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Miocene fossils from the south-eastern Pacific shed light on the last radiation of marine crocodylians

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1 **Miocene fossils from the south-eastern Pacific shed light on the last radiation**
2 **of marine crocodylians**

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25

26 Abstract

27 The evolution of crocodylians as sea dwellers remains obscure because living representatives are
28 basically freshwater inhabitants and fossil evidence lacks crucial aspects about crocodylian
29 occupation of marine ecosystems. New fossils from marine deposits of Peru reveal that
30 crocodylians **were habitual coastal residents** of the south-eastern Pacific (SEP) for approximately
31 14 million years within the Miocene (*ca.* 19-5 Ma), an epoch including the highest **global** peak of
32 marine crocodylian **diversity**. The assemblage of the SEP comprised two long and slender-
33 snouted (longirostrine) taxa **of the Gavialidae: the giant *Piscogavialis* and a new early diverging**
34 **species, *Sacacosuchus cordovai*. Although living gavialids (*Gavialis* and *Tomistoma*) are**
35 **freshwater forms, this remarkable fossil record and a suite of evolutionary morphological**
36 **analyses reveal that the whole evolution of marine crocodylians pertained to the gavialids and**
37 **their stem relatives (Gavialoidea). This adaptive radiation produced two longirostrine ecomorphs**
38 **with dissimilar trophic roles in seawaters and involved multiple transmarine dispersals to South**
39 **America and most landmasses. Marine gavialoids were shallow sea dwellers, and their Cenozoic**
40 **diversification** was influenced by the availability of coastal habitats. Soon after the richness peak
41 of the Miocene, **gavialoid** crocodylians disappeared from the sea, probably as part of the marine
42 megafauna extinction of the Pliocene.

43

44 1. Introduction

45 During the Mesozoic, archaic crocodylomorphs achieved anatomical and physiological
46 specialisations for a pelagic marine lifestyle as in no other time in the history of Earth [1-4]. In
47 contrast, extant members of the crown clade (i.e. crocodylians) are mostly semi-aquatic,
48 freshwater animals and only some species of the genus *Crocodylus* (e.g. *Cr. porosus*, *Cr. acutus*)
49 regularly wander into coastal, saltwater settings [5-7]. Adaptations to withstand different
50 salinities (e.g. presence of lingual salt glands or a keratinised buccal cavity), however, occur not
51 only in *Crocodylus*, but also in strictly freshwater taxa, such as the Malayan and the Indian
52 gharials, *Gavialis gangeticus* (Gmelin, 1789) and *Tomistoma schlegelii* (Muller, 1838) [8,9],
53 suggesting that the common ancestor of Longirostres [sensu 10] had a marine ecology [11].

54 *Gavialis*, *Tomistoma* and their fossil kin (crown clade Gavialidae) typically possess long
55 and slender snouts. Fossils suggest that several extinct gavialids had marine habits since they
56 have been recovered from contexts depicting a wide range of salinities, including marginal to
57 fully marine areas (e.g. [12-19]). These fossils are documented from most landmasses and such
58 broad distribution requires crossing sea barriers to be explained [20-22]. Recent studies
59 established that the last radiation of crocodylomorphs into marine environments occurred in the
60 late Cretaceous with little or no marine diversity throughout the Cenozoic [3,4,23,24].

61 The rich fossil record from the south-eastern Pacific (SEP) in the coastal desert of Peru
62 has revealed invaluable data about the evolution of marine vertebrates and their ecosystems for
63 the last 42 million years (e.g. [25-27]). Along with whales, earless seals, penguins, and aquatic
64 sloths, most of the Neogene localities of the Pisco Formation have yielded well-preserved
65 remains of crocodylians [26,27], until now represented by one giant gavialid species,
66 *Piscogavialis jugaliperforatus* Kraus, 1998 [13].

67 Here, we present a **new gavialid** from the **same** marine deposits of the East Pisco Basin.
68 In contrast to *Piscogavialis*, **which is part of a widely diversified clade of gavialids in South**
69 **America**, this second **taxon** is **related to species from other landmasses that were formerly allied**
70 **to *Tomistoma* within the tomistomines (*sensu* [17]), emphasising the competence of gavialid**
71 **crocodylians as marine voyagers**. New finely preserved fossils of both taxa reveal that this
72 crocodylian assemblage had a prolonged residence **along the coasts** of the SEP, an area
73 dominated by the nutrient-rich waters of the Humboldt Current System where these cold-blooded
74 animals are now lacking [28]. We investigated the phylogenetic relationships of the **new gavialid**
75 and the evolutionary and environmental implications of the long-lasting occupation of
76 crocodylians in the SEP. Based on this record and a comprehensive fossil database, we use
77 phylogenetic, biogeographic, richness, and geometric morphometric analyses to characterise the
78 evolution, diversification, and decline of crocodylians in marine environments.

79

80 **2. Geological context, palaeoenvironment, and age**

81 The Chilcatay and Pisco formations of the East Pisco Basin document long-lasting marine
82 transgressions that affected about 350 km of the SEP (southern Peru) during the Neogene
83 (**electronic supplementary material**) [26,27,29]. Recent radiometric datings improved the
84 chronological constraints on these deposits in the Ica-Pisco Valleys and the Sacaco area (figure
85 1a), which as a whole range from the early Miocene (*ca.* 25 Ma) to the late Pliocene (*ca.* 2.7 Ma)
86 [30-32]. Fossils of the **new gavialid** and *Piscogavialis* are documented since ~19 Ma in the
87 Chilcatay Formation and extensively recovered in the late Miocene deposits of the Pisco
88 Formation in both areas (figures 1a,b, **S2 and S3**). The Peruvian record is particularly rich in the
89 late Miocene-earliest Pliocene strata of the Pisco Formation at Sacaco, with the last crocodylian

90 remains documented at *ca.* 4.85 Ma (figure 1*a,b*) [27]. During this time interval, the Sacaco area
91 was a shallow marine environment connected to the open ocean and comprising protected
92 embayments, rocky headlands, and small islands (figure 1*b*) [26,27]. A similar environment is
93 depicted for most fossiliferous deposits of the Chilcatay and Pisco formations at the Ica-Pisco
94 valley [31,32].

95

96 **3. Systematic Palaeontology**

97 Crocodyliformes Hay, 1930; Crocodylia Gmelin, 1789; **Longirostres (Cuvier, 1807) as defined**
98 **by [10]; Gavialidae (Adams, 1854)**

99 *Sacacosuchus cordovai* gen. et sp. nov.

100 *Etymology:* *Sacaco* after the rich fossiliferous area from where most remains were found;
101 *cordovai* after colleague and professor Jesús Córdova, to honour his brave and unconditional
102 support to develop palaeontology in Peru.

103 *Holotype:* Vertebrate Palaeontology Collection of the Natural History Museum of San
104 Marcos University (MUSM) 162, nearly complete skull (figure 2*a,b,e,f* and S4)

105 *Type Locality and Horizon:* Sud-Sacaco west (SAS-w; figure 1), Sacaco sub-basin,
106 northern Arequipa, Peru; Pisco Formation, late Miocene, dated to *ca.* 6.33 Ma [27].

107 *Referred specimens:* MUSM 160, partial skull of a juvenile, Locality SAS-w (figure 2*i*);
108 MUSM 161, partial skull of a sub-adult, Locality Montemar north (MTM-n; figure 2*c,d,g,h* and
109 S5), late Miocene, *ca.* 8.0 Ma; MUSM 163, left dentary preserved until the fourteenth dentary
110 alveolus, Locality Aguada de Lomas (AGL; figure S2), late Miocene, *ca.* 8.85 Ma; ([electronic](#)
111 [supplementary material](#)).

112 *Diagnosis: Sacacosuchus cordovai* is a relatively medium to large, longirostrine **gavialid**
113 diagnosed by the following unique combination of characters: premaxillae not expanded relative
114 to the maxillae; nasals in contact with the external naris; 14 maxillary teeth; fifth and ninth to
115 twelfth maxillary tooth alveoli enlarged; large, roughly circular orbits; deep splenial symphysis.
116 Differs from all other **gavialids** by having ventral margins of the orbit low and barrel vault-
117 shaped; postorbital bar lanceolate in cross-section with the external plane facing anterolaterally;
118 rostral process of quadratojugal long along the ventral margin of the infratemporal fenestrae and
119 no dorsal process bordering its posterior margin.

120 *General comparative description: Sacacosuchus cordovai* possesses a slender, long, and
121 parallel-sided snout that expands gradually posterolaterally into a robust, triangular orbital and
122 postrostral cranium (figure 2*a,c,i*). The snout is tubular in cross-section with slightly sinuate
123 margins along the dental series. In lateral view, the snout describes a wide dorsal curvature
124 (figure 2*e,g*). The rostral length/skull length index is 0.79, similar to that of *Gavialis gangeticus*
125 (0.76-0.79). However, the rostral width/postorbital width index is 0.22, lower than those of *T.*
126 *schlegelii* (0.34), *Piscogavialis* (0.27) and *G. gangeticus* (0.25), and equivalent to ‘thoracosaurus’
127 (0.22-0.23). The skull table is wide and rectangular in outline, **like *Gavialis***, in contrast to the
128 trapezoidal and relatively smaller one of *T. schlegelii*. The supratemporal fenestrae are wider
129 than long and bear sharp, overhanging borders with the skull table, as in *Paratomistoma* and
130 ‘*Tomistoma*’ *coppensi* [14]. The parietal interfenestral bar is relatively slender. The
131 infratemporal fenestrae are roughly triangular, with a gentle curve at the dorsal angle. The
132 choana is relatively large and basically triangular in outline. The dorsally oriented narial opening
133 is elongated and heart-shaped. The occipital plate is vertical and not visible in dorsal view.
134 Although not fully preserved, suborbital fenestrae show an elongated teardrop shape. The skull

135 bears five and 14 alveoli in the premaxilla and maxilla, respectively. The fifth maxillary alveoli
136 are larger than the fourth and the sixth, but the largest alveoli consist of the ninth, tenth, eleventh,
137 and twelfth tooth positions.

138 The prefrontals, the single frontal, and the postorbitals are not raised along the orbital
139 margins, thus the typical everted orbital margins of most crocodylians are not present in
140 *Sacacosuchus* (character 137-0). The demarcation between the parietal on the skull table and the
141 anterior border of the fenestrae is sharp, with the parietal even overhanging these fenestrae, as in
142 ‘*Tomistoma*’ *coppensi* and *Paratomistoma* (character 152-3). The squamosal surface of the skull
143 table slopes lateroventrally, as in *Gryposuchus* and *Paratomistoma* (character 156-0), and in
144 contrast to the planar skull table of *T. schlegelii* and *Crocodylus*.

145 The dentary bears ~17-18 alveoli and the dentary symphysis extends posteriorly up to the
146 level of the ninth-tenth dentary tooth loci (character 49-2), where they meet the wedge-like
147 rostral process of the united splenials, as in *T. schlegelii*. Body length estimation [33] for
148 *Sacacosuchus* type specimen is 432 cm (details in electronic supplementary material).

149

150 **4. Results and discussion**

151 **(a) Two Neogene crocodylians in the south-eastern Pacific**

152 The Lagerstätte fossil record of the East Pisco Basin reveals that two crocodylian taxa had
153 occupied coastal marine environments of the SEP for approximately 14 million years (*ca.* 19 to 5
154 Ma), an interval that comprises much of the Miocene (figure 1a). This record spans the warm
155 phase of the middle Miocene and the following global cooling trend [34]. Warm conditions
156 likely prevailed in the shallow, coastal marine environments of the SEP during the whole interval
157 [27]. Environmental and climatic conditions during the late Miocene were optimal for marine

158 crocodylians even **in Chile**, 1600 km south of Sacaco, where *Piscogavialis* bones (SGO-PV-834;
159 RS-G personal observation) have been documented [35].

160 The crocodylian remains of the East Pisco Basin were recovered in association with a
161 typical marine vertebrate fauna, including whales, earless seals, seabirds, sharks, and bony fishes
162 [26,27]. Remains of *Sacacosuchus* and *Piscogavialis* consist of cranial and postcranial bones in
163 partial or full anatomical connection (figures **S2 and S3**). The *Sacacosuchus* record includes
164 individuals at various ontogenetic stages (figure 2), suggesting that these crocodylians actually
165 lived, died, and were buried in marine waters. In contrast to the finely preserved marine
166 vertebrate remains [13,27,29], fossils of continental origin in the Pisco Basin are limited to a
167 handful of isolated bones [27].

168 With an estimated body length of 431 cm, *Sacacosuchus* was a medium-sized
169 crocodylian while *Piscogavialis* was a giant, almost twice as long (~776 cm; see [electronic](#)
170 [supplementary material](#)). Despite its large size, the latter was probably a specialist in acquiring
171 rapid small targets (e.g. fishes) while *Sacacosuchus* had a more generalized diet (see below).
172 Isolated bones of large individuals (cf. *Piscogavialis*) document the existence of crocodylians **up**
173 **to** the youngest vertebrate-bearing deposits, dated at 4.85 Ma (early Pliocene; figure 1a). The
174 sedimentary record was commenced again in Sacaco by *ca.* 2.7 Ma with no more crocodylian
175 remains [27]. Andean tectonics at *ca.* 4.5 Ma [36] and a eustatic drop of sea level in the Pliocene
176 [37] likely contributed to the end of Pisco sedimentation and the disruption of the coastal
177 environments. The extirpation (and extinction) of crocodylians from the SEP thus happened at
178 some point during the Pliocene and was probably caused by the reduction of continental flooding
179 and the establishment of cool waters of the Humboldt **current** system [27,37,38].

180

181 **(b) *Sacacosuchus* and gavialid phylogeny**

182 We conducted tip-dated Bayesian and maximum parsimony analyses of morphological
183 characters to determine evolutionary relationships of *Sacacosuchus cordovai* within the
184 crocodylians (methods in [electronic supplementary material](#)). We included in the data matrix the
185 slender-snouted South American taxon *Charactosuchus fieldsi* [39]. However, initial analyses
186 proved that currently known fragments of this taxon are uninformative for establishing its
187 phylogenetic affinities, thus it was excluded from the following searches. Our tip-dated
188 approaches retrieved distant relationships between living *Gavialis* and *Tomistoma*, as suggested
189 by other morphological analysis using this method [40]. Instead, our maximum parsimony
190 analysis with equal weighting recovered close relationships of *Tomistoma* and *Gavialis* among
191 living crocodylians, in line with molecular analyses [10,41,42] and a recent morphological
192 approach [43]. Morphological ‘tomistomines’ (*sensu* [43,44]) are the earliest diverging
193 gavialoids (*sensu* [45]), yet low supported. The long and slender-snouted ‘thoracosaurus’ from the
194 Cretaceous-early Eocene interval have been usually allied to ‘gharials’ (*sensu* [46]) in
195 morphology-based analyses [47,48]. Here, they are positioned deeply nested within the
196 Gavialidae, as a clade sister to ‘gharials.’ However, we identified several plesiomorphic features
197 in ‘thoracosaurus’ [43] lacking in ‘gharials’ and even across *Longirostres* (see [electronic](#)
198 [supplementary material](#)). As their position also provides significant temporal incongruence to the
199 crown clade Gavialidae [40,43], we constrained searches to force ‘thoracosaurus’ outside of
200 *Longirostres* and set the Palaeocene species *Argochampsa krebsi* as a floating taxon. This
201 constraint resulted in a tree insignificantly longer ($p > 0.05$), in which ‘thoracosaurus’ are
202 recovered as the sister clade of *Borealosuchus* + *Crocodylia* and *Argochampsa* within

203 *Gavialidae*. *Eogavialis* from the Eocene of Africa is recovered as the closest relative of *Gavialis*.
204 Subsequent analyses and discussions follow this phylogenetic hypothesis (figure 3a).

205 *Sacacosuchus* is deeply nested within the *Gavialidae*, as part of a polytomy (node 90)
206 with some morphological ‘tomistomines’ (i.e. *Gavialosuchus eggenburgensis* and
207 *Thecachampa*), and a large clade leading to advanced gavialids. Node 90 is supported by having
208 a vomer entirely obscured by maxillae and premaxillae (character 100-0), pterygoid surface and
209 choanal margins flushed (character 123-0), and quadrangular, wider than long, supratemporal
210 fenestrae (character 191-1). The divergence of *Sacacosuchus* occurred after that of *T. schlegelii*
211 but much earlier than the divergence of any other clade of Neotropical gavialids known so far.
212 Indeed, our analysis supports for independent origins of *Sacacosuchus*, *Aktiogavialis*,
213 gryposuchines (*sensu* [21]), and an Eocene Peruvian form coded for these analyses and currently
214 under study (MUSM 1513; figure 3a). Thus, phylogenetics cluster *Sacacosuchus* within
215 morphological ‘tomistomines’ and suggest a complex evolutionary history for Neotropical
216 gavialids.

217

218 **(c) Marine crocodylian biogeographic history and diversity**

219 Phylogenetic analysis indicates that crocodylians recovered from estuarine or marine
220 depositional settings exclusively pertain to the gavialoid clade (figure 3a; node 96). Although
221 extant *Gavialis* and *Tomistoma* species are freshwater forms, marine habits were widely
222 distributed among gavialoids and were probably the ancestral condition of the group [49]. The
223 optimal biogeographic reconstruction provided by a statistical dispersal-vicariance analysis (S-
224 DIVA; [electronic supplementary material](#)) points to the northern European (D) and Peri-Tethyan
225 coasts (C) as the most likely ancestral ranges for gavialoids (node 96) [18,43]. Standing diversity

226 and estimated richness analyses (electronic supplementary material) show that the diversity of
227 marine gavialoids increased from their origination to the early Eocene (figures 3a and 4), when
228 non-crocodylian crocodylomorphs (i.e. dyrosaurids and thoracosaurids) thrived in marine
229 environments [4,47,48,50]. The group soon dispersed to Asia and declined in northern Europe by
230 the late Eocene.

231 Presumed ancestral ranges of the Gavialidae (node 92) might have included the Peri-
232 Tethys and Asia (CF; figure 3a,b), with 100% of marginal probability. Because the Palaeocene
233 *Argochampsa* is deeply nested within the Gavialidae, a late Cretaceous origin for the clade is
234 suggested, in contrast to the Eocene origination proposed by molecular clock estimates [42].
235 Other gavialids recovered in our analysis are no older than Eocene.

236 From the Peri-Tethys, gavialids colonised North America (A) and South America (B), the
237 latter movement giving rise to *Sacacosuchus cordovai* (node 90). *Aktiogavialis*, gryposuchines,
238 and MUSM 1513 are additional clades from the Americas that might have originated within the
239 Peri-Tethys [20,45]. In the late Eocene, ancestors of gryposuchines and *Eogavialis* + *Gavialis*
240 (node 80) occupied BC, BF or BCF, each range with equal marginal probability (figure 3a,b).

241 The late Eocene and Oligocene seem to be characterised by low crocodylian standing
242 diversity in marine environments (figure 4a,b) [4,51]. However, the middle and late Miocene
243 witnessed pronounced origination rates (figure S14b), leading to the largest richness peak of
244 marine forms in the crocodylian history (figures 3a and 4a,b). This richness reflects the extensive
245 adaptive radiation of gavialids in most landmasses, particularly in the Americas and the Peri-
246 Tethys [13,16,20,21]. The East Pisco Basin record of *Sacacosuchus* and *Piscogavialis*
247 corresponds with this time interval, which is characterised by the Middle Miocene Climatic

248 **Optimum (17 to 15 Ma) and** a progressive global cooling with relatively small sea-level
249 fluctuations compared to the Oligocene or Plio-Pleistocene values [34,37,38].

250 A rapid and sustained **global** decline of marine **gavialids** started in the late Miocene and
251 continued until their complete vanishing at the middle or late Pliocene, probably as part of the
252 marine megafauna extinction of that epoch [38]. **Non-marine gavialids survived in Asia but**
253 **declined elsewhere [20]. In general,** freshwater crocodylians show a subtle demise at this time-
254 lapse but their richness was recovered by the end of the Pliocene, with the diversification of
255 *Crocodylus* (figure 3a).

256 **Ancestrally, gavialoids had marine habits, dispersed across marine barriers, and invaded**
257 **freshwater environments multiple times in different landmasses (figure 3a). The Peri-Tethys**
258 **might have been the centre for multidirectional marine dispersals of the gavialids, yet timing**
259 **incongruence on the origin of the clade persists.**

260

261 **(d) What is a marine crocodylian?**

262 **The phylogenetic Principal Component Analysis (pPCA;** methods in **electronic supplementary**
263 **material)** indicates **that marine taxa were all longirostrine forms.** Disparate morphospace
264 occupations within this rostral shape suggest additionally that two different ecomorphs roamed
265 **ancient** marine environments (figure 5). **Advanced marine** gavialoids, such as *Piscogavialis* and
266 *Eogavialis*, had an extremely long rostrum, enlarged teeth restricted to the tip of the snout and an
267 adductor chamber resembling that of the living *Gavialis gangeticus* [52]. These animals
268 performed low-bite-force and fast movements of the jaws and **were** predators of small and rapid
269 targets [20]. **‘Thoracosaur’ might belong to this ecomorph (figure 5).** In comparison,
270 morphological ‘tomistomines’, **such as *Thecachampsa*,** had a more powerful bite, larger teeth

271 close to the jaw joints, and their snout was usually less attenuated than in **advanced** gavialoids,
272 suggesting a diet composed of a wider range of prey sizes [20].

273 Marine crocodylians were essentially shallow marine inhabitants. These environments
274 have been proposed for several taxa of **gavialoids** by taphonomic, geologic, and **isotopic** data
275 [12-19,22,53, **electronic supplementary material**] and are consistent with their locomotion-related
276 anatomy. Because marine crocodylians show no significant differences in the axial skeleton and
277 the hindlimbs relative to living forms, they are inferred to have swum by using axial undulatory
278 movements and terrestrial-adapted limbs (plesiopedal) [54]. This locomotion pattern is
279 incompatible with breathing during prolonged or fast swimming and thus restricts predation to an
280 explosive ambushing behaviour in shallow waters, as has been proposed for other reptiles during
281 incipient adaptations to a marine lifestyle [54].

282 If marine crocodylians were limited to shallow marine environments, their diversification
283 and extinction would have been driven by the availability of coastal habitats and might have
284 been extensively disturbed by global sea-level changes. We would also expect that marine
285 crocodylians and open-ocean predators (hydropedal with a stiff trunk: e.g. odontocete cetaceans)
286 responded differently to evolutionary drivers. For example, changes in odontocete communities
287 are documented worldwide and attributed to a mix of physical and biological factors, in which
288 niche scalation and a pelagic lifestyle played distinct roles [23,55]. Instead, sea-level fluctuations
289 with effects on coastal habitats have been identified as a main driver of crocodylomorph
290 diversification in marine environments [3,4,51]. The peaks in origination rates and standing
291 diversity of the Miocene coincide with a period of relatively high and stable sea level, and
292 **essentially corresponds to** the flourishing of **gavialid** crocodylians in extensive continental
293 flooding areas across the Peri-Tethys and the SEP [26,27,30,31,56]. By the Pliocene, the rapid

294 demise of marine crocodylians concurs with lower sea surface temperature, decreasing sea-level
295 [37] and, a drastic reduction of neritic habitats [38].

296 Bones show no features unique to marine crocodylians. Similar patterns of longirostry
297 and locomotion anatomy are also observed in freshwater taxa [20] (figure 5). However, certain
298 morphologies, such as protruding orbital margins or blunt snouts, would not be found in marine
299 crocodylians because these evolved exclusively associated with an ecology of freshwater
300 environments [46,57]. Intriguingly, the sole living genus with populations in marine areas,
301 *Crocodylus*, does not have a longirostrine condition (figures 3a and 5). Dispersal across marine
302 barriers occurred widely within this taxon but most (if not all) of the fossil record from America,
303 Europe, Asia, Oceania, and Africa was recovered from deposits indicating fluvial and lacustrine
304 environments [58,59]. Even fossils of the saltwater crocodile, *Crocodylus porosus*, come from
305 freshwater deposits [60,61] and the late Miocene *Crocodylus checchiai*, the species linking
306 Neotropical and African *Crocodylus*, was recovered from a marginal marine formation in which
307 vertebrates of continental origin prevail [62]. Fossils examined under multiple assessments
308 (taphonomy, stable isotopes, palaeohistology) should provide further insights on the functional
309 roles of ancient and modern marine crocodylians.

310

311 5. Conclusions

312 *Sacacosuchus cordovai* belongs to the crown clade Gavialidae with ancestors in the Peri-Tethys
313 that migrated to South America crossing marine barriers. This kind of dispersal was
314 multidirectional and characterised the diversification of gavialids in coastal areas, although the
315 timing is still poorly constrained. Extant *Gavialis* and *Tomistoma* are freshwater survivors within
316 a predominantly marine group. The crocodylian marine ecology was restricted to longirostrine

317 forms of the gavialoids, in contrast to the variety of clades and rostral shapes that evolved in
318 freshwater ecosystems. Within this longirostrine morphotype, two distinct ecomorphs with
319 dissimilar trophic roles thrived in seawaters. The evolution of *Sacacosuchus* and *Piscogavialis* in
320 the coastal, flooded areas of the SEP is an exemplar of the adaptive radiation of gavialoids in
321 marine ecosystems. As semi-aquatic predators, gavialoids occupied shallow coastal habitats and
322 got a peak in marine richness during the Miocene, when relatively high and stable sea levels
323 occurred. Soon after, these marine crocodylians suffered a drastic decline, probably triggered by
324 the global loss of shallow marine areas. The demise of the longirostrine, marine crocodylians
325 roughly coincides with the marine megafauna extinction of the Pliocene.

326

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335 **Author contributions.** R.S.-G. designed the research, wrote the manuscript and performed
336 systematic and morphometric research, with additional writing contributions from all authors.
337 R.S.-G. and S.J. performed anatomical studies. D.O., T.D.V, and P.B. provided geological data
338 and DO performed diversity analyses. P.R. performed tree calibration and biogeographic
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343

344 **References**

- 345 1. Hua S, De Buffrenil V. 1996 Bone histology as a clue in the interpretation of functional
346 adaptations in the Thalattosuchia (Reptilia, Crocodylia). *J. Vertebr. Paleontol.* **16**, 703-717.
347 (doi:10.1080/02724634.1996.10011359)
- 348 2. Herrera Y, Fernández MS, Gasparini Z. 2013 The snout of *Cricosaurus araucanensis*: a case
349 study in novel anatomy of the nasal region of metriorhynchids. *Lethaia* **3**, 331-340.
350 (doi:10.1111/let.12011)
- 351 3. Martin JE, Amiot R, Lécuyer C, Benton MJ. 2014 Sea surface temperature contributes to
352 marine crocodylomorph evolution. *Nat. Commun.* **5**, 1–7. (doi:10.1038/ncomms5658)
- 353 4. Mannion PD, Benson RB, Carrano MT, Tennant JP, Judd J, Butler RJ. 2015 Climate
354 constrains the evolutionary history and biodiversity of crocodylians. *Nat. Commun.* **6**, 1–9.
355 (doi:10.1038/ncomms9438)
- 356 5. Mazzotti FJ, Dunson WA. 1989 Osmoregulation in crocodylians. *Am. Zool.* **29**, 903-920
357 (doi:10.1093/icb/29.3.903)
- 358 6. Wheatley PV, Peckham H, Newsome SD, Koch PL. 2012 Estimating marine resource use by
359 the American crocodile *Crocodylus acutus* in southern Florida, USA. *Mar. Ecol. Prog. Ser.*
360 **447**, 211-229 (doi:10.3354/meps09503)
- 361 7. Grigg G, Kirshner D. 2015 Biology and evolution of crocodylians. Ithaca and London:
362 Cornell University Press.

- 363 8. Taplin LE. 1988 Osmoregulation in crocodylians. *Biol. Rev.* **63**, 333-377.
364 (doi:10.1111/j.1469-185X.1988.tb00721.x)
- 365 9. Leslie AJ, Taplin LE. 2000 Recent developments in osmoregulation of crocodylians. In
366 *Crocodylian Biology and Evolution* (eds GC Grigg, F Seebacher, GE Franklin), pp. 265–279.
367 Chipping Norton: Survey Beatty & Sons.
- 368 10. Harshman J, Huddleston CJ, Bollback JP, Parsons TJ, Braun MJ. 2003 True and false
369 gharials: a nuclear gene phylogeny of Crocodylia. *Syst. Biol.* **52**, 386-402.
- 370 11. Wheatley PV. 2012 Understanding saltwater tolerance and marine resource use in the
371 Crocodylia: a stable isotope approach. PhD. thesis, University of California.
- 372 12. Erickson BR, Sawyer GT. 1996 The estuarine crocodile *Gavialosuchus carolinensis* n. sp.
373 (Crocodylia: Eusuchia) from the late Oligocene of South Carolina, North America.
374 *Monographs Sci. Mus. Minnesota (Paleontology)* **3**, 1-47.
- 375 13. Kraus R. 1998 The cranium of *Piscogavialis jugaliperforatus* n. gen., n. sp. (Gavialidae,
376 Crocodylia) from the Miocene of Peru. *Paläontol. Z.* **72**, 389–405.
377 (doi:10.1007/BF02988368)
- 378 14. Brochu CA, Gingerich PD. 2000 New tomistomine crocodylian from the middle Eocene
379 (Bartonian) of Wadi Hitan, Fayum Province, Egypt. *Contr. Mus. Pal. Uni. Michigan* **30**, 251-
380 268.
- 381 15. Brochu CA. 2007 Systematics and taxonomy of Eocene tomistomine crocodylians from
382 Britain and Northern Europe. *Palaeontology* **50**, 917-928. (doi:10.1111/j.1475-
383 4983.2007.00679.x)

- 384 16. Piras P, Delfino M, Del Favero L, Kotsakis T. 2007 Phylogenetic position of the crocodylian
385 *Megadontosuchus arduini* and tomistomine palaeobiogeography. *Acta Palaeontol. Pol.* **52**,
386 315–328.
- 387 17. Jouve S, Bardet N, Jalil NE, Suberbiola XP, Bouya B, Amaghazaz M. 2008 The oldest
388 African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine
389 reptiles through the Cretaceous-Tertiary boundary. *J. Vertebr. Paleontol.* **28**, 409-421.
390 (doi:10.1671/0272- 4634(2008)28[409:TOACPP]2.0.CO;2)
- 391 18. Jouve S, Bouya B, Amaghazaz M, Meslouh S. 2015 *Maroccosuchus zennaroi* (Crocodylia:
392 Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical
393 implications of the basalmost tomistomine. *J. Syst. Palaeontol.* **13**, 421-445.
394 (doi:10.1111/zoj.12357)
- 395 19. Jouve S, Khalloufi B, Zouhri S. 2019 Longirostrine crocodylians from the Bartonian of
396 Morocco and Paleogene climatic and sea level oscillations in the Peri-Tethys area. *J. Vertebr.*
397 *Paleontol.* **39**, e1617723. (doi:10.1080/02724634.2019.1617723)
- 398 20. Salas-Gismondi R, Moreno-Bernal JW, Scheyer TM, Sánchez-Villagra MR, Jaramillo C.
399 2019 New Miocene Caribbean gavialoids and patterns of longirostry in crocodylians. *J. Syst.*
400 *Palaeontol.* **17**, 1049-1075. (doi.org/10.1080/14772019.2018.1495275)
- 401 21. Vélez-Juarbe J, Brochu CA, Santos H. 2007 A gharial from the Oligocene of Puerto Rico:
402 transoceanic dispersal in the history of a non-marine reptile. *Proc. R. Soc. B* **274**, 1245-1254.
403 (doi:10.1098/rspb.2006.0455)
- 404 22. Ristevski J, Price GJ, Weisbecker V, Salisbury SW. 2021 First record of a tomistomine
405 crocodylian from Australia. *Sci. Rep.* **11**, 12158. (doi:10.1038/541598-021-91717-y)

- 406 23. Pyenson ND, Kelley NP, Parham JF. 2014 Marine tetrapod macroevolution: physical and
407 biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeogr.*
408 *Palaeoclimatol. Palaeoecol.* **400**, 1-8. (doi:10.1016/j.palaeo.2014.02.018)
- 409 24. Stubbs TL, Pierce SE, Elsler A, Anderson PS, Rayfield EJ, Benton MJ. 2021 Ecological
410 opportunity and the rise and fall of crocodylomorph evolutionary innovation. *Proc. R. Soc.*
411 *B*, **288**, 20210069. (doi:10.1098/rspb.2021.0069)
- 412 25. Lambert O, Bianucci G, Salas-Gismondi R, Di Celma C, Steurbaut E, Urbina M, Muizon C
413 2019. An amphibious whale from the middle Eocene of Peru reveals early South Pacific
414 dispersal of quadrupedal cetaceans. *Curr. Biol.* **29**, 1352-1359.
415 (doi:10.1016/j.cub.2019.02.050)
- 416 26. Muizon C de, DeVries TJ. 1985 Geology and paleontology of late Cenozoic marine deposits
417 in the Sacaco area (Peru). *Geol. Rundsch.* **74**, 547-563. (doi:10.1007/BF01821211)
- 418 27. Ochoa D *et al.* 2021 Late Neogene evolution of the Peruvian margin and its ecosystems: a
419 synthesis from the Sacaco record. *Int. J. Earth Sci.* 1-31. (doi:10.1007/s00531-021-02003-1)
- 420 28. Chavez FP, Bertrand A, Guevara Carrasco R, Soler P, Csirke J. 2008. The northern
421 Humboldt Current System: Brief history, present status and a view towards the future. *Prog.*
422 *Oceanogr.* **79**, 95-105. (doi:10.1016/j.pocean.2008.10.012)
- 423 29. Di Celma C *et al.* 2018 Facies analysis, stratigraphy and marine vertebrate assemblage of the
424 lower Miocene Chilcatay Formation at Ullujaya (Pisco basin, Peru). *J. Maps* **14**, 257-268.
425 (doi:10.1080/17445647.2018.1456490)
- 426 30. DeVries TJ, Jud NA. 2018 Lithofacies patterns and paleogeography of the Miocene
427 Chilcatay and lower Pisco depositional sequences (East Pisco Basin, Peru). *Bol. Soc. Geol.*
428 *Perú* **8**, 124-167.

- 429 31. DeVries TJ, Schrader H. 1997 Middle Miocene marine sediments in the Pisco basin
430 (Peru). *Bol. Soc. Geol. Perú* **87**, 1-13.
- 431 32. Bosio G *et al.* 2020 Strontium Isotope Stratigraphy and the thermophilic fossil fauna from
432 the middle Miocene of the East Pisco Basin (Peru). *J. S. Am. Earth Sci.* **97**, 102399
433 (doi:10.1016/j.jsames.2019.102399)
- 434 33. Sereno PC, Larsson HC, Sidor CA, Gado B. 2001 The giant crocodyliform *Sarcosuchus* from
435 the Cretaceous of Africa. *Science* **294**, 1516–1519. (doi:10.1126/science.1066521)
- 436 34. Zachos J, Pagani M, Sloan L, Thomas E, Billups K 2001. Trends, rhythms, and aberrations in
437 global climate 65 Ma to present. *Science* **292**, 686-693. (doi:10.1126/science.1059412)
- 438 35. Walsh SA, Suárez M. 2005 First post-Mesozoic record of Crocodyliformes from Chile. *Acta*
439 *Palaeontol. Pol.* **50**, 595-600.
- 440 36. Espurt N, Baby P, Brusset S, Roddaz M, Hermoza W, Regard V, Antoine P-O, Salas-
441 Gismondi R, Bolanos R. 2007 How does the Nazca Ridge subduction influence the modern
442 Amazonian foreland basin? *Geology* **35**, 515-518. (doi:10.1130/G23237A.1)
- 443 37. Miller KG, Browning JV, Schmelz WJ, Kopp RE, Mountain GS, Wright JD. 2020 Cenozoic
444 sea-level and cryospheric evolution from deep-sea geochemical and continental margin
445 records. *Sci. Adv.* **6**, eaaz1346. (doi:10.1126/sciadv.aaz1346)
- 446 38. Pimiento C, Griffin JN, Clements CF, Silvestro D, Varela S, Uhen MD, Jaramillo C. 2017
447 The Pliocene marine megafauna extinction and its impact on functional diversity. *Nat. Ecol.*
448 *Evol.* **1**, 1100-1106. (doi:10.1038/s41559-017-0223-6)
- 449 39. Langston Jr W. 1965 Fossil crocodilians from Colombia and the Cenozoic history of the
450 Crocodilia in South America. *Univ. Calif. Publ. Geol. Sci.* **52**, 1–157.

- 451 40. Lee MSY, Yates AM. 2018 Tip-dating and homoplasy: reconciling the shallow molecular
452 divergences of modern gharials with their long fossil record. *Proc. R. Soc. B* **285**: 20181071
453 (doi:10.1098/rspb.2018.1071)
- 454 41. Gatesy JG, Amato G, Norell M, DeSalle R, Hayashi C. 2003 Total evidence support for
455 extreme atavism in gavialine crocodylians. *Syst. Biol.* **52**, 403–422.
456 (doi:10.1080/10635150390197037)
- 457 42. Oaks JR. 2011 A time-calibrated species tree of Crocodylia reveals a recent radiation of the
458 true crocodiles. *Evolution* **65**, 3285–3297. (doi: 10.1111/j.1558-5646.2011.01373.x)
- 459 43. Rio JP, Mannion PD. 2021 Phylogenetic analysis of a new morphological dataset elucidates
460 the evolutionary history of Crocodylia and resolves the long-standing gharial problem. *PeerJ*
461 **9**:e12094 doi: 10.7717/PeerJ.12094
- 462 44. Iijima M, Kobayashi Y. 2019 Mosaic nature in the skeleton of East Asian crocodylians fills
463 the morphological gap between “Tomistominae” and Gavialinae. *Cladistics* **35**, 623-632.
464 (doi:10.1111/cla.12372)
- 465 45. Norell MA, Clark JM, Hutchison JH. 1994 The Late Cretaceous alligatoroid *Brachychamps*
466 *montana* (Crocodylia): new material and putative relationships. *Am. Mus. Novit.* **3116**, 1–26.
- 467 46. Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara J, Claude J, Antoine P-O. 2016 A new 13
468 million year old gavialoid crocodylian from proto-Amazonian mega- wetlands reveals
469 parallel evolutionary trends in skull shape linked to longirostry. *PLoS ONE* **11**, e0152453.
470 (doi:10.1371/journal.pone.0152453)
- 471 47. Brochu CA. 2004 A new Late Cretaceous gavialoid crocodylian from eastern North America
472 and the phylogenetic relationships of thoracosaurids. *J. Vertebr. Paleontol.* **24**, 610–633.
473 (doi:10.1671/0272-4634(2004)024[0610:ANLGC]2.0.CO;2)

- 474 48. Brochu CA. 2006 Osteology and phylogenetic significance of *Eosuchus minor* (Marsh, 1870)
475 new combination, a longirostrine crocodylian from the late Paleocene of North America. *J.*
476 *Paleontol.* **80**, 162-186.
- 477 49. Wilberg EW, Turner AH, Brochu CA. 2019 Evolutionary structure and timing of major
478 habitat shifts in Crocodylomorpha. *Sci. Rep.* **9**, 514. (doi:10.1038/s41598-018-36795-1)
- 479 50. Jouve S. 2021. Differential diversification through the K-Pg boundary, and post-crisis
480 opportunism in longirostrine crocodyliforms. *Gondwana Research* **99**, 110–130.
481 (doi:10.1016/j.gr.2021.06.020)
- 482 51. De Celis A, Narváez I, Ortega F. 2020 Spatiotemporal palaeodiversity patterns of modern
483 crocodiles (Crocodyliformes: Eusuchia). *Zool. J. Linn. Soc.* **189**, 635-656.
484 (doi:10.1093/zoolinnean/zlz038)
- 485 52. Erickson GM, Gignac PM, Stepan SJ, Lappin AK, Vliet KA, Brueggen JD, Inouye BD,
486 Kledzik D, Webb GJ. 2012 Insights into the ecology and evolutionary success of crocodylians
487 revealed through bite-force and tooth-pressure experimentation. *PLoS ONE*, **7**, e31781.
488 (doi:10.1371/journal.pone.0031781)
- 489 53. Whiting ET, Steadman DW, Krigbaum J. 2016 Paleoeology of Miocene crocodylians in
490 Florida: insights from stable isotope analysis. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*
491 **451**, 23-34. (doi:10.1016/j.palaeo.2016.03.009)
- 492 54. Benson RB, Butler RJ. 2011 Uncovering the diversification history of marine tetrapods:
493 ecology influences the effect of geological sampling biases. *Geol. Soc. Spec. Publ.* **358**, 191-
494 208. (doi:10.1144/SP358.13)
- 495 55. Marx FG, Uhen MD 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution
496 of modern whales. *Science* **327**, 993-996. (doi:10.1126/science.1185581)

- 497 56. Sant K, Palcu DV, Mandic O, Krijgsman W. 2017 Changing seas in the early-middle
498 Miocene of Central Europe: a Mediterranean approach to Paratethyan stratigraphy. *Terra*
499 *Nova* **29**, 273-281. (doi:10.1111/ter.12273)
- 500 57. Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara JV, Wesselingh FP, Antoine P-O. 2015 A
501 Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-
502 Amazonian mega-wetlands. *Proc. R. Soc. B* **282**, 20142490. (doi:10.1098/rspb.2014.2490)
- 503 58. Brochu CA. 2000 Phylogenetic relationships and divergence timing of *Crocodylus* based on
504 morphology and the fossil record. *Copeia* **3**, 657-673. (doi:10.1643/0045-
505 8511(2000)000[0657:PRADTO]2.0.CO;2)
- 506 59. Scheyer TM, Aguilera OA, Delfino M, Fortier DC, Carlini AA, Sánchez R, Carrillo-Briceño
507 JD, Quiroz L, Sánchez-Villagra MR. 2013 Crocodylian diversity peak and extinction in the
508 late Cenozoic of the northern Neotropics. *Nat. Commun.* **4**, 1907. (doi:10.1038/ncomms2940)
- 509 60. Molnar RE. 1982 *Pallimnarchus* and other Cenozoic crocodiles in Queensland. *Mem. Qd.*
510 *Mus.* **20**, 657-673.
- 511 61. Hocknull SA *et al.* 2020 Extinction of eastern Sahul megafauna coincides with sustained
512 environmental deterioration. *Nat. Commun.* **11**, 1-14. (doi:10.1038/s41467-020-15785-w)
- 513 62. Delfino M, Iurino DA, Mercurio B, Piras P, Rook L, Sardella R. 2020 Old African fossils
514 provide new evidence for the origin of the American crocodiles. *Sci. Rep.* **10**, 1-11.
515 (doi:10.1038/s41598-020-68482-5)
- 516 63. Blakey RC. 2008 Gondwana paleogeography from assembly to breakup—A 500 m.y.
517 odyssey. In *Resolving the Late Paleozoic Ice Age in Time and Space* (eds CR Fielding, TD
518 Frank, JL Isbell), pp. 1-28. Boulder: Geological Society of America Special Paper.
519

520 **Figure captions**

521 **Figure 1.** Fossil record of *Sacacosuchus* and *Piscogavialis* in the Neogene deposits of the Pisco
 522 Basin, southern Peru. (a) Schematic stratigraphic columns of the Chilcatay (yellow) and Pisco
 523 (light blue) formations with crocodylian-bearing localities at the Ica-Pisco Valleys (left; from *ca.*
 524 20 to 7 Ma) and the Sacaco area (from *ca.* 9.38 to 4.85 Ma). (b) Location and map of the East
 525 Pisco basin showing the Chilcatay (yellow) and Pisco (blue) deposits within putative continental
 526 flooded areas (in white). Map modified from [31]. AGL, Aguada de Lomas; CCO-n, Cerro
 527 Colorado norte; CCO-s, Cerro Colorado sur; CLQ, Cerro Los Quesos; COM, Comatrana; CVT,
 528 Correviento; ELJ, EL Jahuay; MTM, Montemar; MTM-n, Montemar norte; MTM, Montemar;
 529 SAO-e, Sacaco east; SAS-w, Sud-Sacaco west; SUL, Sula Site; YAU, Yauca; ZAM, Zamaca.

530 **Figure 2.** Photograph and schematic drawing of the skulls of *Sacacosuchus cordovai* gen. et sp.
 531 nov. from Sacaco at different ontogenetic stages. Adult specimen (holotype: MUSM 162) in
 532 dorsal (a), ventral (b), right lateral (e), and occipital (f) views. Sub-adult specimen (MUSM 161)
 533 in dorsal (c), ventral (d), left lateral (g; inverted), and occipital (h) views. Juvenile specimen
 534 (MUSM 160) in dorsal (i) view. ba, basioccipital; bs, basisphenoid; CH, choana; cq,
 535 cranioquadrate foramen; ec, ectopterygoid; ec.mx, maxilla surface for ectopterygoid; EN,
 536 external naris; eo, exoccipital; f, frontal; fcp, foramen carotideum posterior; IF, incisive foramen;
 537 ITF, infratemporal fenestra; j, jugal; j.la, lacrimal surface for jugal; j.mx, maxilla surface for
 538 jugal; l, lacrimal;; ls, laterosphenoid; m5, m,9, m14, maxillary tooth positions; mx, maxilla;
 539 n.pm, premaxilla surface for nasal; na, nasal; OR, orbit; p, parietal; pa, palatine; pa.mx, maxilla
 540 surface for palatine; pf, prefrontal; pm, premaxilla; p3, p4, premaxillary tooth positions; po,
 541 postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; qj.q, quadrate surface for quadratojugal;

542 s, shelf; so, supraoccipital; sq, squamosal; STF, supratemporal fenestra; SOF, suborbital fenestra;
 543 v, foramen vagus; xii, foramen for hypoglossal nerve. All photographs to the same scale. Scale
 544 bar equals 5 cm.

545 **Figure 3.** Phylogenetic position of *Sacacosuchus cordovai* and other marine taxa (represented by
 546 their skulls) within the Crocodylia, with ancestral range reconstructions provided by S-DIVA. (a)
 547 **Time-calibrated, strict consensus tree on the constrained and equal weighted analysis.**
 548 **Crocodylians found in marine deposits pertain to the gavialoid clade.** The ancestral range
 549 reconstructions are summarised as pie charts and shown for critical nodes of **the Gavialoidea (73:**
 550 ***Eogavialis* + *Gavialis*; 79: *Gryposuchinae*; 81: *Aktiogavialis*; 82: *Argochampsia*, *Aktiogavialis*,**
 551 **advanced gavialids; 83: ‘gharials’ + MUSM 1513; 86: Miocene African forms; 89:**
 552 ***Thecachampsia* species; 90: *Sacacosuchus*, *Gavialosuchus*, *Thecachampsia* + unnamed node 88;**
 553 **92: Gavialidae; 96: Gavialoidea), Crocodylidae (99: node 97 + *Cr. porosus*); and ‘thoracosaurus’**
 554 **(121).** Geographic areas of distribution are represented by colours and capital letters. Wide bars
 555 within branches show stratigraphic range of taxa. **White arrows at the branches of gryposuchines,**
 556 ***Gavialis*, and *Tomistoma schlegelii* indicate major shifts from marine to freshwater habitats.**
 557 Eocene palaeomap (b) is from Blackey [63].

558 **Figure 4.** Diversity of crocodylians during the last 90 my. (a) Observed range-through
 559 (OR) diversity of crocodylian genera (OR bys: red dashed line), OR of marine (OR mg: blue
 560 solid line) and non-marine genera (OR n-mg: black solid line) **calculated per chronostratigraphic**
 561 **stages.** (b) Estimated richness based on the Chao1 extrapolation estimator calculated per
 562 chronostratigraphic stages (red dots) and second-order Jackknife richness estimator calculated
 563 using 3-million years time bins for marine (mg: blue line) and non-marine (n-mg: black line)

564 **crocodylia** genera. Grey solid line represents a smoothed global sea level curve after Miller et
565 al. [37] and the orange solid line a global mean temperature curve after Zachos et al. [34]. The
566 time span of the south-eastern Pacific **gavialid** crocodylia record (SEP C) encompasses the
567 estimated highest peak of genera and species of marine forms. PLI, Pliocene.

568 **Figure 5.** The **pPCA of the snout of the** Crocodylia defined by PC1 and PC2. Black dots denote
569 non marine taxa and blue dots (with or without skulls) correspond to extinct taxa (gavialoids and
570 *Thoracosaurus*) recovered from marginal to fully marine environments and the living saltwater
571 crocodile, *Crocodylus porosus*. **Positive values of PC1 depict forms with longirostrine**
572 **ecomorphs. All gavialoids pertain to these ecomorphs but bearing large variation along positive**
573 **and negatives values of PC2, with morphological ‘tomistomines’ restricted to the positive values**
574 **and ‘gharials’ confined to the negative values. The sole ‘thoracosaur’ included in this analysis is**
575 **positioned close to the ‘gharial’ ecomorph. Grey polygon encompasses the gavialoid**
576 **morphospace and blue areas correspond to distinct ecomorphs of marine gavialoids within the**
577 **morphological ‘tomistomines’ (upper) and ‘gharials’ (lower).**

1 **Miocene fossils from the south-eastern Pacific shed light on the last radiation**
2 **of marine crocodylians**

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25

26 **Abstract**

27 The evolution of crocodylians as sea dwellers remains obscure because living representatives are
28 basically freshwater inhabitants and fossil evidence lacks crucial aspects about crocodylian
29 occupation of marine ecosystems. New fossils from marine deposits of Peru reveal that
30 crocodylians were habitual coastal residents of the south-eastern Pacific (SEP) for approximately
31 14 million years within the Miocene (*ca.* 19-5 Ma), an epoch including the highest global peak of
32 marine crocodylian diversity. The assemblage of the SEP comprised two long and slender-
33 snouted (longirostrine) taxa of the Gavialidae: the giant *Piscogavialis* and a new early diverging
34 species, *Sacacosuchus cordovai*. Although living gavialids (*Gavialis* and *Tomistoma*) are
35 freshwater forms, this remarkable fossil record and a suite of evolutionary morphological
36 analyses reveal that the whole evolution of marine crocodylians pertained to the gavialids and
37 their stem relatives (Gavialoidea). This adaptive radiation produced two longirostrine ecomorphs
38 with dissimilar trophic roles in seawaters and involved multiple transmarine dispersals to South
39 America and most landmasses. Marine gavialoids were shallow sea dwellers, and their Cenozoic
40 diversification was influenced by the availability of coastal habitats. Soon after the richness peak
41 of the Miocene, gavialoid crocodylians disappeared from the sea, probably as part of the marine
42 megafauna extinction of the Pliocene.

43

44 **1. Introduction**

45 During the Mesozoic, archaic crocodylomorphs achieved anatomical and physiological
46 specialisations for a pelagic marine lifestyle as in no other time in the history of Earth [1-4]. In
47 contrast, extant members of the crown clade (i.e. crocodylians) are mostly semi-aquatic,
48 freshwater animals and only some species of the genus *Crocodylus* (e.g. *Cr. porosus*, *Cr. acutus*)
49 regularly wander into coastal, saltwater settings [5-7]. Adaptations to withstand different
50 salinities (e.g. presence of lingual salt glands or a keratinised buccal cavity), however, occur not
51 only in *Crocodylus*, but also in strictly freshwater taxa, such as the Malayan and the Indian
52 gharials, *Gavialis gangeticus* (Gmelin, 1789) and *Tomistoma schlegelii* (Muller, 1838) [8,9],
53 suggesting that the common ancestor of Longirostres (*sensu* [10]) had a marine ecology [11].

54 *Gavialis*, *Tomistoma* and their fossil kin (crown clade Gavialidae) typically possess long
55 and slender snouts. Fossils suggest that several extinct gavialids had marine habits since they
56 have been recovered from contexts depicting a wide range of salinities, including marginal to
57 fully marine areas (e.g. [12-19]). These fossils are documented from most landmasses and such
58 broad distribution requires crossing sea barriers to be explained [20-22]. Recent studies
59 established that the last radiation of crocodylomorphs into marine environments occurred in the
60 late Cretaceous with little or no marine diversity throughout the Cenozoic [3,4,23,24].

61 The rich fossil record from the south-eastern Pacific (SEP) in the coastal desert of Peru
62 has revealed invaluable data about the evolution of marine vertebrates and their ecosystems for
63 the last 42 million years (e.g. [25-27]). Along with whales, earless seals, penguins, and aquatic
64 sloths, most of the Neogene localities of the Pisco Formation have yielded well-preserved
65 remains of crocodylians [26,27], until now represented by one giant gavialid species,
66 *Piscogavialis jugaliperforatus* Kraus, 1998 [13].

67 Here, we present a new gavialid from the same marine deposits of the East Pisco Basin.
68 In contrast to *Piscogavialis*, which is part of a widely diversified clade of gavialids in South
69 America, this second taxon is related to species from other landmasses that were formerly allied
70 to *Tomistoma* within the tomistomines (*sensu* [17]), emphasising the competence of gavialid
71 crocodylians as marine voyagers. New finely preserved fossils of both taxa reveal that this
72 crocodylian assemblage had a prolonged residence along the coasts of the SEP, an area
73 dominated by the nutrient-rich waters of the Humboldt Current System where these cold-blooded
74 animals are now lacking [28]. We investigated the phylogenetic relationships of the new gavialid
75 and the evolutionary and environmental implications of the long-lasting occupation of
76 crocodylians in the SEP. Based on this record and a comprehensive fossil database, we use
77 phylogenetic, biogeographic, richness, and geometric morphometric analyses to characterise the
78 evolution, diversification, and decline of crocodylians in marine environments.

79

80 **2. Geological context, palaeoenvironment, and age**

81 The Chilcatay and Pisco formations of the East Pisco Basin document long-lasting marine
82 transgressions that affected about 350 km of the SEP (southern Peru) during the Neogene
83 (electronic supplementary material) [26,27,29]. Recent radiometric datings improved the
84 chronological constraints on these deposits in the Ica-Pisco Valleys and the Sacaco area (figure
85 1a), which as a whole range from the early Miocene (*ca.* 25 Ma) to the late Pliocene (*ca.* 2.7 Ma)
86 [30-32]. Fossils of the new gavialid and *Piscogavialis* are documented since ~19 Ma in the
87 Chilcatay Formation and extensively recovered in the late Miocene deposits of the Pisco
88 Formation in both areas (figures 1a,b, S2 and S3). The Peruvian record is particularly rich in the
89 late Miocene-earliest Pliocene strata of the Pisco Formation at Sacaco, with the last crocodylian

90 remains documented at *ca.* 4.85 Ma (figure 1*a,b*) [27]. During this time interval, the Sacaco area
91 was a shallow marine environment connected to the open ocean and comprising protected
92 embayments, rocky headlands, and small islands (figure 1*b*) [26,27]. A similar environment is
93 depicted for most fossiliferous deposits of the Chilcatay and Pisco formations at the Ica-Pisco
94 valley [31,32].

95

96 **3. Systematic Palaeontology**

97 Crocodyliformes Hay, 1930; Crocodylia Gmelin, 1789; Longirostres (Cuvier, 1807) as defined
98 by [10]; Gavialidae (Adams, 1854)

99 *Sacacosuchus cordovai* gen. et sp. nov.

100 *Etymology:* *Sacaco* after the rich fossiliferous area from where most remains were found;
101 *cordovai* after colleague and professor Jesús Córdova, to honour his brave and unconditional
102 support to develop palaeontology in Peru.

103 *Holotype:* Vertebrate Palaeontology Collection of the Natural History Museum of San
104 Marcos University (MUSM) 162, nearly complete skull (figure 2*a,b,e,f* and S4)

105 *Type Locality and Horizon:* Sud-Sacaco west (SAS-w; figure 1), Sacaco sub-basin,
106 northern Arequipa, Peru; Pisco Formation, late Miocene, dated to *ca.* 6.33 Ma [27].

107 *Referred specimens:* MUSM 160, partial skull of a juvenile, Locality SAS-w (figure 2*i*);
108 MUSM 161, partial skull of a sub-adult, Locality Montemar north (MTM-n; figure 2*c,d,g,h* and
109 S5), late Miocene, *ca.* 8.0 Ma; MUSM 163, left dentary preserved until the fourteenth dentary
110 alveolus, Locality Aguada de Lomas (AGL; figure S2), late Miocene, *ca.* 8.85 Ma; ([electronic
111 supplementary material](#)).

112 *Diagnosis: Sacacosuchus cordovai* is a relatively medium to large, longirostrine gavialid
113 diagnosed by the following unique combination of characters: premaxillae not expanded relative
114 to the maxillae; nasals in contact with the external naris; 14 maxillary teeth; fifth and ninth to
115 twelfth maxillary tooth alveoli enlarged; large, roughly circular orbits; deep splenial symphysis.
116 Differs from all other gavialids by having ventral margins of the orbit low and barrel vault-
117 shaped; postorbital bar lanceolate in cross-section with the external plane facing anterolaterally;
118 rostral process of quadratojugal long along the ventral margin of the infratemporal fenestrae and
119 no dorsal process bordering its posterior margin.

120 *General comparative description: Sacacosuchus cordovai* possesses a slender, long, and
121 parallel-sided snout that expands gradually posterolaterally into a robust, triangular orbital and
122 postrostral cranium (figure 2*a,c,i*). The snout is tubular in cross-section with slightly sinuate
123 margins along the dental series. In lateral view, the snout describes a wide dorsal curvature
124 (figure 2*e,g*). The rostral length/skull length index is 0.79, similar to that of *Gavialis gangeticus*
125 (0.76-0.79). However, the rostral width/postorbital width index is 0.22, lower than those of *T.*
126 *schlegelii* (0.34), *Piscogavialis* (0.27) and *G. gangeticus* (0.25), and equivalent to ‘thoracosaurus’
127 (0.22-0.23). The skull table is wide and rectangular in outline, like *Gavialis*, in contrast to the
128 trapezoidal and relatively smaller one of *T. schlegelii*. The supratemporal fenestrae are wider
129 than long and bear sharp, overhanging borders with the skull table, as in *Paratomistoma* and
130 ‘*Tomistoma*’ *coppensi* [14]. The parietal interfenestral bar is relatively slender. The
131 infratemporal fenestrae are roughly triangular, with a gentle curve at the dorsal angle. The
132 choana is relatively large and basically triangular in outline. The dorsally oriented narial opening
133 is elongated and heart-shaped. The occipital plate is vertical and not visible in dorsal view.
134 Although not fully preserved, suborbital fenestrae show an elongated teardrop shape. The skull

135 bears five and 14 alveoli in the premaxilla and maxilla, respectively. The fifth maxillary alveoli
136 are larger than the fourth and the sixth, but the largest alveoli consist of the ninth, tenth, eleventh,
137 and twelfth tooth positions.

138 The prefrontals, the single frontal, and the postorbitals are not raised along the orbital
139 margins, thus the typical everted orbital margins of most crocodylians are not present in
140 *Sacacosuchus* (character 137-0). The demarcation between the parietal on the skull table and the
141 anterior border of the fenestrae is sharp, with the parietal even overhanging these fenestrae, as in
142 ‘*Tomistoma*’ *coppensi* and *Paratomistoma* (character 152-3). The squamosal surface of the skull
143 table slopes lateroventrally, as in *Gryposuchus* and *Paratomistoma* (character 156-0), and in
144 contrast to the planar skull table of *T. schlegelii* and *Crocodylus*.

145 The dentary bears ~17-18 alveoli and the dentary symphysis extends posteriorly up to the
146 level of the ninth-tenth dentary tooth loci (character 49-2), where they meet the wedge-like
147 rostral process of the united splenials, as in *T. schlegelii*. Body length estimation [33] for
148 *Sacacosuchus* type specimen is 432 cm (details in [electronic supplementary material](#)).

149

150 **4. Results and discussion**

151 **(a) Two Neogene crocodylians in the south-eastern Pacific**

152 The Lagerstätte fossil record of the East Pisco Basin reveals that two crocodylian taxa had
153 occupied coastal marine environments of the SEP for approximately 14 million years (*ca.* 19 to 5
154 Ma), an interval that comprises much of the Miocene (figure 1a). This record spans the warm
155 phase of the middle Miocene and the following global cooling trend [34]. Warm conditions
156 likely prevailed in the shallow, coastal marine environments of the SEP during the whole interval
157 [27]. Environmental and climatic conditions during the late Miocene were optimal for marine

158 crocodylians even in Chile, 1600 km south of Sacaco, where *Piscogavialis* bones (SGO-PV-834;
159 RS-G personal observation) have been documented [35].

160 The crocodylian remains of the East Pisco Basin were recovered in association with a
161 typical marine vertebrate fauna, including whales, earless seals, seabirds, sharks, and bony fishes
162 [26,27]. Remains of *Sacacosuchus* and *Piscogavialis* consist of cranial and postcranial bones in
163 partial or full anatomical connection (figures S2 and S3). The *Sacacosuchus* record includes
164 individuals at various ontogenetic stages (figure 2), suggesting that these crocodylians actually
165 lived, died, and were buried in marine waters. In contrast to the finely preserved marine
166 vertebrate remains [13,27,29], fossils of continental origin in the Pisco Basin are limited to a
167 handful of isolated bones [27].

168 With an estimated body length of 431 cm, *Sacacosuchus* was a medium-sized
169 crocodylian while *Piscogavialis* was a giant, almost twice as long (~776 cm; see electronic
170 supplementary material). Despite its large size, the latter was probably a specialist in acquiring
171 rapid small targets (e.g. fishes) while *Sacacosuchus* had a more generalized diet (see below).
172 Isolated bones of large individuals (cf. *Piscogavialis*) document the existence of crocodylians up
173 to the youngest vertebrate-bearing deposits, dated at 4.85 Ma (early Pliocene; figure 1a). The
174 sedimentary record was commenced again in Sacaco by ca. 2.7 Ma with no more crocodylian
175 remains [27]. Andean tectonics at ca. 4.5 Ma [36] and a eustatic drop of sea level in the Pliocene
176 [37] likely contributed to the end of Pisco sedimentation and the disruption of the coastal
177 environments. The extirpation (and extinction) of crocodylians from the SEP thus happened at
178 some point during the Pliocene and was probably caused by the reduction of continental flooding
179 and the establishment of cool waters of the Humboldt current system [27,37,38].

180

181 **(b) *Sacacosuchus* and gavialid phylogeny**

182 We conducted tip-dated Bayesian and maximum parsimony analyses of morphological
183 characters to determine evolutionary relationships of *Sacacosuchus cordovai* within the
184 crocodylians (methods in [electronic supplementary material](#)). We included in the data matrix the
185 slender-snouted South American taxon *Charactosuchus fieldsi* [39]. However, initial analyses
186 proved that currently known fragments of this taxon are uninformative for establishing its
187 phylogenetic affinities, thus it was excluded from the following searches. Our tip-dated
188 approaches retrieved distant relationships between living *Gavialis* and *Tomistoma*, as suggested
189 by other morphological analysis using this method [40]. Instead, our maximum parsimony
190 analysis with equal weighting recovered close relationships of *Tomistoma* and *Gavialis* among
191 living crocodylians, in line with molecular analyses [10,41,42] and a recent morphological
192 approach [43]. Morphological ‘tomistomines’ (*sensu* [43,44]) are the earliest diverging
193 gavialoids (*sensu* [45]), yet low supported. The long and slender-snouted ‘thoracosaurus’ from the
194 Cretaceous-early Eocene interval have been usually allied to ‘gharials’ (*sensu* [46]) in
195 morphology-based analyses [47,48]. Here, they are positioned deeply nested within the
196 Gavialidae, as a clade sister to ‘gharials.’ However, we identified several plesiomorphic features
197 in ‘thoracosaurus’ [43] lacking in ‘gharials’ and even across *Longirostres* (see [electronic](#)
198 [supplementary material](#)). As their position also provides significant temporal incongruence to the
199 crown clade Gavialidae [40,43], we constrained searches to force ‘thoracosaurus’ outside of
200 *Longirostres* and set the Palaeocene species *Argochampsa krebsi* as a floating taxon. This
201 constraint resulted in a tree insignificantly longer ($p > 0.05$), in which ‘thoracosaurus’ are
202 recovered as the sister clade of *Borealosuchus* + Crocodylia and *Argochampsa* within

203 Gavialidae. *Eogavialis* from the Eocene of Africa is recovered as the closest relative of *Gavialis*.
204 Subsequent analyses and discussions follow this phylogenetic hypothesis (figure 3a).

205 *Sacacosuchus* is deeply nested within the Gavialidae, as part of a polytomy (node 90)
206 with some morphological ‘tomistomines’ (i.e. *Gavialosuchus eggenburgensis* and
207 *Thecachampa*), and a large clade leading to advanced gavialids. Node 90 is supported by having
208 a vomer entirely obscured by maxillae and premaxillae (character 100-0), pterygoid surface and
209 choanal margins flushed (character 123-0), and quadrangular, wider than long, supratemporal
210 fenestrae (character 191-1). The divergence of *Sacacosuchus* occurred after that of *T. schlegelii*
211 but much earlier than the divergence of any other clade of Neotropical gavialids known so far.
212 Indeed, our analysis supports for independent origins of *Sacacosuchus*, *Aktiogavialis*,
213 gryposuchines (*sensu* [21]), and an Eocene Peruvian form coded for these analyses and currently
214 under study (MUSM 1513; figure 3a). Thus, phylogenetics cluster *Sacacosuchus* within
215 morphological ‘tomistomines’ and suggest a complex evolutionary history for Neotropical
216 gavialids.

217

218 **(c) Marine crocodylian biogeographic history and diversity**

219 Phylogenetic analysis indicates that crocodylians recovered from estuarine or marine
220 depositional settings exclusively pertain to the gavialoid clade (figure 3a; node 96). Although
221 extant *Gavialis* and *Tomistoma* species are freshwater forms, marine habits were widely
222 distributed among gavialoids and were probably the ancestral condition of the group [49]. The
223 optimal biogeographic reconstruction provided by a statistical dispersal-vicariance analysis (S-
224 DIVA; [electronic supplementary material](#)) points to the northern European (D) and Peri-Tethyan
225 coasts (C) as the most likely ancestral ranges for gavialoids (node 96) [18,43]. Standing diversity

226 and estimated richness analyses ([electronic supplementary material](#)) show that the diversity of
227 marine gavialoids increased from their origination to the early Eocene (figures 3*a* and 4), when
228 non-crocodylian crocodylomorphs (i.e. dyrosaurids and thoracosaurids) thrived in marine
229 environments [4,47,48,50]. The group soon dispersed to Asia and declined in northern Europe by
230 the late Eocene.

231 Presumed ancestral ranges of the Gavialidae (node 92) might have included the Peri-
232 Tethys and Asia (CF; figure 3*a,b*), with 100% of marginal probability. Because the Palaeocene
233 *Argochampsa* is deeply nested within the Gavialidae, a late Cretaceous origin for the clade is
234 suggested, in contrast to the Eocene origination proposed by molecular clock estimates [42].
235 Other gavialids recovered in our analysis are no older than Eocene.

236 From the Peri-Tethys, gavialids colonised North America (A) and South America (B), the
237 latter movement giving rise to *Sacacosuchus cordovai* (node 90). *Aktiogavialis*, gryposuchines,
238 and MUSM 1513 are additional clades from the Americas that might have originated within the
239 Peri-Tethys [20,45]. In the late Eocene, ancestors of gryposuchines and *Eogavialis* + *Gavialis*
240 (node 80) occupied BC, BF or BCF, each range with equal marginal probability (figure 3*a,b*).

241 The late Eocene and Oligocene seem to be characterised by low crocodylian standing
242 diversity in marine environments (figure 4*a,b*) [4,51]. However, the middle and late Miocene
243 witnessed pronounced origination rates (figure S14*b*), leading to the largest richness peak of
244 marine forms in the crocodylian history (figures 3*a* and 4*a,b*). This richness reflects the extensive
245 adaptive radiation of gavialids in most landmasses, particularly in the Americas and the Peri-
246 Tethys [13,16,20,21]. The East Pisco Basin record of *Sacacosuchus* and *Piscogavialis*
247 corresponds with this time interval, which is characterised by the Middle Miocene Climatic

248 Optimum (17 to 15 Ma) and a progressive global cooling with relatively small sea-level
249 fluctuations compared to the Oligocene or Plio-Pleistocene values [34,37,38].

250 A rapid and sustained global decline of marine gavialids started in the late Miocene and
251 continued until their complete vanishing at the middle or late Pliocene, probably as part of the
252 marine megafauna extinction of that epoch [38]. Non-marine gavialids survived in Asia but
253 declined elsewhere [20]. In general, freshwater crocodylians show a subtle demise at this time-
254 lapse but their richness was recovered by the end of the Pliocene, with the diversification of
255 *Crocodylus* (figure 3a).

256 Ancestrally, gavialoids had marine habits, dispersed across marine barriers, and invaded
257 freshwater environments multiple times in different landmasses (figure 3a). The Peri-Tethys
258 might have been the centre for multidirectional marine dispersals of the gavialids, yet timing
259 incongruence on the origin of the clade persists.

260

261 **(d) What is a marine crocodylian?**

262 The phylogenetic Principal Component Analysis (pPCA; methods in [electronic supplementary](#)
263 [material](#)) indicates that marine taxa were all longirostrine forms. Disparate morphospace
264 occupations within this rostral shape suggest additionally that two different ecomorphs roamed
265 ancient marine environments (figure 5). Advanced marine gavialoids, such as *Piscogavialis* and
266 *Eogavialis*, had an extremely long rostrum, enlarged teeth restricted to the tip of the snout and an
267 adductor chamber resembling that of the living *Gavialis gangeticus* [52]. These animals
268 performed low-bite-force and fast movements of the jaws and were predators of small and rapid
269 targets [20]. ‘Thoracosaurus’ might belong to this ecomorph (figure 5). In comparison,
270 morphological ‘tomistomines’, such as *Thecachampsa*, had a more powerful bite, larger teeth

271 close to the jaw joints, and their snout was usually less attenuated than in advanced gavialoids,
272 suggesting a diet composed of a wider range of prey sizes [20].

273 Marine crocodylians were essentially shallow marine inhabitants. These environments
274 have been proposed for several taxa of gavialoids by taphonomic, geologic, and isotopic data
275 [12-19,22,53] and are consistent with their locomotion-related anatomy. Because marine
276 crocodylians show no significant differences in the axial skeleton and the hindlimbs relative to
277 living forms, they are inferred to have swum by using axial undulatory movements and
278 terrestrial-adapted limbs (plesiopedal) [54]. This locomotion pattern is incompatible with
279 breathing during prolonged or fast swimming and thus restricts predation to an explosive
280 ambushing behaviour in shallow waters, as has been proposed for other reptiles during incipient
281 adaptations to a marine lifestyle [54].

282 If marine crocodylians were limited to shallow marine environments, their diversification
283 and extinction would have been driven by the availability of coastal habitats and might have
284 been extensively disturbed by global sea-level changes. We would also expect that marine
285 crocodylians and open-ocean predators (hydropedal with a stiff trunk: e.g. odontocete cetaceans)
286 responded differently to evolutionary drivers. For example, changes in odontocete communities
287 are documented worldwide and attributed to a mix of physical and biological factors, in which
288 niche scalation and a pelagic lifestyle played distinct roles [23,55]. Instead, sea-level fluctuations
289 with effects on coastal habitats have been identified as a main driver of crocodylomorph
290 diversification in marine environments [3,4,51]. The peaks in origination rates and standing
291 diversity of the Miocene coincide with a period of relatively high and stable sea level, and
292 essentially corresponds to the flourishing of gavialid crocodylians in extensive continental
293 flooding areas across the Peri-Tethys and the SEP [26,27,30,31,56]. By the Pliocene, the rapid

294 demise of marine crocodylians concurs with lower sea surface temperature, decreasing sea-level
295 [37] and, a drastic reduction of neritic habitats [38].

296 Bones show no features unique to marine crocodylians. Similar patterns of longirostry
297 and locomotion anatomy are also observed in freshwater taxa [20] (figure 5). However, certain
298 morphologies, such as protruding orbital margins or blunt snouts, would not be found in marine
299 crocodylians because these evolved exclusively associated with an ecology of freshwater
300 environments [46,57]. Intriguingly, the sole living genus with populations in marine areas,
301 *Crocodylus*, does not have a longirostrine condition (figures 3a and 5). Dispersal across marine
302 barriers occurred widely within this taxon but most (if not all) of the fossil record from America,
303 Europe, Asia, Oceania, and Africa was recovered from deposits indicating fluvial and lacustrine
304 environments [58,59]. Even fossils of the saltwater crocodile, *Crocodylus porosus*, come from
305 freshwater deposits [60,61] and the late Miocene *Crocodylus checchiai*, the species linking
306 Neotropical and African *Crocodylus*, was recovered from a marginal marine formation in which
307 vertebrates of continental origin prevail [62]. Fossils examined under multiple assessments
308 (taphonomy, stable isotopes, palaeohistology) should provide further insights on the functional
309 roles of ancient and modern marine crocodylians.

310

311 **5. Conclusions**

312 *Sacacosuchus cordovai* belongs to the crown clade Gavialidae with ancestors in the Peri-Tethys
313 that migrated to South America crossing marine barriers. This kind of dispersal was
314 multidirectional and characterised the diversification of gavialids in coastal areas, although the
315 timing is still poorly constrained. Extant *Gavialis* and *Tomistoma* are freshwater survivors within
316 a predominantly marine group. The crocodylian marine ecology was restricted to longirostrine

317 forms of the gavialoids, in contrast to the variety of clades and rostral shapes that evolved in
318 freshwater ecosystems. Within this longirostrine morphotype, two distinct ecomorphs with
319 dissimilar trophic roles thrived in seawaters. The evolution of *Sacacosuchus* and *Piscogavialis* in
320 the coastal, flooded areas of the SEP is an exemplar of the adaptive radiation of gavialoids in
321 marine ecosystems. As semi-aquatic predators, gavialoids occupied shallow coastal habitats and
322 got a peak in marine richness during the Miocene, when relatively high and stable sea levels
323 occurred. Soon after, these marine crocodylians suffered a drastic decline, probably triggered by
324 the global loss of shallow marine areas. The demise of the longirostrine, marine crocodylians
325 roughly coincides with the marine megafauna extinction of the Pliocene.

326

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336 systematic and morphometric research, with additional writing contributions from all authors.
337 R.S.-G. and S.J. performed anatomical studies. D.O., T.D.V, and P.B. provided geological data
338 and DO performed diversity analyses. P.R. performed tree calibration and biogeographic
339 analyses. All authors contributed to the discussions and interpretation of the results.

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343

344 **References**

- 345 1. Hua S, De Buffrenil V. 1996 Bone histology as a clue in the interpretation of functional
346 adaptations in the Thalattosuchia (Reptilia, Crocodylia). *J. Vertebr. Paleontol.* **16**, 703-717.
347 (doi:10.1080/02724634.1996.10011359)
- 348 2. Herrera Y, Fernández MS, Gasparini Z. 2013 The snout of *Cricosaurus araucanensis*: a case
349 study in novel anatomy of the nasal region of metriorhynchids. *Lethaia* **3**, 331-340.
350 (doi:10.1111/let.12011)
- 351 3. Martin JE, Amiot R, Lécuyer C, Benton MJ. 2014 Sea surface temperature contributes to
352 marine crocodylomorph evolution. *Nat. Commun.* **5**, 1–7. (doi:10.1038/ncomms5658)
- 353 4. Mannion PD, Benson RB, Carrano MT, Tennant JP, Judd J, Butler RJ. 2015 Climate
354 constrains the evolutionary history and biodiversity of crocodylians. *Nat. Commun.* **6**, 1–9.
355 (doi:10.1038/ncomms9438)
- 356 5. Mazzotti FJ, Dunson WA. 1989 Osmoregulation in crocodylians. *Am. Zool.* **29**, 903-920
357 (doi:10.1093/icb/29.3.903)
- 358 6. Wheatley PV, Peckham H, Newsome SD, Koch PL. 2012 Estimating marine resource use by
359 the American crocodile *Crocodylus acutus* in southern Florida, USA. *Mar. Ecol. Prog. Ser.*
360 **447**, 211-229 (doi:10.3354/meps09503)
- 361 7. Grigg G, Kirshner D. 2015 Biology and evolution of crocodylians. Ithaca and London:
362 Cornell University Press.

- 363 8. Taplin LE. 1988 Osmoregulation in crocodylians. *Biol. Rev.* **63**, 333-377.
364 (doi:10.1111/j.1469-185X.1988.tb00721.x)
- 365 9. Leslie AJ, Taplin LE. 2000 Recent developments in osmoregulation of crocodylians. In
366 *Crocodylian Biology and Evolution* (eds GC Grigg, F Seebacher, GE Franklin), pp. 265–279.
367 Chipping Norton: Survey Beatty & Sons.
- 368 10. Harshman J, Huddleston CJ, Bollback JP, Parsons TJ, Braun MJ. 2003 True and false
369 gharials: a nuclear gene phylogeny of Crocodylia. *Syst. Biol.* **52**, 386-402.
- 370 11. Wheatley PV. 2012 Understanding saltwater tolerance and marine resource use in the
371 Crocodylia: a stable isotope approach. PhD. thesis, University of California.
- 372 12. Erickson BR, Sawyer GT. 1996 The estuarine crocodile *Gavialosuchus carolinensis* n. sp.
373 (Crocodylia: Eusuchia) from the late Oligocene of South Carolina, North America.
374 *Monographs Sci. Mus. Minnesota (Paleontology)* **3**, 1-47.
- 375 13. Kraus R. 1998 The cranium of *Piscogavialis jugaliperforatus* n. gen., n. sp. (Gavialidae,
376 Crocodylia) from the Miocene of Peru. *Paläontol. Z.* **72**, 389–405.
377 (doi:10.1007/BF02988368)
- 378 14. Brochu CA, Gingerich PD. 2000 New tomistomine crocodylian from the middle Eocene
379 (Bartonian) of Wadi Hitan, Fayum Province, Egypt. *Contr. Mus. Pal. Uni. Michigan* **30**, 251-
380 268.
- 381 15. Brochu CA. 2007 Systematics and taxonomy of Eocene tomistomine crocodylians from
382 Britain and Northern Europe. *Palaeontology* **50**, 917-928. (doi:10.1111/j.1475-
383 4983.2007.00679.x)

- 384 16. Piras P, Delfino M, Del Favero L, Kotsakis T. 2007 Phylogenetic position of the crocodylian
385 *Megadontosuchus arduini* and tomistomine palaeobiogeography. *Acta Palaeontol. Pol.* **52**,
386 315–328.
- 387 17. Jouve S, Bardet N, Jalil NE, Suberbiola XP, Bouya B, Amaghazaz M. 2008 The oldest
388 African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine
389 reptiles through the Cretaceous-Tertiary boundary. *J. Vertebr. Paleontol.* **28**, 409-421.
390 (doi:10.1671/0272- 4634(2008)28[409:TOACPP]2.0.CO;2)
- 391 18. Jouve S, Bouya B, Amaghazaz M, Meslouh S. 2015 *Maroccosuchus zennaroi* (Crocodylia:
392 Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical
393 implications of the basalmost tomistomine. *J. Syst. Palaeontol.* **13**, 421-445.
394 (doi:10.1111/zoj.12357)
- 395 19. Jouve S, Khalloufi B, Zouhri S. 2019 Longirostrine crocodylians from the Bartonian of
396 Morocco and Paleogene climatic and sea level oscillations in the Peri-Tethys area. *J. Vertebr.*
397 *Paleontol.* **39**, e1617723. (doi:10.1080/02724634.2019.1617723)
- 398 20. Salas-Gismondi R, Moreno-Bernal JW, Scheyer TM, Sánchez-Villagra MR, Jaramillo C.
399 2019 New Miocene Caribbean gavialoids and patterns of longirostry in crocodylians. *J. Syst.*
400 *Palaeontol.* **17**, 1049-1075. (doi.org/10.1080/14772019.2018.1495275)
- 401 21. Vélez-Juarbe J, Brochu CA, Santos H. 2007 A gharial from the Oligocene of Puerto Rico:
402 transoceanic dispersal in the history of a non-marine reptile. *Proc. R. Soc. B* **274**, 1245-1254.
403 (doi:10.1098/rspb.2006.0455)
- 404 22. Ristevski J, Price GJ, Weisbecker V, Salisbury SW. 2021 First record of a tomistomine
405 crocodylian from Australia. *Sci. Rep.* **11**, 12158. (doi:10.1038/541598-021-91717-y)

- 406 23. Pyenson ND, Kelley NP, Parham JF. 2014 Marine tetrapod macroevolution: physical and
407 biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeogr.*
408 *Palaeoclimatol. Palaeoecol.* **400**, 1-8. (doi:10.1016/j.palaeo.2014.02.018)
- 409 24. Stubbs TL, Pierce SE, Elsler A, Anderson PS, Rayfield EJ, Benton MJ. 2021 Ecological
410 opportunity and the rise and fall of crocodylomorph evolutionary innovation. *Proc. R. Soc.*
411 *B*, **288**, 20210069. (doi:10.1098/rspb.2021.0069)
- 412 25. Lambert O, Bianucci G, Salas-Gismondi R, Di Celma C, Steurbaut E, Urbina M, Muizon C
413 2019. An amphibious whale from the middle Eocene of Peru reveals early South Pacific
414 dispersal of quadrupedal cetaceans. *Curr. Biol.* **29**, 1352-1359.
415 (doi:10.1016/j.cub.2019.02.050)
- 416 26. Muizon C de, DeVries TJ. 1985 Geology and paleontology of late Cenozoic marine deposits
417 in the Sacaco area (Peru). *Geol. Rundsch.* **74**, 547-563. (doi:10.1007/BF01821211)
- 418 27. Ochoa D *et al.* 2021 Late Neogene evolution of the Peruvian margin and its ecosystems: a
419 synthesis from the Sacaco record. *Int. J. Earth Sci.* 1-31. (doi:10.1007/s00531-021-02003-1)
- 420 28. Chavez FP, Bertrand A, Guevara Carrasco R, Soler P, Csirke J. 2008. The northern
421 Humboldt Current System: Brief history, present status and a view towards the future. *Prog.*
422 *Oceanogr.* **79**, 95-105. (doi:10.1016/j.pocean.2008.10.012)
- 423 29. Di Celma C *et al.* 2018 Facies analysis, stratigraphy and marine vertebrate assemblage of the
424 lower Miocene Chilcatay Formation at Ullujaya (Pisco basin, Peru). *J. Maps* **14**, 257-268.
425 (doi:10.1080/17445647.2018.1456490)
- 426 30. DeVries TJ, Jud NA. 2018 Lithofacies patterns and paleogeography of the Miocene
427 Chilcatay and lower Pisco depositional sequences (East Pisco Basin, Peru). *Bol. Soc. Geol.*
428 *Perú* **8**, 124-167.

- 429 31. DeVries TJ, Schrader H. 1997 Middle Miocene marine sediments in the Pisco basin
430 (Peru). *Bol. Soc. Geol. Perú* **87**, 1-13.
- 431 32. Bosio G *et al.* 2020 Strontium Isotope Stratigraphy and the thermophilic fossil fauna from
432 the middle Miocene of the East Pisco Basin (Peru). *J. S. Am. Earth Sci.* **97**, 102399
433 (doi:10.1016/j.jsames.2019.102399)
- 434 33. Sereno PC, Larsson HC, Sidor CA, Gado B. 2001 The giant crocodyliform *Sarcosuchus* from
435 the Cretaceous of Africa. *Science* **294**, 1516–1519. (doi:10.1126/science.1066521)
- 436 34. Zachos J, Pagani M, Sloan L, Thomas E, Billups K 2001. Trends, rhythms, and aberrations in
437 global climate 65 Ma to present. *Science* **292**, 686-693. (doi:10.1126/science.1059412)
- 438 35. Walsh SA, Suárez M. 2005 First post-Mesozoic record of Crocodyliformes from Chile. *Acta*
439 *Palaeontol. Pol.* **50**, 595-600.
- 440 36. Espurt N, Baby P, Brusset S, Roddaz M, Hermoza W, Regard V, Antoine P-O, Salas-
441 Gismondi R, Bolanos R. 2007 How does the Nazca Ridge subduction influence the modern
442 Amazonian foreland basin? *Geology* **35**, 515-518. (doi:10.1130/G23237A.1)
- 443 37. Miller KG, Browning JV, Schmelz WJ, Kopp RE, Mountain GS, Wright JD. 2020 Cenozoic
444 sea-level and cryospheric evolution from deep-sea geochemical and continental margin
445 records. *Sci. Adv.* **6**, eaaz1346. (doi:10.1126/sciadv.aaz1346)
- 446 38. Pimiento C, Griffin JN, Clements CF, Silvestro D, Varela S, Uhen MD, Jaramillo C. 2017
447 The Pliocene marine megafauna extinction and its impact on functional diversity. *Nat. Ecol.*
448 *Evol.* **1**, 1100-1106. (doi:10.1038/s41559-017-0223-6)
- 449 39. Langston Jr W. 1965 Fossil crocodylians from Colombia and the Cenozoic history of the
450 Crocodylia in South America. *Univ. Calif. Publ. Geol. Sci.* **52**, 1–157.

- 451 40. Lee MSY, Yates AM. 2018 Tip-dating and homoplasy: reconciling the shallow molecular
452 divergences of modern gharials with their long fossil record. *Proc. R. Soc. B* **285**: 20181071
453 (doi:10.1098/rspb.2018.1071)
- 454 41. Gatesy JG, Amato G, Norell M, DeSalle R, Hayashi C. 2003 Total evidence support for
455 extreme atavism in gavialine crocodylians. *Syst. Biol.* **52**, 403–422.
456 (doi:10.1080/10635150390197037)
- 457 42. Oaks JR. 2011 A time-calibrated species tree of Crocodylia reveals a recent radiation of the
458 true crocodiles. *Evolution* **65**, 3285–3297. (doi: 10.1111/j.1558-5646.2011.01373.x)
- 459 43. Rio JP, Mannion PD. 2021 Phylogenetic analysis of a new morphological dataset elucidates
460 the evolutionary history of Crocodylia and resolves the long-standing gharial problem. *PeerJ*
461 **9**:e12094 doi: 10.7717/PeerJ.12094
- 462 44. Iijima M, Kobayashi Y. 2019 Mosaic nature in the skeleton of East Asian crocodylians fills
463 the morphological gap between “Tomistominae” and Gavialinae. *Cladistics* **35**, 623-632.
464 (doi:10.1111/cla.12372)
- 465 45. Norell MA, Clark JM, Hutchison JH. 1994 The Late Cretaceous alligatoroid *Brachychamps*
466 *montana* (Crocodylia): new material and putative relationships. *Am. Mus. Novit.* **3116**, 1–26.
- 467 46. Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara J, Claude J, Antoine P-O. 2016 A new 13
468 million year old gavialoid crocodylian from proto-Amazonian mega- wetlands reveals
469 parallel evolutionary trends in skull shape linked to longirostry. *PLoS ONE* **11**, e0152453.
470 (doi:10.1371/journal.pone.0152453)
- 471 47. Brochu CA. 2004 A new Late Cretaceous gavialoid crocodylian from eastern North America
472 and the phylogenetic relationships of thoracosaurids. *J. Vertebr. Paleontol.* **24**, 610–633.
473 (doi:10.1671/0272-4634(2004)024[0610:ANLGC]2.0.CO;2)

- 474 48. Brochu CA. 2006 Osteology and phylogenetic significance of *Eosuchus minor* (Marsh, 1870)
475 new combination, a longirostrine crocodylian from the late Paleocene of North America. *J.*
476 *Paleontol.* **80**, 162-186.
- 477 49. Wilberg EW, Turner AH, Brochu CA. 2019 Evolutionary structure and timing of major
478 habitat shifts in Crocodylomorpha. *Sci. Rep.* **9**, 514. (doi:10.1038/s41598-018-36795-1)
- 479 50. Jouve S. 2021. Differential diversification through the K-Pg boundary, and post-crisis
480 opportunism in longirostrine crocodyliforms. *Gondwana Research* **99**, 110–130.
481 (doi:10.1016/j.gr.2021.06.020)
- 482 51. De Celis A, Narváez I, Ortega F. 2020 Spatiotemporal palaeodiversity patterns of modern
483 crocodiles (Crocodyliformes: Eusuchia). *Zool. J. Linn. Soc.* **189**, 635-656.
484 (doi:10.1093/zoolinnean/zlz038)
- 485 52. Erickson GM, Gignac PM, Stepan SJ, Lappin AK, Vliet KA, Brueggen JD, Inouye BD,
486 Kledzik D, Webb GJ. 2012 Insights into the ecology and evolutionary success of crocodylians
487 revealed through bite-force and tooth-pressure experimentation. *PLoS ONE*, **7**, e31781.
488 (doi:10.1371/journal.pone.0031781)
- 489 53. Whiting ET, Steadman DW, Krigbaum J. 2016 Paleoecology of Miocene crocodylians in
490 Florida: insights from stable isotope analysis. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*
491 **451**, 23-34. (doi:10.1016/j.palaeo.2016.03.009)
- 492 54. Benson RB, Butler RJ. 2011 Uncovering the diversification history of marine tetrapods:
493 ecology influences the effect of geological sampling biases. *Geol. Soc. Spec. Publ.* **358**, 191-
494 208. (doi:10.1144/SP358.13)
- 495 55. Marx FG, Uhen MD 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution
496 of modern whales. *Science* **327**, 993-996. (doi:10.1126/science.1185581)

- 497 56. Sant K, Palcu DV, Mandic O, Krijgsman W. 2017 Changing seas in the early-middle
498 Miocene of Central Europe: a Mediterranean approach to Paratethyan stratigraphy. *Terra*
499 *Nova* **29**, 273-281. (doi:10.1111/ter.12273)
- 500 57. Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara JV, Wesselingh FP, Antoine P-O. 2015 A
501 Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-
502 Amazonian mega-wetlands. *Proc. R. Soc. B* **282**, 20142490. (doi:10.1098/rspb.2014.2490)
- 503 58. Brochu CA. 2000 Phylogenetic relationships and divergence timing of *Crocodylus* based on
504 morphology and the fossil record. *Copeia* **3**, 657-673. (doi:10.1643/0045-
505 8511(2000)000[0657:PRADTO]2.0.CO;2)
- 506 59. Scheyer TM, Aguilera OA, Delfino M, Fortier DC, Carlini AA, Sánchez R, Carrillo-Briceño
507 JD, Quiroz L, Sánchez-Villagra MR. 2013 Crocodylian diversity peak and extinction in the
508 late Cenozoic of the northern Neotropics. *Nat. Commun.* **4**, 1907. (doi:10.1038/ncomms2940)
- 509 60. Molnar RE. 1982 *Pallimnarchus* and other Cenozoic crocodiles in Queensland. *Mem. Qd.*
510 *Mus.* **20**, 657-673.
- 511 61. Hocknull SA *et al.* 2020 Extinction of eastern Sahul megafauna coincides with sustained
512 environmental deterioration. *Nat. Commun.* **11**, 1-14. (doi:10.1038/s41467-020-15785-w)
- 513 62. Delfino M, Iurino DA, Mercurio B, Piras P, Rook L, Sardella R. 2020 Old African fossils
514 provide new evidence for the origin of the American crocodiles. *Sci. Rep.* **10**, 1-11.
515 (doi:10.1038/s41598-020-68482-5)
- 516 63. Blakey RC. 2008 Gondwana paleogeography from assembly to breakup—A 500 m.y.
517 odyssey. In *Resolving the Late Paleozoic Ice Age in Time and Space* (eds CR Fielding, TD
518 Frank, JL Isbell), pp. 1-28. Boulder: Geological Society of America Special Paper.
519

520 **Figure captions**

521 **Figure 1.** Fossil record of *Sacacosuchus* and *Piscogavialis* in the Neogene deposits of the Pisco
 522 Basin, southern Peru. (a) Schematic stratigraphic columns of the Chilcatay (yellow) and Pisco
 523 (light blue) formations with crocodylian-bearing localities at the Ica-Pisco Valleys (left; from *ca.*
 524 20 to 7 Ma) and the Sacaco area (from *ca.* 9.38 to 4.85 Ma). (b) Location and map of the East
 525 Pisco basin showing the Chilcatay (yellow) and Pisco (blue) deposits within putative continental
 526 flooded areas (in white). Map modified from [31]. AGL, Aguada de Lomas; CCO-n, Cerro
 527 Colorado norte; CCO-s, Cerro Colorado sur; CLQ, Cerro Los Quesos; COM, Comatrana; CVT,
 528 Correviento; ELJ, EL Jahuay; MTM, Montemar; MTM-n, Montemar norte; MTM, Montemar;
 529 SAO-e, Sacaco east; SAS-w, Sud-Sacaco west; SUL, Sula Site; YAU, Yauca; ZAM, Zamaca.

530 **Figure 2.** Photograph and schematic drawing of the skulls of *Sacacosuchus cordovai* gen. et sp.
 531 nov. from Sacaco at different ontogenetic stages. Adult specimen (holotype: MUSM 162) in
 532 dorsal (a), ventral (b), right lateral (e), and occipital (f) views. Juvenile specimen (MUSM 160)
 533 in dorsal (c), ventral (d), left lateral (g; inverted), and occipital (h) views. Sub-adult specimen
 534 (MUSM 161) in dorsal (i) view. ba, basioccipital; bs, basisphenoid; CH, choana; cq,
 535 cranioquadrate foramen; ec, ectopterygoid; ec.mx, maxilla surface for ectopterygoid; EN,
 536 external naris; eo, exoccipital; f, frontal; fcp, foramen carotideum posterior; IF, incisive foramen;
 537 ITF, infratemporal fenestra; j, jugal; j.la, lacrimal surface for jugal; j.mx, maxilla surface for
 538 jugal; l, lacrimal;; ls, laterosphenoid; m5, m,9, m14, maxillary tooth positions; mx, maxilla;
 539 n.pm, premaxilla surface for nasal; na, nasal; OR, orbit; p, parietal; pa, palatine; pa.mx, maxilla
 540 surface for palatine; pf, prefrontal; pm, premaxilla; p3, p4, premaxillary tooth positions; po,
 541 postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; qj.q, quadrate surface for quadratojugal;

542 s, shelf; so, supraoccipital; sq, squamosal; STF, supratemporal fenestra; SOF, suborbital fenestra;
543 v, foramen vagus; xii, foramen for hypoglossal nerve. All photographs to the same scale. Scale
544 bar equals 5 cm.

545 **Figure 3.** Phylogenetic position of *Sacacosuchus cordovai* and other marine taxa (represented by
546 their skulls) within the Crocodylia, with ancestral range reconstructions provided by S-DIVA. (a)
547 Time-calibrated, strict consensus tree on the constrained and equal weighted analysis.
548 Crocodylians found in marine deposits pertain to the gavialoid clade. The ancestral range
549 reconstructions are summarised as pie charts and shown for critical nodes of the Gavialoidea (73:
550 *Eogavialis* + *Gavialis*; 79: Gryposuchinae; 81: *Aktiogavialis*; 82: *Argochampsa*, *Aktiogavialis*,
551 advanced gavialids; 83: ‘gharials’ + MUSM 1513; 86: Miocene African forms; 89:
552 *Thecachampsa* species; 90: *Sacacosuchus*, *Gavialosuchus*, *Thecachampsa* + unnamed node 88;
553 92: Gavialidae; 96: Gavialoidea), Crocodylidae (99: node 97 + *Cr. porosus*); and ‘thoracosaurus’
554 (121). Geographic areas of distribution are represented by colours and capital letters. Wide bars
555 within branches show stratigraphic range of taxa. White arrows at the branches of gryposuchines,
556 *Gavialis*, and *Tomistoma schlegelii* indicate major shifts from marine to freshwater habitats.
557 Eocene palaeomap (b) is from Blackey [63].

558 **Figure 4.** Diversity of crocodylians during the last 90 my. (a) Observed range-through
559 (OR) diversity of crocodylian genera (OR bys: red dashed line), OR of marine (OR mg: blue
560 solid line) and non-marine genera (OR n-mg: black solid line) calculated per chronostratigraphic
561 stages. (b) Estimated richness based on the Chao1 extrapolation estimator calculated per
562 chronostratigraphic stages (red dots) and second-order Jackknife richness estimator calculated
563 using 3-million years time bins for marine (mg: blue line) and non-marine (n-mg: black line)

564 crocodylian genera. Grey solid line represents a smoothed global sea level curve after Miller et
565 al. [37] and the orange solid line a global mean temperature curve after Zachos et al. [34]. The
566 time span of the south-eastern Pacific gavialid crocodylians record (SEP C) encompasses the
567 estimated highest peak of genera and species of marine forms. PLI, Pliocene.

568 **Figure 5.** The pPCA of the snout of the Crocodylia defined by PC1 and PC2. Black dots denote
569 non marine taxa and blue dots (with or without skulls) correspond to extinct taxa (gavialoids and
570 *Thoracosaurus*) recovered from marginal to fully marine environments and the living saltwater
571 crocodile, *Crocodylus porosus*. Positive values of PC1 depict forms with longirostrine
572 ecomorphs. All gavialoids pertain to these ecomorphs but bearing large variation along positive
573 and negatives values of PC2, with morphological ‘tomistomines’ restricted to the positive values
574 and ‘gharials’ confined to the negative values. The sole ‘thoracosaur’ included in this analysis is
575 positioned close to the ‘gharial’ ecomorph. Grey polygon encompasses the gavialoid
576 morphospace and blue areas correspond to distinct ecomorphs of marine gavialoids within the
577 morphological ‘tomistomines’ (upper) and ‘gharials’ (lower).

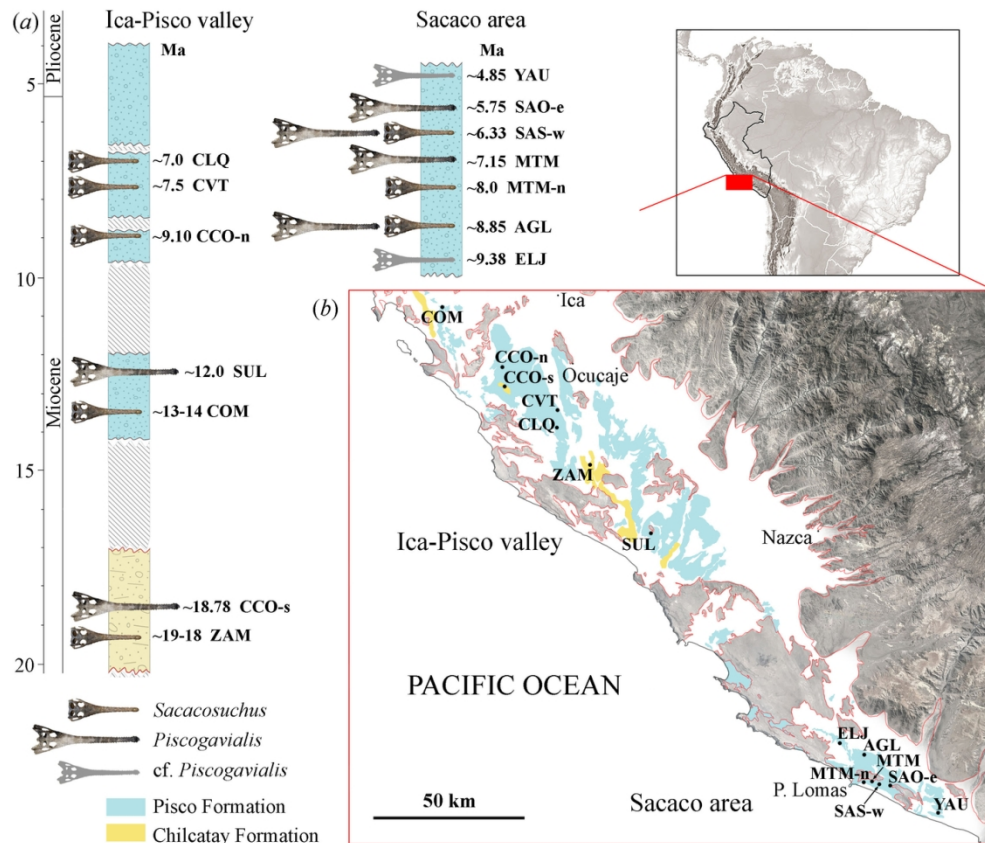


Figure 1. Fossil record of *Sacacosuchus* and *Piscogavialis* in the Neogene deposits of the Pisco Basin, southern Peru. (a) Schematic stratigraphic columns of the Chilcatay (yellow) and Pisco (light blue) formations with crocodylian-bearing localities at the Ica-Pisco Valleys (left; from ca. 20 to 7 Ma) and the Sacaco area (from ca. 9.38 to 4.85 Ma). (b) Location and map of the East Pisco basin showing the Chilcatay (yellow) and Pisco (blue) deposits within putative continental flooded areas (in white). Map modified from [31]. AGL, Aguada de Lomas; CCO-n, Cerro Colorado norte; CCO-s, Cerro Colorado sur; CLQ, Cerro Los Quesos; COM, Comatrana; CVT, Correviento; ELJ, EL Jahuay; MTM, Montemar; MTM-n, Montemar norte; MTM, Montemar; SAO-e, Sacaco east; SAS-w, Sud-Sacaco west; SUL, Sula Site; YAU, Yauca; ZAM, Zamaca.

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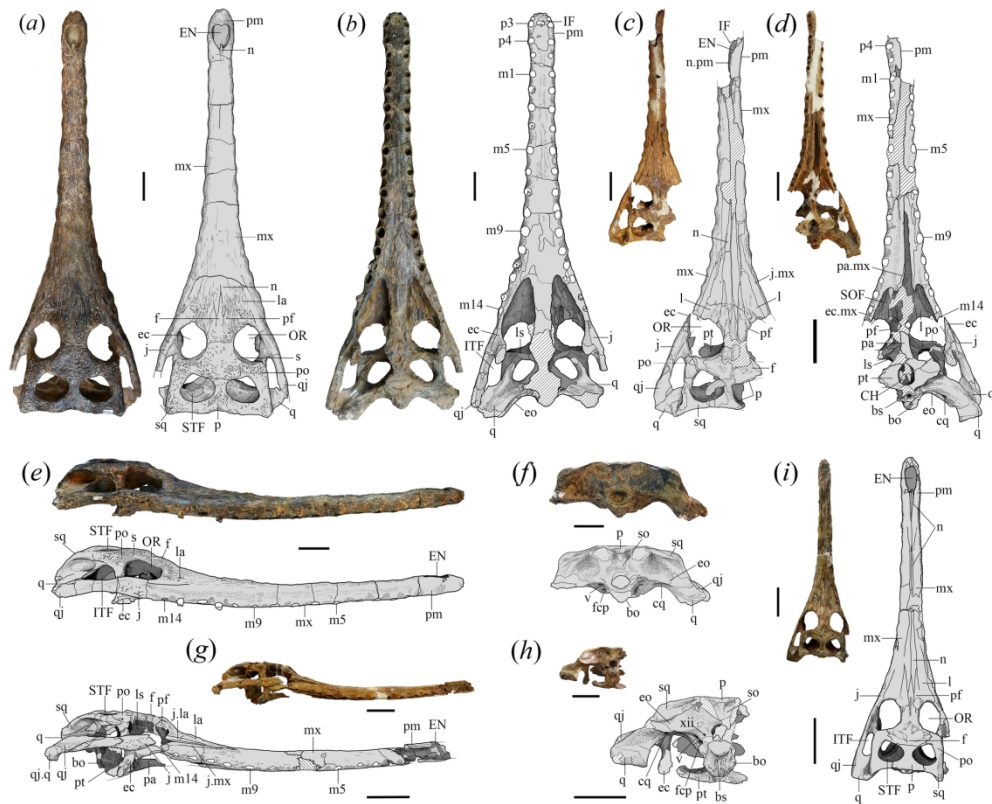


Figure 2. Photograph and schematic drawing of the skulls of *Sacacosuchus cordovai* gen. et sp. nov. from Sacaco at different ontogenetic stages. Adult specimen (holotype: MUSM 162) in dorsal (a), ventral (b), right lateral (e), and occipital (f) views. Juvenile specimen (MUSM 160) in dorsal (c), ventral (d), left lateral (g; inverted), and occipital (h) views. Sub-adult specimen (MUSM 161) in dorsal (i) view. ba, basioccipital; bs, basisphenoid; CH, choana; cq, cranioquadrate foramen; ec, ectopterygoid; ec.mx, maxilla surface for ectopterygoid; EN, external naris; eo, exoccipital; f, frontal; fcp, foramen carotideum posterior; IF, incisive foramen; ITF, infratemporal fenestra; j, jugal; j.la, lacrimal surface for jugal; j.mx, maxilla surface for jugal; l, lacrimal;; ls, laterosphenoid; m5, m9, m14, maxillary tooth positions; mx, maxilla; n.pm, premaxilla surface for nasal; na, nasal; OR, orbit; p, parietal; pa, palatine; pa.mx, maxilla surface for palatine; pf, prefrontal; pm, premaxilla; p3, p4, premaxillary tooth positions; po, postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; qj.q, quadrate surface for quadratojugal; s, shelf; so, supraoccipital; sq, squamosal; STF, supratemporal fenestra; SOF, suborbital fenestra; v, foramen vagus; xii, foramen for hypoglossal nerve. All photographs to the same scale. Scale bar equals 5 cm.

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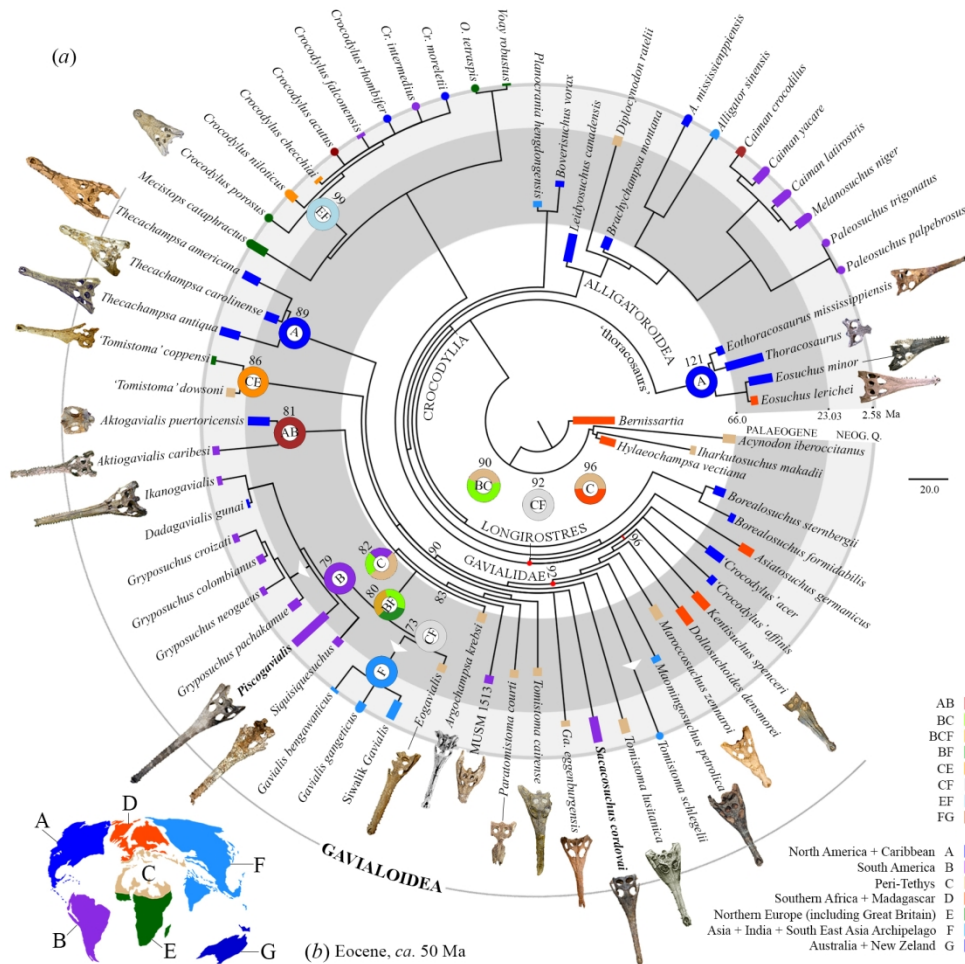


Figure 3. Phylogenetic position of *Sacacosuchus cordovai* and other marine taxa (represented by their skulls) within the Crocodylia, with ancestral range reconstructions provided by S-DIVA. (a) Time-calibrated, strict consensus tree on the constrained and equal weighted analysis. Crocodylians found in marine deposits pertain to the gavialoid clade. The ancestral range reconstructions are summarised as pie charts and shown for critical nodes of the Gavialoidea (73: *Eogavialis* + *Gavialis*; 79: Gryposuchinae; 81: *Aktiogavialis*; 82: *Argochampsa*, *Aktiogavialis*, advanced gavialids; 83: 'gharials' + MUSM 1513; 86: Miocene African forms; 89: *Thecachampsa* species; 90: *Sacacosuchus*, *Gavialosuchus*, *Thecachampsa* + unnamed node 88; 92: Gavialidae; 96: Gavialoidea), Crocodylidae (99: node 97 + *Cr. porosus*); and 'thoracosaurus' (121). Geographic areas of distribution are represented by colours and capital letters. Wide bars within branches show stratigraphic range of taxa. White arrows at the branches of gryposuchines, *Gavialis*, and *Tomistoma schlegelii* indicate major shifts from marine to freshwater habitats. Eocene palaeomap (b) is from Blackey [63].

161x157mm (300 x 300 DPI)

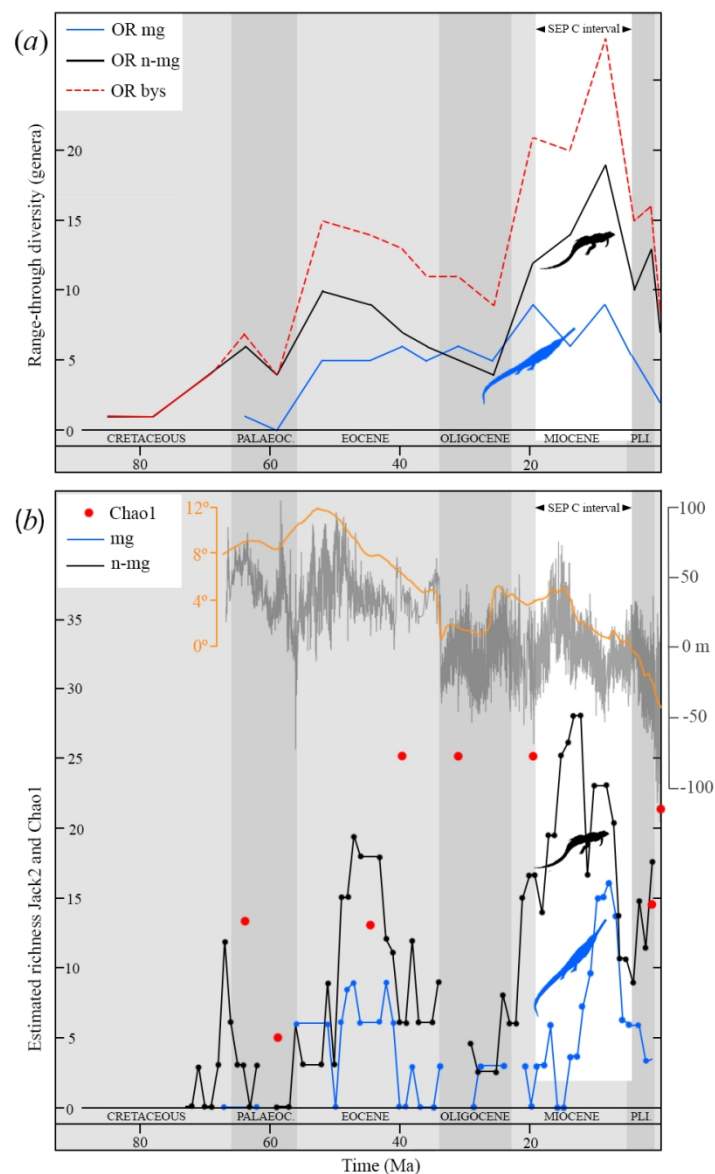


Figure 4. Diversity of crocodylians during the last 90 my. (a) Observed range-through (OR) diversity of crocodylian genera (OR bys: red dashed line), OR of marine (OR mg: blue solid line) and non-marine genera (OR n-mg: black solid line) calculated per chronostratigraphic stages. (b) Estimated richness based on the

Chao1 extrapolation estimator calculated per chronostratigraphic stages (red dots) and second-order Jackknife richness estimator calculated using 3-million years time bins for marine (mg: blue line) and non-marine (n-mg: black line) crocodylian genera. Grey solid line represents a smoothed global sea level curve after Miller et al. [37] and the orange solid line a global mean temperature curve after Zachos et al. [34]. The time span of the south-eastern Pacific gavialid crocodylians record (SEP C) encompasses the estimated highest peak of genera and species of marine forms. PLI, Pliocene.

82x139mm (300 x 300 DPI)

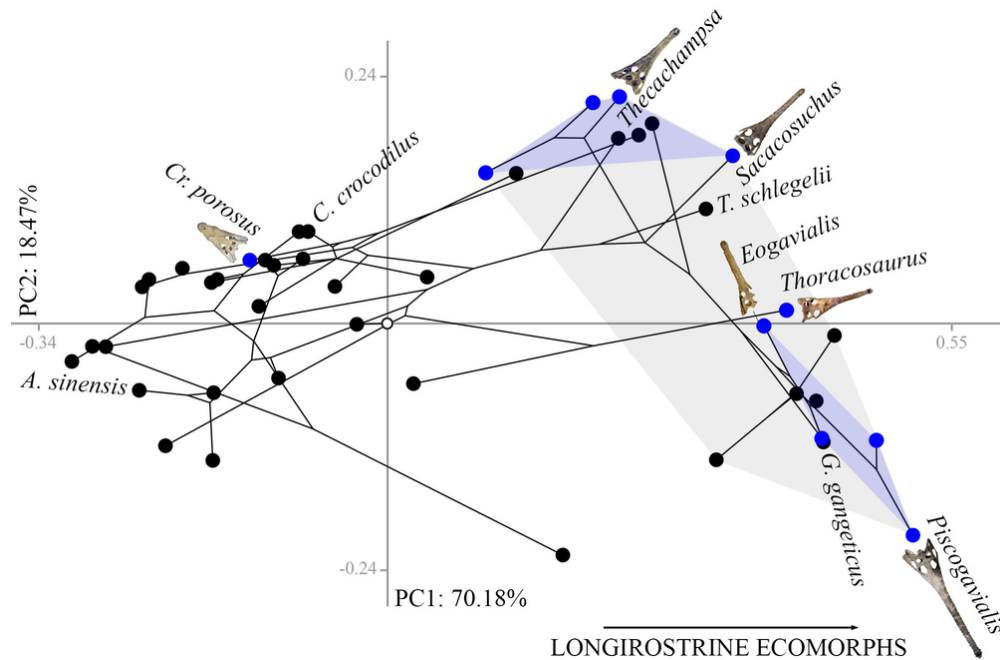


Figure 5. The pPCA of the snout of the Crocodylia defined by PC1 and PC2. Black dots denote non marine taxa and blue dots (with or without skulls) correspond to extinct taxa (gavialoids and *Thoracosaurus*) recovered from marginal to fully marine environments and the living saltwater crocodile, *Crocodylus porosus*. Positive values of PC1 depict forms with longirostrine ecomorphs. All gavialoids pertain to these ecomorphs but bearing large variation along positive and negatives values of PC2, with morphological 'tomistomines' restricted to the positive values and 'gharials' confined to the negative values. The sole 'thoracosaur' included in this analysis is positioned close to the 'gharial' ecomorph. Grey polygon encompasses the gavialoid morphospace and blue areas correspond to distinct ecomorphs of marine gavialoids within the morphological 'tomistomines' (upper) and 'gharials' (lower).

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