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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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1	Acynodon adriaticus from Villaggio del Pescatore (Campanian of Italy): anatomical
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4	
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22	
23	

ABSTRACT

The hylaeochampsid crocodylomorph Acynodon adriaticus, from the uppermost Cretaceous 26 'Villaggio del Pescatore' site, belongs to an early diverging lineage in Eusuchia. Here an additional 27 specimen, MCSNT 57031, is osteologically and osteohistologically described in detail. After 28 integrating this morphological information together with the recent chronostratigraphic recalibration 29 of the site to the lower-middle Campanian, the tip-dated Bayesian phylogenetic analysis recovers this 30 31 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 32 assigned to A. adriaticus highlights the need for a detailed morphological description and integration 33 34 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 35 morpho- and osteo-skeletal maturity suggest unique ecomorphological adaptations in this Campanian 36 crocodylomorph. 37

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1. Introduction

The Villaggio del Pescatore Lagerstätte (VdP hereafter), located in the municipality of Duino-40 Aurisina, Trieste (NE Italy), is a world-renown paleontological site due to its well-preserved 41 42 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; 43 Chiarenza et al., 2021), remains of the small hylaeochampsid crocodylomorph Acynodon adriaticus 44 45 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 46 similar to that of small alligatoroids (Brochu, 2010) although with larger and 'molariform' dentition. 47 48 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 49 Acynodon in Eusuchia has been problematic (Rio and Mannion, 2021). Acynodon was previously 50 considered as an example of 'archaic' alligatoroid, one of the oldest and most primitive 51 representatives of the entire Globidonta (Santonian-Campanian) (Buscalioni et al., 1997; Brochu, 52 53 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, 54 with conflicting results regarding the monophyly of the genus (Brochu, 2011, 2012; Brochu et al., 55 56 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, 57 with referred material from Spain, southern France and Romania (with remains from these latter two 58 countries represented by multiple, fairly complete crania), and A. lopezi based on isolated teeth found 59 60 in Spain (Buscalioni et al. 1997). Other occurrences of this genus come from several European 61 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 62 (Spain), Laño (Spain), Arén (Spain), Massecaps (France), Quarante (France), Fox-Ampoux (France), 63 Hateg Basin (Romania) and VdP (Italy). Only A. adriaticus and A. iberoccitanus have been analysed 64

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

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

All crocodilian remains from the VdP were collected between 1996 and 1999 (*see* Table 1) and are currently housed at the Museo Civico di Storia Naturale in Trieste (MCSNT). Specimens 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).

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98 3.1.1 New specimens assigned to Acynodon adriaticus and discussed in this study

99 MCSNT 57031: ventrally exposed, articulated, sub-complete specimen (main focus of this study;

100 Fig. 1); Initially described by <u>Delfino and Buffetaut, 2006.</u>

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.

114

- 115 *3.1.2 Specimens assigned to Crocodylomorpha 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 (Fig. S1A).
- 118 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 (Fig. S1B).
- 120 MCSNT 57036: a ~2 cm anteroposteriorly long vertebra, possibly a fragmented cervical, three-
- dimensionally prepared out of the matrix (Fig. S1C).

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 (Fig. S1D).

125

3.2 Stratigraphy and age

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

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

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3.3 Taphonomy

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

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

188

189 *3.4 Osteohistological sampling*

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

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3.5 Phylogenetic analyses

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

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

Characters were treated as unordered and equally weighted. Maximum Parsimony analyses 217 were computed in TNT 1.5 beta (Goloboff et al., 2008), using a 'New Technology' search, with Sect 218 Search, Ratchet, Drift, and Tree Fusing algorithms, and 10 random addition sequences (Chiarenza et 219 220 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 absolute frequencies for 1000 replicates. The analysis recovered 9 trees with best step length score of 223 224 807. Notably, the use of TBR after the 'New Technology' search further explores the tree space (Barrett et al., 2014; Raven and Maidment, 2018). Notably, while this procedure differs from those 225 226 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.

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

'strap' by Bell and Lloyd (2015), which was also used to calculate values of stratigraphic congruence
of different tree outputs compared to randomly generated trees using the Stratigraphic Consistency
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

4.2 Description of MCSNT 57031

255 Skull

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

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

splenial is located on a deep groove on the ventromedial surface of this distal portion of the 266 267 mandibular ramus (Fig. 4B). The splenial 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 268 the mandible and skull elements. The angular, surangular and articular bones are heavily fragmented 269 and hardly distinguishable. The right retroarticular process is partially damaged but better preserved 270 271 than the left one, at least in its general outline (Fig. 4). From the posterior end of the retroarticular 272 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 273 represented only by small, hardly identifiable proximal fragments, most likely the angular and 274 275 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. 276

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Axial skeleton

The preserved cervical vertebrae are lateroventrally exposed on their left side (Fig. 7): centra 279 280 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 281 an anterior neural spine and a few overlapping or nearby fragments corresponding to cervical c2 or 282 283 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 284 partially overlapped with the holotypic cervical one. Centra are twice anteroposteriorly long as 285 dorsoventrally high. Centra are mediolaterally wide with relatively short and lateroventrally directed 286 parapophyses. The putative c2 centrum is partially lateroventrally rotated, exposing either a convex 287 288 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. 289 290 Ribs have short tubercula and capitula, and they are hatchet-shaped in overall morphology, with a 291 smooth surface and with curved and relatively thick inferior margins. Neural arches are apparently

292 not articulated to each other in cervicals 4-6, and in c5 and c6 they are clearly unfused from their 293 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 294 295 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, 296 297 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 298 299 vertebral centrum, possibly one of the first dorsal vertebrae, is partially preserved posteriorly to the last cervical neural spine, apparently rotated by almost 180°. 300

301

302 **Ribs**

Assessing the exact number of preserved ribs is challenging due to the fragmentary nature of 303 304 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, 305 306 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 307 shape or eccentrically D-shaped section. The distal epiphysis is preserved in some ribs, appearing to 308 309 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 gastralia. At least 310 three small, elongated structures overlapping with the unidentified clusters of dark bone portions in 311 312 the abdominal region of the specimen might represent small fragments of gastralia or other sternal ribs (Fig. 8). The dark amorphous mass that partially engulfs them, already described by Delfino 313 (2008) as a "uniformly vermicular surface", most likely is here identifiable as a cluster of small lateral 314 or ventral osteoderms exposed on their visceral surface, heavily overlapped and crushed together. 315

316

317 **Pectoral girdle**

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

333

Right forelimb

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

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

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

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

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

375

376 Left forelimb

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

385

386 Osteoderms

Many osteoderms are preserved in MCSNT 57031 (Fig. 1). A few oval, cervical osteoderms 387 are preserved in ventral view around the cervical area. The largest and most articulated osteoderm 388 389 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. Single osteoderms of this area are partially overlapping their neighboring elements on their right and 391 posterior end. This arrangement suggests a 180° rotation of the entire dorsal and lateral osteoderm 392 armor. Ventrally to the anterior elements, however, a smooth surface may in fact represent the 393 somewhat smoother ventral surface of the osteoderms from the row of the right side. Following this 394

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

408

409 *4.3 Osteohistology*

410 **Dorsal rib (6th)**

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

418

419 Osteoderm

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

428

429 **5.** Phylogenetics

The phylogenetic relationships of MCSNT 57031 and the holotype of A. adriaticus MCSNT 430 57248 were tested with Maximum Parsimony and Bayesian analyses (Fig. 16). The maximum 431 parsimony strict consensus of 9 trees (Fig. 16A, Fig. S2) is 807 steps long, with a Consistency Index 432 433 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 Hylaeochampsa vectiana and Iharkutosuchus makadii [Bremer (decay) Index of DI = 1]. Acynodon iberoccitanus is found as sister group of this polytomy (DI = 2). 435 Shamosuchus djadochtaensis and Pietraroiasuchus ormezzanoi are found in a polytomy with the 436 437 Acynodon + Hylaeochampsa clade (DI = 1). The Majority rule tree (Fig. 16B, Fig. S3) increases resolution in this 'hylaeochampsid polytomy' placing both specimens of A. adriaticus (bootstrap 438 support of BS = 77%) as sister group of the clade including *H. vectiana* and *I. makadii* (BS = 100%), 439 but breaking the monophyly of the genus Acynodon, since the Spanish eponym taxon A. iberoccitanus 440 is found as sister taxon of the Hylaeochampsa + A. adriaticus clade (BS = 100%). According to this 441 442 result, a synapomorphy of Hylaeochampsidae is the maxilla with a posterior process between the lacrimal and the prefrontal (character 128, state 2 of Brochu and Storrs, 2012). The synapomorphy 443 444 defining the Acynodon + Hylaeochampsa clade is the presence of anterodorsally projected anterior dentary teeth (character 48, state 1 of <u>Brochu and Storrs, 2012</u>). The *Hylaeochampsa* + *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 <u>Brochu and Storrs, 2012</u>); a prefrontal longer than the
lacrimal (character 130, state 1 of <u>Brochu and Storrs, 2012</u>); and a quadrate bearing a prominent,
mediolaterally thin crest on its dorsal surface (character 179, state 1 of <u>Brochu and Storrs, 2012</u>). *Acynodon iberoccitanus* is diagnosed in this analysis by the unexposed supraoccipital on the dorsal
surface of the skull table (character 160, state 1 of <u>Brochu and Storrs, 2012</u>).

The Bayesian analysis (Fig. 16C; Fig. S4) solves this paraphyletic ambiguity by placing A. 452 adriaticus and A. iberoccitanus in a monophyletic clade, with a Posterior Probability (PP) value of 453 454 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 455 Pietraroiasuchus ormezzanoi and Shamosuchus djadochtaensis (PP=61). The phylogenetic topology 456 found in the Bayesian analysis has as higher stratigraphic congruence (SCI=0.5-1 > 0.45; Fig. S5) 457 than the strict consensus (SCI=0-0.45 > 0.48; Fig. S6) and the majority rule (SCI=0.5-1 vs 0.585; 458 459 Fig. S7) trees from the maximum parsimony analysis.

460

461 **6.** Discussion

462 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 crocodilians (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.

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

As mentioned above, when compared to the holotype, cervical centra in MCSNT 57031 484 appear proportionally longer and more gracile, most likely due to differential preservation. Delfino 485 486 et al. (2008) estimated an anteroposterior length of 17 mm for the holotypic c6 centrum. We measured the putative c6 centrum in MCSNT 57031 reporting the same measurement (17.2 mm long), thus 487 comparable in anteroposterior length. In the holotype, the neurocentral sutures of all visible vertebrae 488 489 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 (Fig. 7). Neurocentral sutures in the crocodilian axial skeleton follow a distinct caudal to cranial 492 closure sequence during ontogeny, with the sutures in caudal vertebrae being fully closed in 493 hatchlings, and closure of remaining sutures toward the cranium occurring progressively later. 494

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

The bone surface on the epiphyisis of long bones and manual elements in MCSNT 57031 is 498 499 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 between bone textures and either body size or skeletal maturity in *Alligator mississippiensis*, possibly 502 due to the extremely plastic environment-induced developmental rates common to most crocodilians. 503 504 This makes the porosities on MCSNT 57031 a weak immaturity signal if considered alone, although it is still widely used for other archosaurs, particularly of the avian lineage (Bennett, 1993; Carr, 1999; 505 Chiappe and Göhlich, 2010; Chiarenza et al., 2020; Hone et al., 2016; Sampson et al., 1997). In 506 507 contrast, the osteoarthropathy of unknown etiology reported by Huchzermeyer et al. (2013) in *Crocodylus niloticus* is not correlated to ontogenetic immaturity, and the reported humeral epiphyseal 508 509 osteolytic lesions are somewhat similar to the condition described for MCSNT 57031. The pathological nature of the epiphyseal porosity discussed here should not be excluded. 510

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 cortex of the dorsal rib, the high number of LAGs, and the decrease of spacing between them suggest 513 that sexual maturity was probably reached in this individual (Fig. 15). These results contrast with the 514 515 osteological observations suggesting an immature ontogenetic stage for MCSNT 57031. Although it is currently unclear why such mismatch between these observations is present, previous studies have 516 517 shown how osteohistological analyses are generally preferable and more reliable than osteological observations (e.g. Griffin et al., 2021). Lack of closure for neurocentral sutures along the axial 518 skeleton and porous epiphyses in the long bones have been previously observed in late ontogenetic 519 stages in aquatic animals, such as marine reptiles: these were described as skeletal paedomorphosis 520

and suggested to be an adaptation to more aquatic ecologies (e.g. Motani et al., 2015; Rieppel, 1989).
A paedomorphic overall skeletal morphology due to the potentially bizarre ecomorphology of *Acynodon adriaticus* is a possibility, although more data and observations are necessary to confirm
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 material in the available character matrix. Character 26 in Brochu and Storrs (2012), related to the 528 529 scapulocoracoid facet anterior to glenoid fossa and previously unscored in the holotype, is scored here from MCSNT 57031 as broad immediately anterior to glenoid fossa, and tapering anteriorly. 530 Similarly, the olecranon process of the ulna (Character 29 in Brochu and Storrs, 2012) is scored as 531 wide and rounded. The dentary is scored as gently curved in MCSNT 57031 (Character 50 in Brochu 532 and Storrs 2012), a feature previously unscored from the holotype. The strict consensus from 533 maximum parsimony analysis recovers a complete polyotomy of the main groups of Eusuchia when 534 the specimen MCSNT 57031 is added to the dataset, while when this OTU is inactive, the topology 535 between the main eusuchian lineages is identical to that reported by Blanco (2021). This is probably 536 due to the low proportion of diagnosable characters in this specimen of A. adriaticus. 537

On a purely morphological basis and under a maximum parsimony approach, the phylogenetic 538 539 integration of the new scoring confirms the paraphyly of Acynodon as shown in several previous analyses (Brochu, 2011; Brochu, 2012; Brochu et al., 2012; Blanco, 2021; Martin et al., 2014, 2016; 540 541 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 including a redescription of the other species included in Acynodon, at the light of several newly 543 described characters of phylogenetic value, is strongly needed. In particular, a better scoring of the 544 545 poorly preserved hylaeochampsids and the retrieval of new remains (above all Hylaeochampsa) would be also recommended in order to properly revaluate the phylogeny and therefore taxonomy of *Acynodon* as well as the phylogenetic position of Hylaeochampsidae and closely related taxa within
Eusuchia.

549 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 550 chronologically older and stratigraphically overlaid by the range of A. iberoccitanus. Furthermore, 551 552 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 553 Hylaeochampsa and A. iberoaccitanus resulting from previous tip-dated Bayesian analyses of 554 555 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 556 of this clade inside Eusuchia (and early diverging eusuchian relationships overall). The morphological 557 redescription and chronostrigraphic datum added herein are preliminary steps to increase the 558 resolution at the base of Eusuchia and provide a better understanding of the palaeobiology and 559 560 evolutionary history of this interesting clade of Mesozoic crocodylomorphs from the Tethyan domain.

561

562 **7.** Conclusions

A detailed description of specimen MCSNT 57031 herein referred to Acynodon adriaticus 563 564 offers a new opportunity to evaluate the variation in the fossil eusuchians from Villaggio del Pescatore 565 locality. The uppermost Cretaceous genus Acynodon is herein found monophyletic by the Bayesian 566 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 567 568 chronostratigraphic range (middle-late Campanian). The Parsimony-based phylogenetic results, though, is in conflict with this interpretation, creating a paraphyletic Acynodon, probably also induced 569 by the poorly phylogenetically sampled sister taxa (e.g. *Hylaeochampsa*), for which a redescription 570

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

578

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599 **References**

- Andrews, C.W., 1913. LVIII.—On the skull and part of the skeleton of a crocodile from the Middle
 Purbeck of Swanage, with a description of a new species (*Pholidosaurus lævis*), and a note
 on the skull of Hylæochampsa. Annals and Magazine of Natural History 11, 485–494.
 https://doi.org/10.1080/00222931308693345
- Arbulla D., Cotza F., Cucchi F., Dalla Vecchia F.M., De Giusto A., Flora O., Masetti D., Palci A.,
 Pittau P., Pugliese N., Stenni B., Tarlao A., Tunis G. & Zini L., 2006. La successione
 Santoniano–Campaniana del Villaggio del Pescatore (Carso Triestino) nel quale sono stati
 rinvenuti i resti di dinosauro, in: Guida Alle Escursioni/Excursions Guide, Società
 Paleontologica Italiana. Presented at the Giornate di Paleontologia 2006, EUT Edizioni
 Università di Trieste, Trieste, pp. 20–27.
- Attura, M., 1999. Aspetti paleontologici e geochimico-isotopici di una successione stratigrafica
 Santoniana-Camapaniana del Villaggio del Pescatore (Ts). Università degli Studi di Trieste,
 Trieste.
- Barrett, P.M., Butler, R.J., Mundil, R., Scheyer, T.M., Irmis, R.B., Sánchez-Villagra, M.R., 2014. A
 palaeoequatorial ornithischian and new constraints on early dinosaur diversification.
 Proceedings of the Royal Society B: Biological Sciences 281, 20141147.
 https://doi.org/10.1098/rspb.2014.1147
- Bell, M.A., Lloyd, G.T., 2015. strap: an R package for plotting phylogenies against stratigraphy and
 assessing their stratigraphic congruence. Palaeontology 58, 379–389.
 https://doi.org/10.1111/pala.12142
- Bennett, S.C., 1993. The ontogeny of *Pteranodon* and other pterosaurs. Paleobiology 19, 92–106.
- Benton, M.J., Clark, J.M., 1988. Archosaur phylogeny and the relationships of the Crocodylia 295–
 338.
- Blanco, A., 2021. Importance of the postcranial skeleton in eusuchian phylogeny: Reassessing the
 systematics of allodaposuchid crocodylians. PLOS ONE 16, e0251900.
 https://doi.org/10.1371/journal.pone.0251900
- Blanco, A., Puértolas-Pascual, E., Marmi, J., Moncunill-Solé, B., Llácer, S., Rössner, G.E., 2020.
 Late Cretaceous (Maastrichtian) crocodyliforms from north-eastern Iberia: a first attempt to
 explain the crocodyliform diversity based on tooth qualitative traits. Zoological Journal of
 the Linnean Society 189, 584–617. https://doi.org/10.1093/zoolinnean/zlz106
- Brinkmann, W., n.d. Die Krokodilier-Fauna aus der Unter-Kreide (Ober-Barremium) von Una
 (Provinz Cuenca, Spanien). Herausgegeben von geowissenschaftlichen Instituten der Freien
 und der Technischen Universität Berlin und der Technischen Fachhochschule Berlin.
- Brochu, C.A., 2012. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status
 of *Pristichampsus* Gervais, 1853. Earth and Environmental Science Transactions of The
 Royal Society of Edinburgh 103, 521–550. https://doi.org/10.1017/S1755691013000200
- Brochu, C.A., 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the
 early history of caimanines. Zoological Journal of the Linnean Society 163, S228–S256.
 https://doi.org/10.1111/j.1096-3642.2011.00716.x
- Brochu, C.A., 2010. A new alligatorid from the lower Eocene Green River Formation of Wyoming
 and the origin of caimans. Journal of Vertebrate Paleontology 30, 1109–1126.
 https://doi.org/10.1080/02724634.2010.483569
- Brochu, C.A., 2003. Phylogenetic Approaches Toward Crocodylian History. Annu. Rev. Earth
 Planet. Sci. 31, 357–397. https://doi.org/10.1146/annurev.earth.31.100901.141308
- Brochu, C.A., 2001. Crocodylian snouts in space and time: phylogenetic approaches toward
 adaptive radiation. American Zoologist 41, 564–585. https://doi.org/10.1093/icb/41.3.564
- Brochu, C.A., 1999. Phylogenetics, Taxonomy, and Historical Biogeography of Alligatoroidea.
 Journal of Vertebrate Paleontology 19, 9–100.
- 648 https://doi.org/10.1080/02724634.1999.10011201

- Brochu, C.A., 1996. Closure of neurocentral sutures during crocodilian ontogeny: Implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16, 49–62.
 https://doi.org/10.1080/02724634.1996.10011283
- Brochu, C.A., Parris, D.C., Grandstaff, B.S., Denton, R.K., Gallagher, W.B., 2012. A new species
 of *Borealosuchus* (Crocodyliformes, Eusuchia) from the Late Cretaceous–early Paleogene
 of New Jersey. null 32, 105–116. https://doi.org/10.1080/02724634.2012.633585
- Brochu, C.A., Storrs, G.W., 2012. A giant crocodile from the Plio-Pleistocene of Kenya, the
 phylogenetic relationships of Neogene African crocodylines, and the antiquity of
 Crocodylus in Africa. Journal of Vertebrate Paleontology 32, 587–602.
 https://doi.org/10.1080/02724634.2012.652324
- Buscalioni, A.D., Ortega, F., Vasse, D., 1997. New crocodiles (Eusuchia: Alligatoroidea) from the
 Upper Cretaceous of southern Europe. Comptes Rendus de l'Académie des Sciences Series
 IIA Earth and Planetary Science 325, 525–530. https://doi.org/10.1016/S12518050(97)89872-2
- Carr, T.D., 1999. Craniofacial ontogeny in tyrannosauridae (Dinosauria, Coelurosauria). Journal of
 vertebrate Paleontology 19, 497–520.
- Cerda, I.A., Desojo, J.B., 2011. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia),
 from the Upper Triassic of Argentina and Brazil. Lethaia 44, 417–428.
 https://doi.org/10.1111/j.1502-3931.2010.00252.x
- Chiappe, L.M., Göhlich, U.B., 2010. Anatomy of *Juravenator starki* (Theropoda: Coelurosauria)
 from the late Jurassic of Germany. Neues Jahrbuch fuer Geologie und Palaeontologie.
 Abhandlungen 258, 257–296.
- Chiarenza, A.A., Fabbri, M., Consorti, L., Muscioni, M., Evans, D.C., Cantalapiedra, J.L., Fanti, F.,
 2021. An Italian dinosaur Lagerstätte reveals the tempo and mode of hadrosauriform body
 size evolution. Scientific Reports 11, 23295. https://doi.org/10.1038/s41598-021-02490-x
- Chiarenza, A.A., Fiorillo, A.R., Tykoski, R.S., McCarthy, P.J., Flaig, P.P., Contreras, D.L., 2020.
 The first juvenile dromaeosaurid (Dinosauria: Theropoda) from Arctic Alaska. PLOS ONE
 15, e0235078. https://doi.org/10.1371/journal.pone.0235078
- 677 Consorti, L., Arbulla, D., Bonini, L., Fabbi, S., Fanti, F., Franceschi, M., Frijia, G., Pini, G.A.,
 678 2021. The Mesozoic palaeoenvironmental richness of the Trieste Karst. GFT&M.
 679 https://doi.org/10.3301/GFT.2021.06
- Dalla Vecchia, F.M., 2009. *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia)
 from the Upper Cretaceous of Italy. Journal of Vertebrate Paleontology 29, 1100–1116.
 https://doi.org/10.1671/039.029.0428
- Dalla Vecchia, F.M., 2008. I dinosauri del Villaggio del Pescatore (Trieste): qualche aggiornamento
 21.
- Dalla Vecchia, F.M., 1999. Relazione scientifica finale, scavo paleontologico del Villaggio del
 Pescatore 1998-1999 & elencazione, identificazione e determinazione preliminare dei
 reperti.
- de Ricqlès, A.J., Padian, K., Horner, J.R., 2003. On the bone histology of some Triassic
 pseudosuchian archosaurs and related taxa. Annales de Paléontologie 89, 67–101.
 https://doi.org/10.1016/S0753-3969(03)00005-3
- Deeming, D.C., Ferguson, M.W.J., 1990. Morphometric analysis of embryonic development in
 Alligator mississippiensis, *Crocodylus johnstoni* and *Crocodylus porosus*. Journal of
 Zoology 221, 419–439. https://doi.org/10.1111/j.1469-7998.1990.tb04011.x
- Delfino, M., Buffetaut, E., 2006. A preliminary description of the crocodylian remains from the
 Late Cretaceous of Villaggio del Pescatore (northeastern Italy).
- Delfino, Massimo, Martin, J.E., Buffetaut, E., 2008a. A new species of *Acynodon* (Crocodylia)
 from the upper cretaceous (Santonian–Campanian) of Villaggio del Pescatore, Italy.
 Palaeontology 51, 1091–1106. https://doi.org/10.1111/j.1475-4983.2008.00800.x

- Delfino, M., Martin, J.E., Buffetaut, E., 2008b. I coccodrilli del Villaggio del Pescatore: una 699 panoramica generale. Atti del Museo Civico di Storia Naturale di Trieste 53, 277-284. 700 701 Dodson, P., 1975. Taxonomic Implications of Relative Growth in Lambeosaurine Hadrosaurs. Systematic Zoology 24, 37-54. https://doi.org/10.2307/2412696 702 Erickson, G.M., Brochu, C.A., 1999. How the 'terror crocodile' grew so big. Nature 398, 205–206. 703 704 https://doi.org/10.1038/18343 705 Frijia, G., Parente, M., Di Lucia, M., Mutti, M., 2015. Carbon and strontium isotope stratigraphy of the Upper Cretaceous (Cenomanian-Campanian) shallow-water carbonates of southern Italy: 706 Chronostratigraphic calibration of larger foraminifera biostratigraphy. Cretaceous Research 707 708 53, 110–139. https://doi.org/10.1016/j.cretres.2014.11.002 Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. 709 Cladistics 24, 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x 710 Gregorovičová, M., Kvasilová, A., Sedmera, D., 2018. Ossification Pattern in Forelimbs of the 711 Siamese Crocodile (Crocodylus siamensis): Similarity in Ontogeny of Carpus Among 712 Crocodylian Species. The Anatomical Record 301, 1159–1168. 713 https://doi.org/10.1002/ar.23792 714 Griffin, C.T., Stocker, M.R., Colleary, C., Stefanic, C.M., Lessner, E.J., Riegler, M., Formoso, K., 715 Koeller, K., Nesbitt, S.J., 2021. Assessing ontogenetic maturity in extinct saurian reptiles. 716 Biological Reviews 96, 470-525. https://doi.org/10.1111/brv.12666 717 Hone, D.W.E., Farke, A.A., Wedel, M.J., 2016. Ontogeny and the fossil record: what, if anything, is 718 an adult dinosaur? Biology Letters 12, 20150947. https://doi.org/10.1098/rsbl.2015.0947 719 Huchzermeyer, F.W., Groenewald, H.B., Myburgh, J.G., Steyl, J.C.A., Crole, M.R., 2013. 720 Osteoarthropathy of unknown aetiology in the long bones of farmed and wild Nile 721 crocodiles (Crocodylus niloticus). Journal of the South African Veterinary Association 84, 722 723 1–5. Jones, L.A., Gearty, W., Allen, B.J., Eichenseer, K., Dean, C.D., Galván, S., Kouvari, M., Godoy, 724 P.L., Nicholl, C.S.C., Buffan, L., Dillon, E.M., Flannery-Sutherland, J.T., Chiarenza, A.A., 725 2023. palaeoverse: A community-driven R package to support palaeobiological analysis. 726 727 Methods in Ecology and Evolution n/a. https://doi.org/10.1111/2041-210X.14099 Jouve, S., Sarıgül, V., Steyer, J.-S., Sen, S., 2019. The first crocodylomorph from the Mesozoic of 728 Turkey (Barremian of Zonguldak) and the dispersal of the eusuchians during the Cretaceous. 729 Journal of Systematic Palaeontology 17, 111–128. 730 https://doi.org/10.1080/14772019.2017.1393469 731 Jurkovšek, B., Biolchi, S., Furlani, S., Kolar-Jurkovšek, T., Zini, L., Jež, J., Tunis, G., Bavec, M., 732 Cucchi, F., 2016. Geology of the Classical Karst Region (SW Slovenia-NE Italy). Journal 733 of Maps 12, 352-362. https://doi.org/10.1080/17445647.2016.1215941 734 Kramer, G., Medem, F., 1955. Über wachstumsbedingte Proportionsänderungen bei Krokodilen. 735 Zoologische Jahrbücher 66, 62–74. 736 Lee, M.S.Y., Cau, A., Naish, D., Dyke, G.J., 2014. Morphological Clocks in Paleontology, and a 737 Mid-Cretaceous Origin of Crown Aves. Systematic Biology 63, 442-449. 738 https://doi.org/10.1093/sysbio/syt110 739
- Lima, F., Santos, A., Vieira, L., Coutinho, M., 2011. Ossification sequence of skull and hyoid in
 embryos of Caiman yacare (Crocodylia, Alligatoridae). Iheringia. Série Zoologia 101, 161–
 172. https://doi.org/10.1590/S0073-47212011000200003
- Mannion, P.D., Chiarenza, A.A., Godoy, P.L., Cheah, Y.N., 2019. Spatiotemporal sampling
 patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact
 on diversity. Palaeontology 62, 615–637. https://doi.org/10.1111/pala.12419
- Martin, J.E., 2007. New Material of the Late Cretaceous Globidontan *Acynodon iberoccitanus* (Crocodylia) from Southern France. Journal of Vertebrate Paleontology 27, 362–372.
- Martin, J.E., Delfino, M., Garcia, G., Godefroit, P., Berton, S., Valentin, X., 2016. New specimens
 of Allodaposuchus precedens from France: intraspecific variability and the diversity of

- European Late Cretaceous eusuchians. Zoological Journal of the Linnean Society 176, 607–
 631. https://doi.org/10.1111/zoj.12331
- Martin, J.E., Smith, T., de Lapparent de Broin, F., Escuillié, F., Delfino, M., 2014. Late Palaeocene
 eusuchian remains from Mont de Berru, France, and the origin of the alligatoroid
 Diplocynodon. Zoological Journal of the Linnean Society 172, 867–891.
 https://doi.org/10.1111/zoj.12195
- Martin, J.E., Smith, T., Salaviale, C., Adrien, J., Delfino, M., 2020. Virtual reconstruction of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–eusuchian transition. Journal of Systematic Palaeontology 18, 1079–1101.
 https://doi.org/10.1080/14772019.2020.1731722
- Motani, R., Jiang, D.-Y., Tintori, A., Rieppel, O., Chen, G.-B., You, H., 2015. First evidence of
 centralia in Ichthyopterygia reiterating bias from paedomorphic characters on marine reptile
 phylogenetic reconstruction. Journal of Vertebrate Paleontology 35, e948547.
 https://doi.org/10.1080/02724634.2014.948547
- Müller, G.B., Alberch, P., 1990. Ontogeny of the limb skeleton in *Alligator mississippiensis*:
 Developmental invariance and change in the evolution of archosaur limbs. Journal of
 Morphology 203, 151–164. https://doi.org/10.1002/jmor.1052030204
- Narváez, I., Brochu, C.A., Escaso, F., Pérez-García, A., Ortega, F., 2016. New Spanish Late
 Cretaceous eusuchian reveals the synchronic and sympatric presence of two
 allodaposuchids. Cretaceous Research 65, 112–125.

770 https://doi.org/10.1016/j.cretres.2016.04.018

- Nesbitt, S.J., 2011. The early evolution of archosaurs : relationships and the origin of major clades.
 (Bulletin of the American Museum of Natural History, no. 352).
- Palci, A., 2003. Ricostruzione Paleoambientale del Sito Fossilifero Senoniano del Villaggio del
 Pescatore (Trieste) (Tesi di Laurea In Paleontologia). Università degli Studi di Trieste,
 Trieste.
- Parker, W.G., Stocker, M.R., Irmis, R.B., 2008. A New Desmatosuchine Aetosaur (Archosauria:
 Suchia) from the Upper Triassic Tecovas Formation (Dockum Group) of Texas. Journal of
 Vertebrate Paleontology 28, 692–701.
- Ponce, D., Cerda, I., Desojo, J., Nesbitt, S., 2017. The osteoderm microstructure in doswelliids and proterochampsids and its implications for palaeobiology of stem archosaurs. APP 62.
 https://doi.org/10.4202/app.00381.2017
- Puértolas-Pascual, E., Young, M.T., Brochu, C.A., 2020. Introducing the First European
 Symposium on the Evolution of Crocodylomorpha. Zoological Journal of the Linnean
 Society 189, 419–427. https://doi.org/10.1093/zoolinnean/zlaa012
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior Summarization
 in Bayesian Phylogenetics Using Tracer 1.7. Systematic Biology 67, 901–904.
 https://doi.org/10.1093/sysbio/syy032
- Raven, T.J., Maidment, S.C.R., 2018. The systematic position of the enigmatic thyreophoran
 dinosaur Paranthodon africanus, and the use of basal exemplifiers in phylogenetic analysis.
 PeerJ 6, e4529. https://doi.org/10.7717/peerj.4529
- Rieppel, O., 1989. The Hind Limd of *Macrocnemus bassanii* (Nopcsa) (Reptilia, Diapsida):
 Deverlopment and Functional Anatomy. Journal of Vertebrate Paleontology 9, 373–387.
- Rio, J.P., Mannion, P.D., 2021. Phylogenetic analysis of a new morphological dataset elucidates the
 evolutionary history of Crocodylia and resolves the long-standing gharial problem. PeerJ 9,
 e12094. https://doi.org/10.7717/peerj.12094
- Ristevski, J., Yates, A.M., Price, G.J., Molnar, R.E., Weisbecker, V., Salisbury, S.W., 2020.
 Australia's prehistoric 'swamp king': revision of the Plio-Pleistocene crocodylian genus
 Pallimnarchus de Vis, 1886. PeerJ 8, e10466. https://doi.org/10.7717/peerj.10466

- Sampson, S.D., Ryan, M.J., Tanke, D.H., 1997. Craniofacial ontogeny in centrosaurine dinosaurs
 (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. Zoological Journal of
 the Linnean Society 121, 293–337.
- Scheyer, T.M., Desojo, J., 2011. Palaeohistology and external microanatomy of rauisuchian
 osteoderms (Archosauria: Pseudosuchia). Palaeontology 54, 1289–1302.
 https://doi.org/10.1111/j.1475-4983.2011.01098.x
- Scheyer, T.M., Sander, P.M., 2009. Bone microstructures and mode of skeletogenesis in osteoderms
 of three pareiasaur taxa from the Permian of South Africa. Journal of Evolutionary Biology
 22, 1153–1162. https://doi.org/10.1111/j.1420-9101.2009.01732.x
- Stubbs, T.L., Pierce, S.E., Elsler, A., Anderson, P.S.L., Rayfield, E.J., Benton, M.J., 2021.
 Ecological opportunity and the rise and fall of crocodylomorph evolutionary innovation.
 Proceedings of the Royal Society B: Biological Sciences 288, 20210069.
 https://doi.org/10.1098/rspb.2021.0069
- Taborda J. R. A., Cerda I. A., Desojo J. B., 2013. Growth curve of Aetosauroides scagliai
 Casamiquela 1960 (Pseudosuchia: Aetosauria) inferred from osteoderm histology.
 Geological Society, London, Special Publications 379, 413–423.
 https://doi.org/10.1144/SP379.19
- Tarlao, A., Tentor, M., Tunis, G., Venturini, S., 1995. Stop 4: Villaggio del Pescatore. Atti Museo
 Geologico Paleontologico Monfalcone 135–142.
- Tarlao A., Tentor M., Tunis G., Venturini S., 1993. Evidenze di una fase tettonica nel Senoniano
 inferiore dell'area del Villaggio del Pescatore (Trieste). Gortania Atti Museo Friulano Storia
 Naturale 23–24.
- Tumarkin-Deratzian, A.R., Vann, D.R., Dodson, P., 2006. Bone surface texture as an ontogenetic indicator in long bones of the Canada goose *Branta canadensis* (Anseriformes: Anatidae).
 Zoological Journal of the Linnean Society 148, 133–168. https://doi.org/10.1111/j.1096-3642.2006.00232.x
- Vieira, L.G., Lima, F.C., Mendonôa, S.H.S.T., Menezes, L.T., Hirano, L.Q.L., Santos, A.L.Q.,
 2018. Ontogeny of the Postcranial Axial Skeleton of *Melanosuchus niger* (Crocodylia,
 Alligatoridae). The Anatomical Record 301, 607–623. https://doi.org/10.1002/ar.23722
- von Baczko, M.B., Desojo, J.B., Ponce, D., 2019. Postcranial anatomy and osteoderm histology of
 Riojasuchus tenuisceps and a phylogenetic update on Ornithosuchidae (Archosauria,
 Pseudosuchia). Journal of Vertebrate Paleontology 39, e1693396.
- 831 https://doi.org/10.1080/02724634.2019.1693396
- Witzmann, F., 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the
 implications for the soft tissue dermis.
- Witzmann, F., Soler-Gijón, R., 2010. The bone histology of osteoderms in temnospondyl
 amphibians and in the chroniosuchian *Bystrowiella*. Acta Zoologica 91, 96–114.
 https://doi.org/10.1111/j.1463-6395.2008.00385.x
- Woodward Ballard, H., Horner, J., Farlow, J., 2011. Osteohistological Evidence for Determinate
 Growth in the American Alligator. Journal of Herpetology 45, 339–342.
 https://doi.org/10.1670/10-274.1
- Woodward, H.N., Horner, J.R., Farlow, J.O., 2014. Quantification of intraskeletal histovariability in
 Alligator mississippiensis and implications for vertebrate osteohistology. PeerJ 2, e422.
 https://doi.org/10.7717/peerj.422
- 843

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

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

Figure 3. Geographic and geological setting of the Villaggio del Pescatore quarry. Geographic location of

the site (A); ortophotographic view of the quarry obtained with UAV and photogrammetric processing (B),

simplified geological map of the site (C) and location of the specimen in the quarry superimposed to GIS-

based orthophoto (D). S, slumped rhythmites, L, laminites. Core S3 is the reference core for biostratigraphic
analyses (*see* Chiarenza et al., 2021).

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

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

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

Figure 7. Cervical series of MCSNT 57031 in lateral view (A) with anatomical labels and outlines

highlighted in B. Abbreviations: c: cervical, cr: cervical ribs. Scale bar: 5 cm.

Figure 8. Ribs of MCSNT 57031 in lateral view with gastralia highlighted in different colours (red) than

dorsal ribs (blue). Abbreviations: rb: ribs. Scale bar: 5 cm.

Figure 9. Pectoral girdle elements of MCSNT 57031 in lateral view. Abbreviations: icl: interclavicle, lco:

left coracoid, lsc: left scapula, rco: right coracoid, rsc: right scapula. Scale bar: 5 cm.

Figure 10. Right forelimb elements of MCSNT 57031. Arrows indicate restoration in the zeugopodium.
Abbreviations: dca: distale carpal, dpc: deltopectoral crest, icl: interclavicle, mc: metacarpal, pca: pisiform
carpal, ph: phalanges, rca: radiale carpal, rco: right coracoid, rhu: right humerus, rr: right radius, rsc: right
scapula, ru: right ulna, uca: ulnare carpal. Scale bar: 5 cm

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

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

Figure 12. Details of right autopodium elements of MCSNT 57031. Arrows indicate osteoporotic articular
surfaces. Abbreviations: dca: distale carpal, mc: metacarpal, pca: pisiform carpal, ph: phalanges, rca: radiale
carpal, uca: ulnare carpal, ?cca, possible fragments of the central carpal (centrale). Scale bar: 1 cm.

Figure 13. Left forelimb elements of MCSNT 57031 (A) with anatomical labels reported in B.
Abbreviations: lhu: left humerus, lr: left radius, lu: left ulna, mc: metacarpals, ph: phalanges, rca: radiale

carpal, uca: ulnare carpal. Scale bar: 5 cm.

Figure 14. Osteodermal series of MCSNT 57031 sketched and in different light direction (A) and
morphological outlines of the best-preserved ones in B. Black triangle points to possible ventrally exposed
osteoderms (*see* section 4.2). Arrows points to the direction towards the cranium of the specimen. Scale bars:
5 cm.

Figure 15. Histological thin sections under polarised light of MCSNT 57031 6th dorsal rib. A, overall rib
histological section; B, detail of secondary osteons, C, lines of arrested growth (LAGs) and annuli in the
outer cortex of the rib section; D, overview of the osteoderm thin section; E, close up of the outer cortex of
the osteoderm. Scale bars in: B, 250 nm; C, 500 nm; E, 200 nm. Abbreviations: An: annuli; cb: cancellous
bone; ec: erosional cavity; hs: haversian system; pv: primary vascularization. Red arrows indicate LAGs.

Figure 16. Phylogenetic position of *Acynodon adriaticus*. Results of Maximum Parsimony with strict
consensus (A) and majority rule (B) trees. Time calibrated Bayesian tree focused on the base of Eusuchia
(C). Yellow box is used to highlight the position of the genus *Acynodon*. Specimens referred to *Acynodon adriaticus* highlighted in red. Abbreviation in the chronological y-axis 'Ma' refers to Mega annum (million)

- years). Numbers in A indicate Bremer support (Decay index) while bootstrap support values are reported forthe Majority rule tree in B.
- **Figure 17.** Skeletal reconstruction of MCSNT 57031 in A with size comparison between the latter specimen
- in ventral view and the holotype (more complete in dorsal view) in B.
- **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	SPECIMEN DESCRIPTION	QUARRY
INVENTORY		INFORMATI
		ON
Acynodon		
adriaticus		
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		
Acynodon		
adriaticus 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	Collected from
	surface of a larger matrix slab with other unidentified bone	Slab 38 in
	fragments. The tuberculum is shorter than the capitulum and	1998-1999

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

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











MCSNT 57031

MCSNT 57248























- 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

 \boxtimes 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: