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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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333 specimens. *Sacacosuchus* and *Piscogavialis* (exclusive of the type) specimens are permanently  
334 deposited at the Museo de Historia Natural, UNMSM (MUSM), Lima, Peru.

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  
339 analyses. All authors contributed to the discussions and interpretation of the results.

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343

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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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24 ecomorphs

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]. ‘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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333 specimens. *Sacacosuchus* and *Piscogavialis* (exclusive of the type) specimens are permanently  
334 deposited at the Museo de Historia Natural, UNMSM (MUSM), Lima, Peru.

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  
339 analyses. All authors contributed to the discussions and interpretation of the results.

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343

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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).

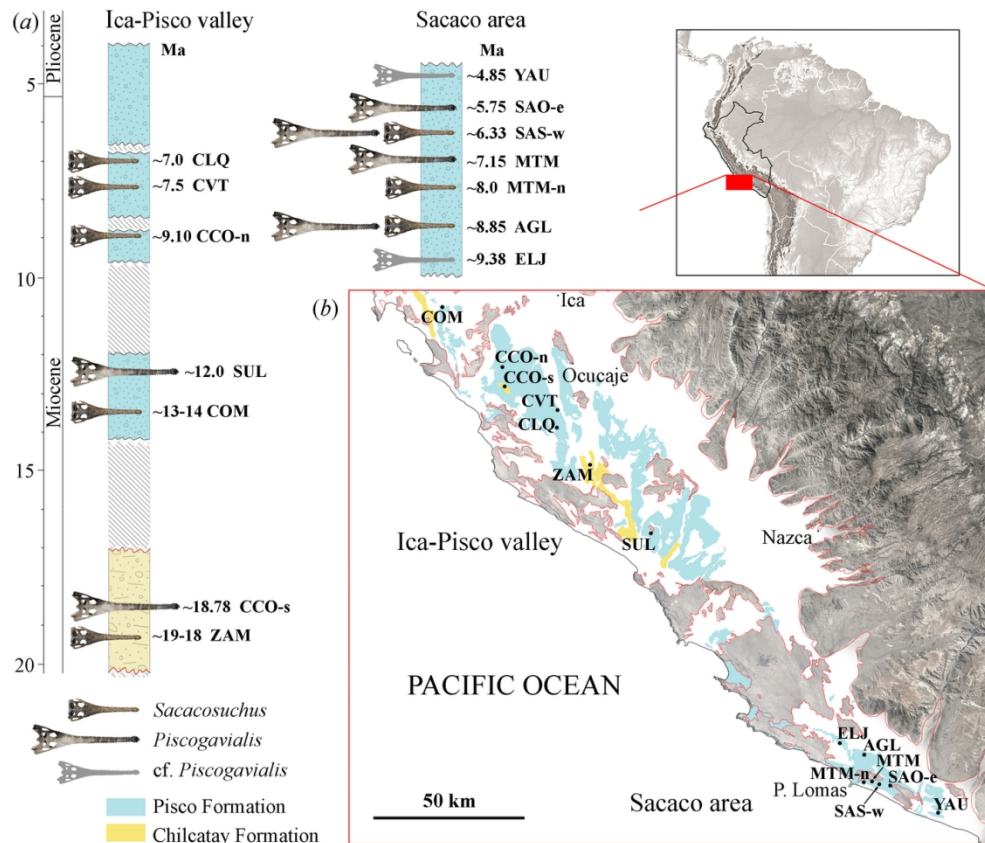


Figure 1. Fossil record of *Sacacosuchus* and *Piscogavialis* in the Neogene deposits of the Pisco Basin, southern Peru. (a) Schematic stratigraphic columns of the Chilcatay (yellow) and Pisco (light blue) formations with crocodylian-bearing localities at the Ica-Pisco Valleys (left; from ca. 20 to 7 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.

122x104mm (300 x 300 DPI)

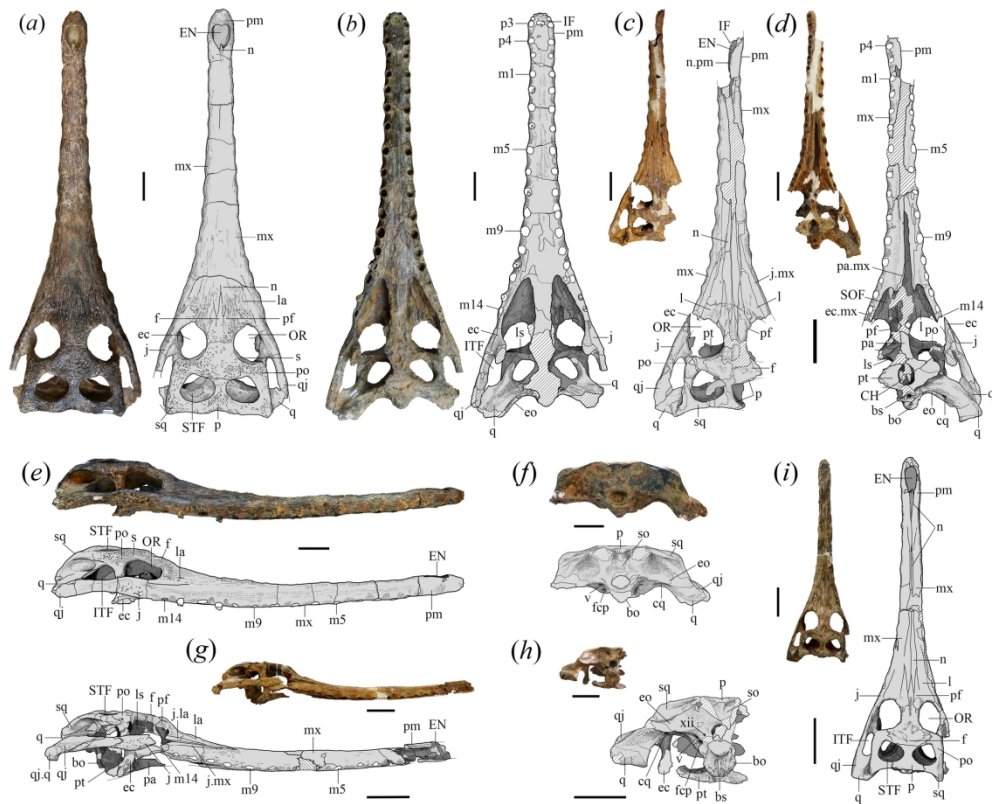


Figure 2. Photograph and schematic drawing of the skulls of *Sacacosuchus cordovai* gen. et sp. nov. from Sacaco at different ontogenetic stages. Adult specimen (holotype: MUSM 162) in dorsal (a), ventral (b), right lateral (e), and occipital (f) views. Juvenile specimen (MUSM 160) in dorsal (c), ventral (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.

182x150mm (300 x 300 DPI)

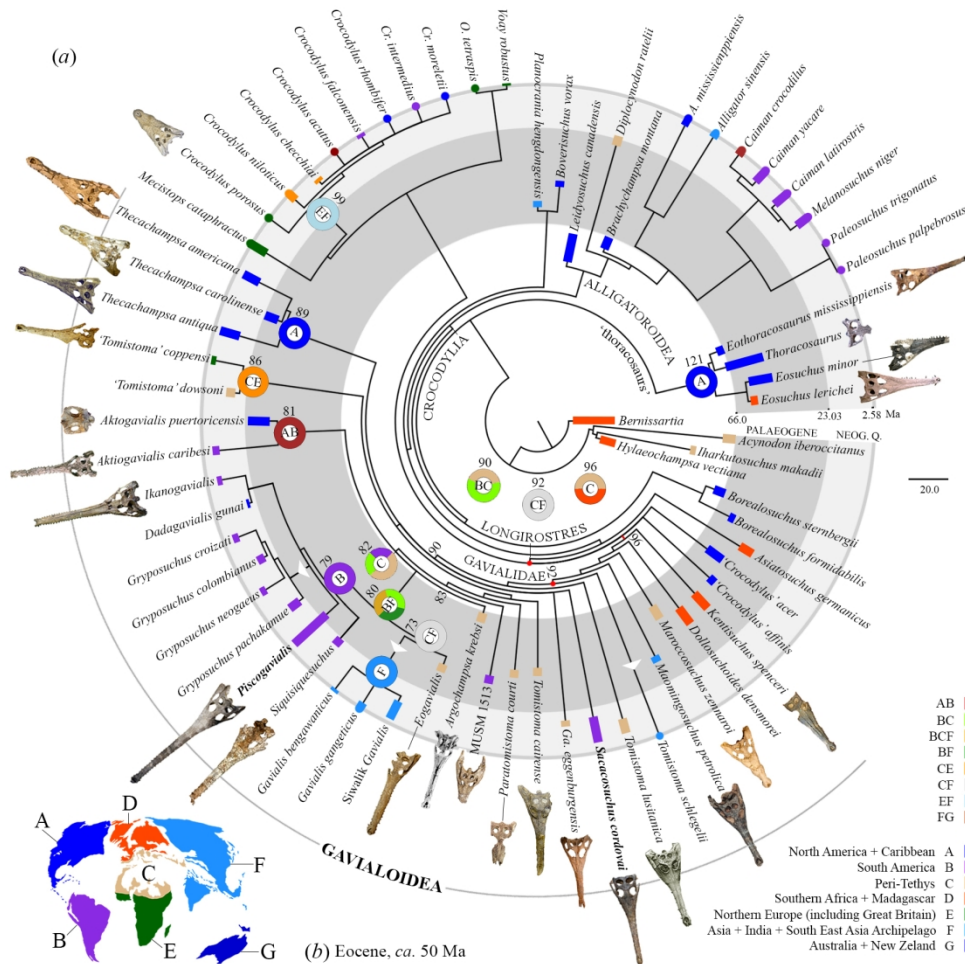


Figure 3. Phylogenetic position of *Sacacosuchus cordovai* and other marine taxa (represented by their skulls) within the Crocodylia, with ancestral range reconstructions provided by S-DIVA. (a) Time-calibrated, strict consensus tree on the constrained and equal weighted analysis. Crocodylians found 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)

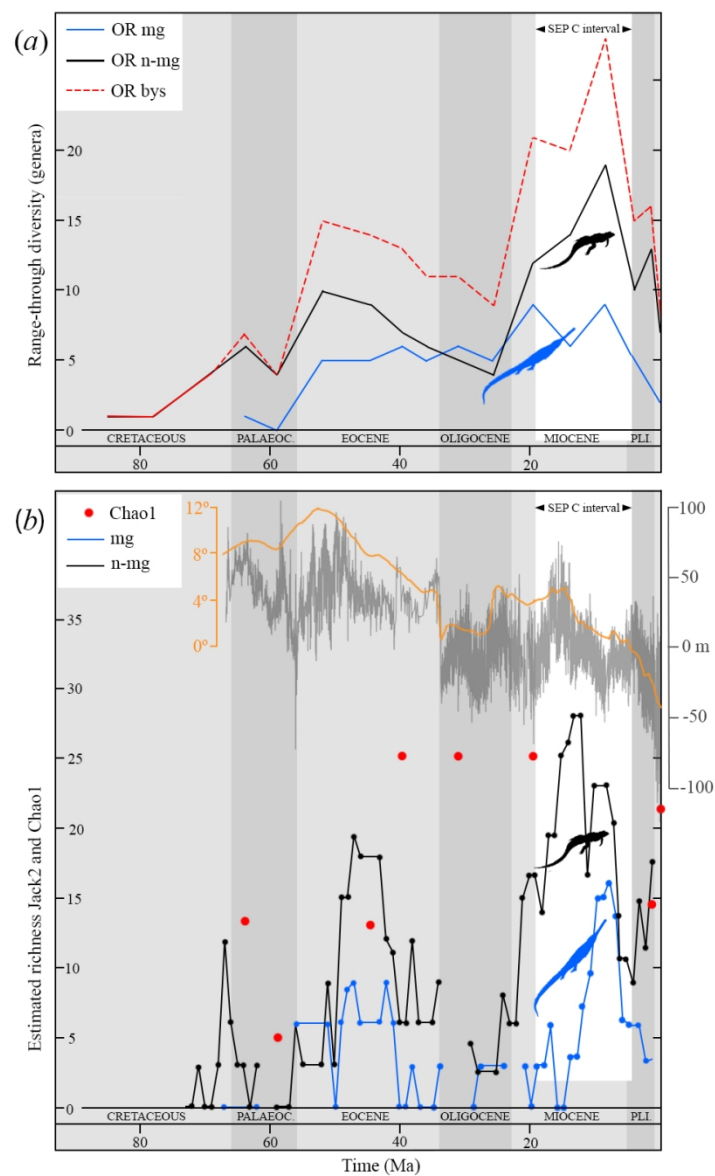


Figure 4. Diversity of crocodylians during the last 90 my. (a) Observed range-through (OR) diversity of crocodylian genera (OR bys: red dashed line), OR of marine (OR mg: blue solid line) and non-marine genera (OR n-mg: black solid line) calculated per chronostratigraphic stages. (b) Estimated richness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

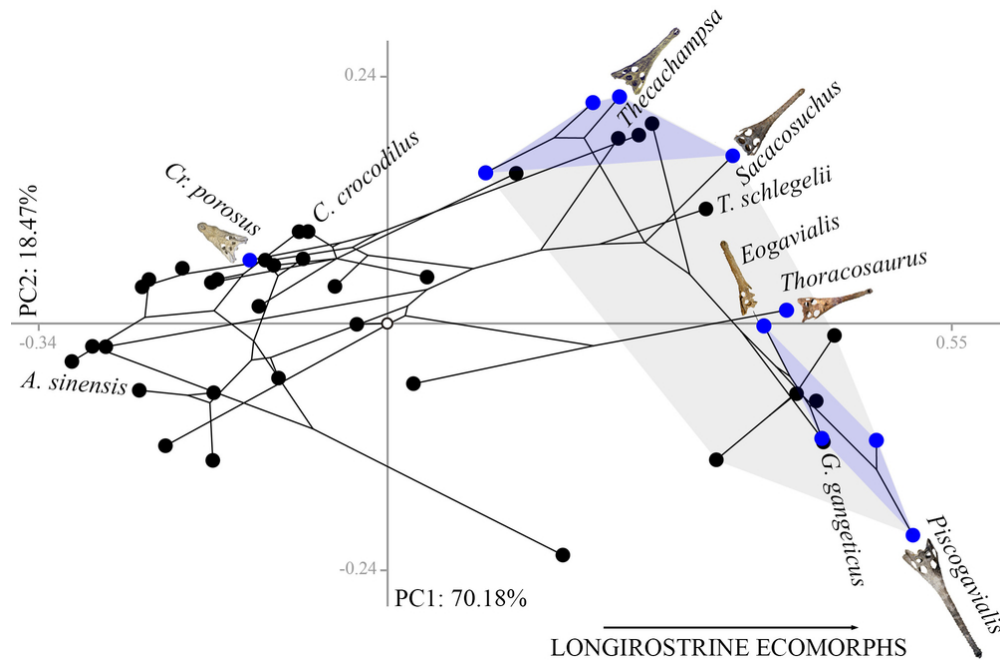


Figure 5. The pPCA of the snout of the Crocodylia defined by PC1 and PC2. Black dots denote non marine taxa and blue dots (with or without skulls) correspond to extinct taxa (gavialoids and *Thoracosaurus*) recovered from marginal to fully marine environments and the living saltwater crocodile, *Crocodylus 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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