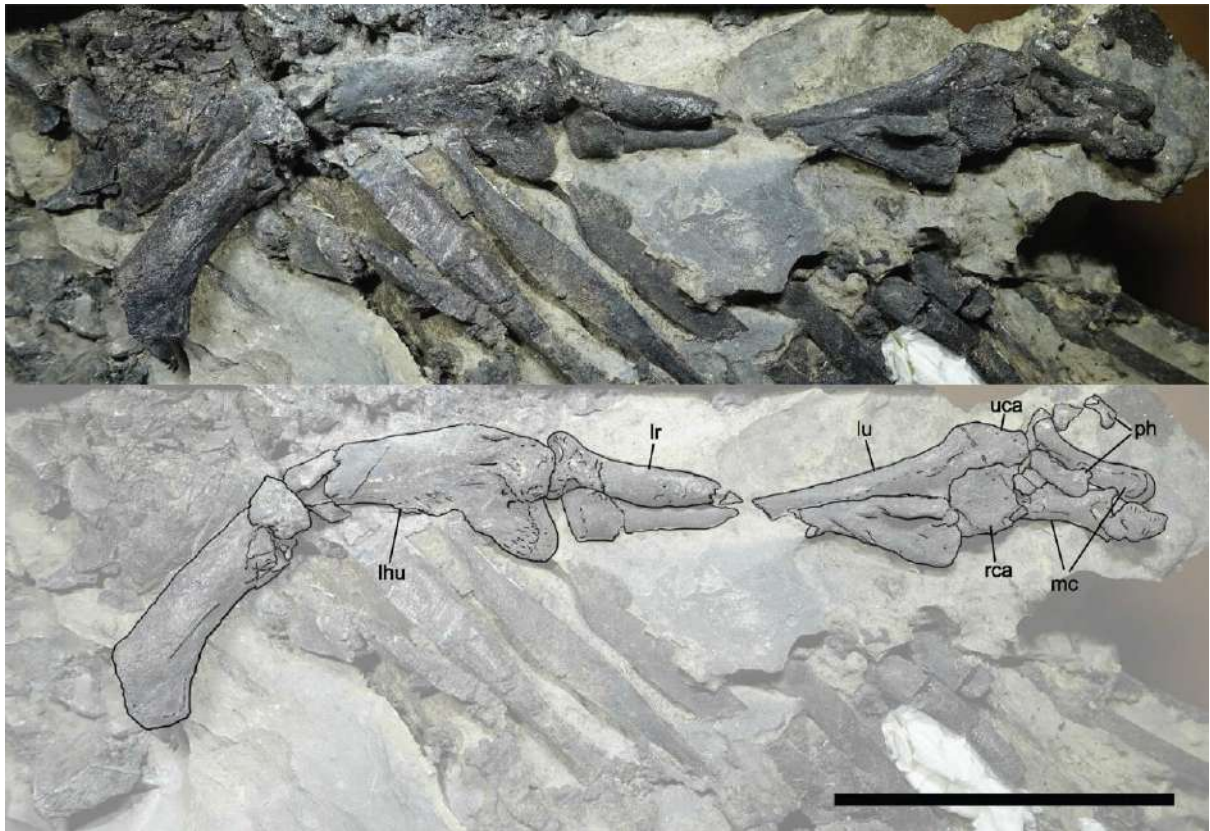


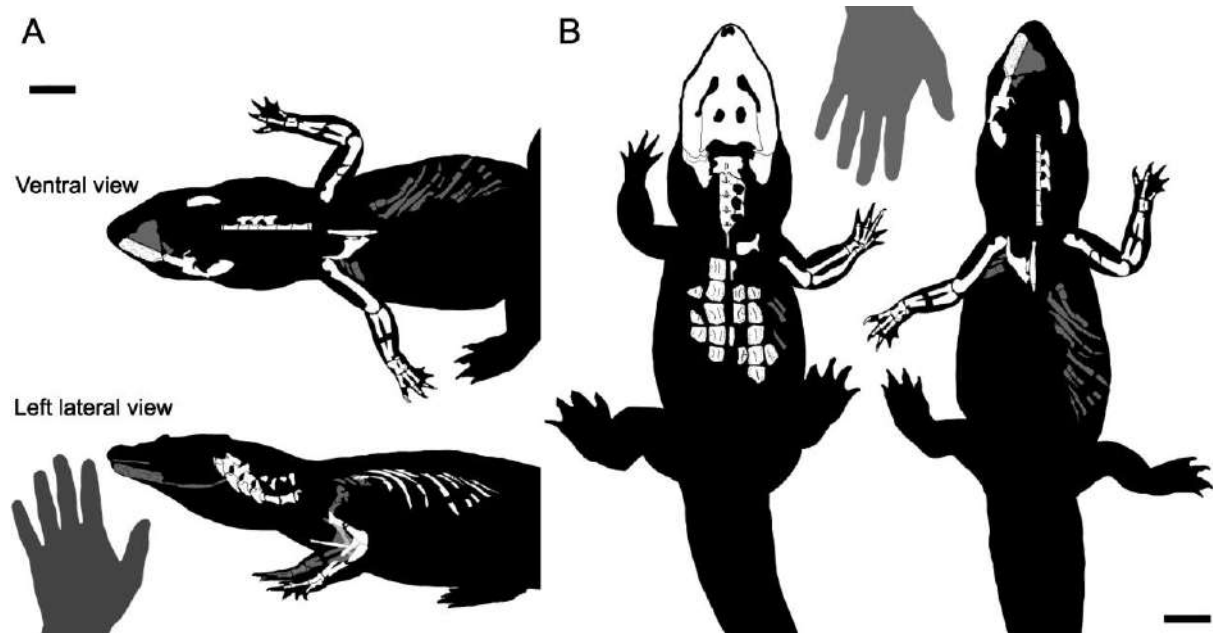
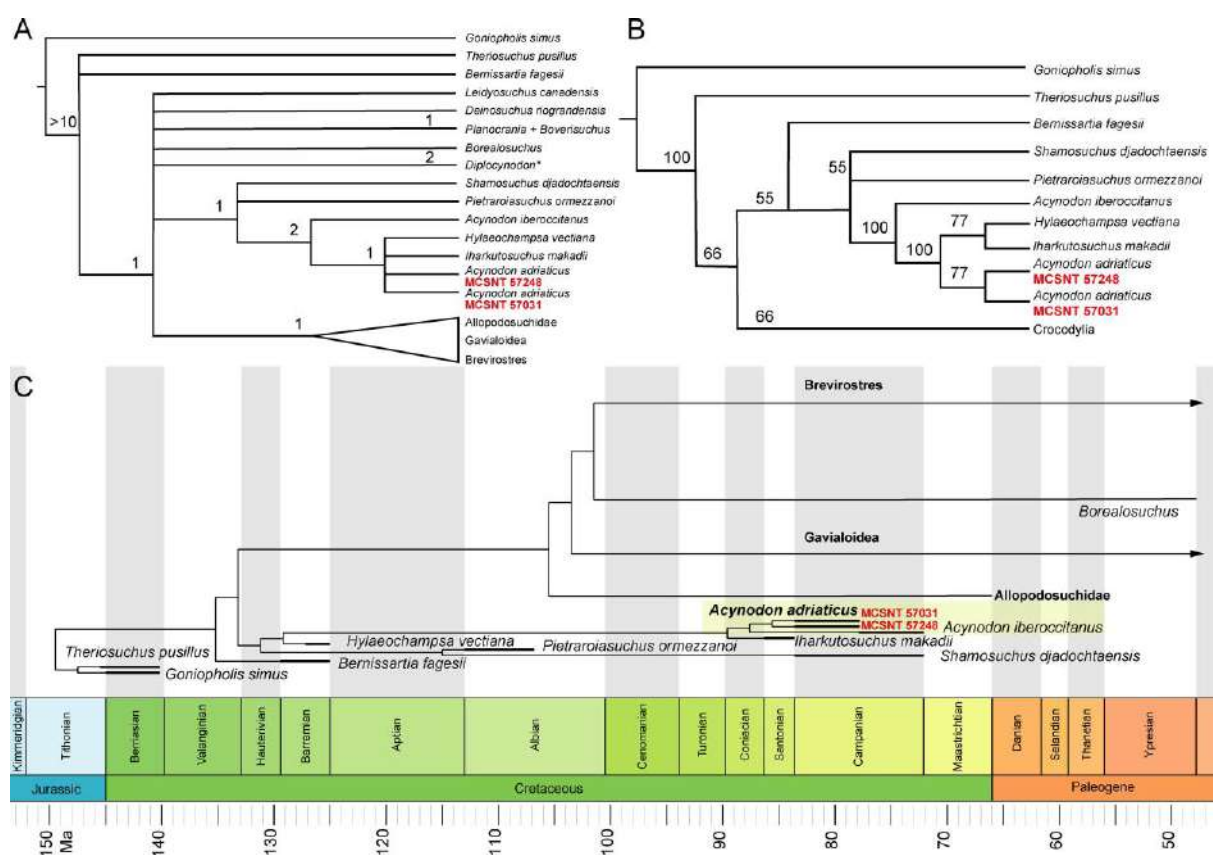
A



B







- New specimen of *Acynodon adriaticus* is herein osteologically and osteohistologically described in detail.
- Results from maximum parsimony phylogenetic analyses indicate a paraphyletic *Acynodon*.
- Results from bayesian phylogenetic analyses indicate a monophyletic *Acynodon*.
- The Middle–Late Campanian age of the Adriatic taxon support the Bayesian results.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: