LIMITED CONVERGENCE IN THE POSTCRANIUM OF AQUATIC CROCODYLOMORPHA

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ABSTRACT. Thalattosuchia (Early Jurassic–Early Cretaceous) and Dyrosauridea (Late Cretaceous–Early Eocene) are crocodylomorph archosaurs which diversified in fluvial and marine environments and endured extinction events (*i.e.* Jurassic–Cretaceous boundary for Thalattosuchia; Cretaceous–Paleogene for Dyrosauridea). Their postcrania remain globally undervalued in anatomical descriptions and diagnoses, shrouding the locomotive adaptations that possibly underpinned their radiations and longevity. We thoroughly surveyed the postcranial morphology of Dyrosauridea and Thalattosuchia, recreated their girdles in three-dimensions using tens of high-precisions 3D scans, and analysed their shape using geometric morphometrics. Dyrosauridea and Thalattosuchia have clearly distinct postcrania, even when found within similar environments, suggesting the existence of clade-specific features limiting the strength of evolutionary convergence. Moreover, the range of postcranial morphologies evolved by dyrosaurids and thalattosuchians is large compared to extant crocodylians, making the latter unsatisfactory functional analogues for every group of extinct crocodylomorphs. Our work reveals the previously unsuspected potential of postcranial anatomy as an abundant source of phylogenetic and taxonomic characters to assess the relationships within Crocodylomorpha. Incorporation of postcranial anatomy therefore appears crucial to fully assess the ecology, disparity, and relationships of crocodylomorphs.

1. INTRODUCTION

Crocodylomorpha is currently restricted to twenty-eight species of semi-aquatic ambush predators (Rasmussen et al., 2011; Grigg and Kirshner, 2015; Stubbs et al., 2021; Griffith et al., 2023). Nevertheless, its considerable fossil record reveals that Crocodylomorpha presented a significant diversity in the past (Toljagìc and Butler, 2013; Bronzati et al., 2015; Tennant et al., 2016; Wilberg et al., 2019; Mannion et al., 2019; Johnson et al., 2020; Young et al., 2020a; Jouve and Jalil, 2020a; Stubbs et al., 2021). Thalattosuchia represents the most remarkable and diverse marine radiation within Crocodylomorpha (Fanti et al., 2015; Wilberg, 2015a; Young et al., 2020a; Johnson et al., 2020), distinguishing itself with its wide range of postcranial morphologies, likely representing several approaches to aquatic life within the clade. Dyrosauridea is another lineage that colonized the aquatic realm. Both clades do not overlap in time, with Thalattosuchia crossing the Jurassic–Cretaceous boundary and disappearing in the Early Cretaceous (Young et al., 2012; Fanti et al., 2015; Chiarenza et al., 2015) while Dyrosauridea radiated by the late Cretaceous and crossed the Cretaceous–Paleogene boundary (Jouve et al., 2006; Hastings et al., 2014; Bronzati et al., 2015; Jouve and Jalil, 2020a). Each clade initially evolved in non-marine settings before transitioning to marine environments (Wilberg et al., 2019; Young et al., 2020a; Johnson et al., 2020; Jouve, 2021).

The postcranial anatomy of extinct crocodylomorphs constitutes an exemplary case of ambivalence. Over their long evolutionary history, crocodylomorphs have colonized various environments from fully terrestrial to fully aquatic (Toljagìc and Butler, 2013; Bronzati et al., 2015; Tennant et al., 2016; Wilberg et al., 2019; Mannion et al., 2019; Johnson et al., 2020; Young et al., 2020a; Jouve and Jalil, 2020a; Godoy, 2020; Stubbs et al., 2021), as revealed by extensive modification of their postcranium. Yet, attention has historically been focused on craniodental anatomy, resulting in the depreciation of postcranial anatomy in diagnoses, anatomical descriptions, phylogenetic analyses, and palaeoecological inferences. Recent studies on different groups of Crocodyliformes have started to shed light on the importance of postcranial anatomy in understanding the lifestyle but also relationships of those extinct clades (Langston, 1995; Herrera et al., 2013; Godoy et al., 2016; Martin et al., 2016; Herrera et al., 2017; de Souza et al., 2019; Jouve

and Jalil, 2020a; Jouve et al., 2021; Blanco, 2021). Withal, the postcranial anatomy of Thalattosuchia and Dyrosauridae remains profoundly overlooked despite an evident disparity. In this study we investigate the shape disparity of the girdle and upper appendicular anatomy of Thalattosuchia and Dyrosauridae using geometrics morphometrics and discuss their potential as a source of taxonomic and phylogenetic characters.

2. ABBREVIATIONS

BRLSI Bath: Bath Royal Literary and Scientific Institute, UK; **BRSMG** Bristol: Bristol City Museum and Art Gallery, UK; **GLAHM** Glasgow: Hunterian Museum and Art Gallery, UK; **GPIT** Tübingen: Geologisch–Paläontologisches Institut Tübingen, Germany; **LRM** Lyme: Lyme Regis Museum, UK; **MLP** La Plata: Museo de La Plata, Buenos Aires, Argentina; **NHMUK** London: Natural History Museum, UK; **MNHN** Paris: Muséum national d'Histoire naturelle, France; **MRAC** Tervuren: Musée Royal de l'Afrique Centrale, Belgium; **NJSM** Trenton: New Jersey State Museum, USA; **NKNB** Bamberg: Naturkunde-Museum Bamberg, Germany; **OCP** Khouribga, Office Chérifien des Phosphates, Direction de l'Exploitation de Khouribga, Geologie-Exploitation, Morocco; **PMU** Uppsala: Evolutionsmuseet, Uppsala Universitet, Sweden; **RBINS** Brussels: Royal Belgian Institute of Natural Sciences, Belgium; **SCR**: 'Sur Combe Ronde', Jurassica Museum, Porrentruy, Switzerland; **SMNS** Stuttgart: Staatliches Museum für Naturkunde, Germany; **UJF** Grenoble: Joseph Fourier University, France; **UF/IGM** Gainesville: **UF**, Florida Museum of Natural History, University of Florida, USA / **IGM**, Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, Minería y Quimica, Bogotá, Colombia; **YPM** New Haven: Yale Peabody Museum, USA.

3. MATERIAL AND METHODS

We created 3D models of the best preserved specimens of key species of Thalattosuchia and Dyrosauridea using high precision surface scanning (see Figure 1). We sampled specimens possessing both postcranial and cranial materials, and some missing cranial remains but with outstanding postcrania (see supplementary table 1 – in total one specimen for Crocodylia, 36 specimens for Thalattosuchia, and five specimens for Dyrosauridae). We assign NHMUK PV R 3169 to *Neosteneosaurus edwardsi* based on the morphology of its girdle elements, similarly to Johnson et al. (2015). We, and additional colleagues (pers. comm. MM Johnson, April 2023) suspect that the coracoid of NHMUK PV R 3169 might actually belong to the holotype of *Lemmysuchus obtusidens* (NHMUK PV R 3168) based on its overall dimensions, type of preservation, and the presence of bite marks on its distal blade. For this reason we included it in the combined analyses. The majority of surface scan data were obtained using the surface laser scanner Creaform HandySCAN 300 (accuracy of 0.2 mm). The surface models for the specimens of *Hyposaurus natator* YPM VP.000753 and YPM VP.000985 were obtained using the white light scanner Artec EVA (accuracy up to 0.5 mm). The surface model of *Acherontisuchus guajiraensis* was modelled using photogrammetry (Meshroom version 2021.1.0) and assembled using Artec Studio 16. Blender (version 3.1.2) was used to mirror bones into the preferred left polarity, and also to repair obvious defects portions (see supplementary table 2 and supplementary figures 1–16). Our entire data set of 3D models comprises a total of: ten scapulae, fourteen coracoids, seventeen humeri, twenty-two ilia, nineteen ischia, seventeen pubes, and twenty-three femora. On each model, we placed a series of type-II landmarks (Bookstein, 1997) and sliding semi-landmarks (see supplementary tables 6–8 and supplementary figures 17–19) using the software Stratovan Checkpoint (version 2020.10.13.0859): scapula (6 type-II; 187 sliding); coracoid (9 type-II; 185 sliding); humerus (8 type-II; 172 sliding); ilium (14 type-II; 195 sliding); ischium (11 type-II; 159 sliding); pubis (8 type-II; 169 sliding); femur (8 type-II; 132 sliding). The landmarks were all placed by the same person. For the humeri phenograms, we used a series of two dimensional measurements (namely length and width) to build our ratios. In total, the humeri phenograms contain 31 specimens with seven crocodylians, four dyrosaurids, eleven metriorhynchoids and nine teleosauroids

(see supplementary table 9 for the complete list).

All subsequent analyses were run in the R statistical environment v4.1.2 (TEAM, 2013). Landmark coordinates were saved as .pts files and imported in R using the READ.PTS function of the MORPHO package (Schlager et al., 2021). The isolated bone morphospaces were performed to allow the inclusion of a greater portion of specimens (see supplementary figures 20–28). To analyse the distribution of landmarks of each bone, we performed the Generalized Procrust Analysis (GPA) (using the GPAGEN function of the GEOMORPH package, with the default option ProcD = FALSE Adams et al. (2022)) followed by a Principal Component Analysis (PCA) (using the GM.PRCOMP function of the GEOMORPH package Adams et al. (2022)). To assess the differences between the clades, we also computed a procrustes ANOVA (Adams et al., 2022). In parallel, we also combined landmark coordinates to create new sets grouping together the different pelvic or thoracic girdle elements (sometimes combining different specimens; see supplementary table 1). Landmark coordinates were grouped after performing separate Generalized Procrust Analysis (GPA) using the COMBINE.SUBSETS function of the GEOMORPH package (Adams et al., 2022). Each new set was then subjected to a Principal Component Analysis (PCA) using the GM.PRCOMP function of the GEOMORPH package (Adams et al., 2022) (see Figures 2 and 3). Again, the differences between the clades for the new sets were assessed through a procrustes ANOVA (Adams et al., 2022).

We created a supertree based on the dataset from Jouve and Jalil (2020a,b), with additional phylogenetic relations for Teleosauroidea obtained from Johnson et al. (2020) and for Metriorhynchoidea from Young et al. (2020a). We reanalysed this dataset using our parsimony protocol (TNT version 1.5; see Bennion et al. (2023) for protocol) and randomly selected one most parsimonious tree. To fit our taxa from our combined thoracic and pelvic morphometric analyses, and because sampling differs for each bone, we removed and added tips to the tree using ADDTIP and DROPTIP functions from the TREETOOLS package (Smith, 2022) in R. Each newly created tree was calibrated in time with the minimum branch length method and minimum value of three million years using the function TIMEPALEOPHY from the PALEOTREE package (v.4.1.3; Bapst (2012)) based on taxon occurrences obtained from https://paleobiodb.org. The estimations for Dyrosauridea–Thalattosuchia and Dyrosauridea–Crocodylia roots were taken from Jouve and Jalil (2020a). These dates were combined with morphological data to produce phylomorphospaces (see supplementary figure 29) using the PHYTOOLS package (Revell, 2012).

For each bone, the degree of phylogenetic signal was assessed using the K_{mult} method from the PHYSIGNAL function (GEOMORPH package Adams et al. (2022)). K_{mult} corresponds to the multivariate version of the K-statistic (Adams, 2014). It determines the degree of phylogenetic signal under a Brownian motion model of evolution, and K_{mult} values close to 1 indicate strong phylogenetic signal (Adams et al., 2022). In parallel, we conducted, per bone, the updated Stayton distance-based convergence measure tests (Ct metrics; Grossnickle et al. (2023)) on several pairs of crocodylomorphs. These pairs were selected as the closest taxa in morphospaces regardless of their phylogenetic affinities. Ct metrics close to 1 indicate convergence whereas negative values reflect divergence (Grossnickle et al., 2023). We also analysed the correlation between the phenotypic and the phylogenetic distance by computing Mantel tests (1000 permutations using the mantel function of the vegan v.2.5-6 package; Oksanen et al. (2019)).

4. RESULTS

4.1. **Morphospace occupation.** Thalattosuchia, Dyrosauridea and Crocodylia cover clearly distinct portions of the morphospace for both girdles (see Figures 2 and 3; ANOVA p values <0.001). Teleosauroidea and Metriorhynchoidea are also found in specific regions of the morphospaces, resulting in a large morphospace occupation for Thalattosuchia, as also shown in individual bone analyses (see supplementary figures 20–28). On the combined morphospaces, the clades appear markedly distinct from one another, although the sampling is reduced. In addition, the thoracic and pelvic combined sets hint at the potential
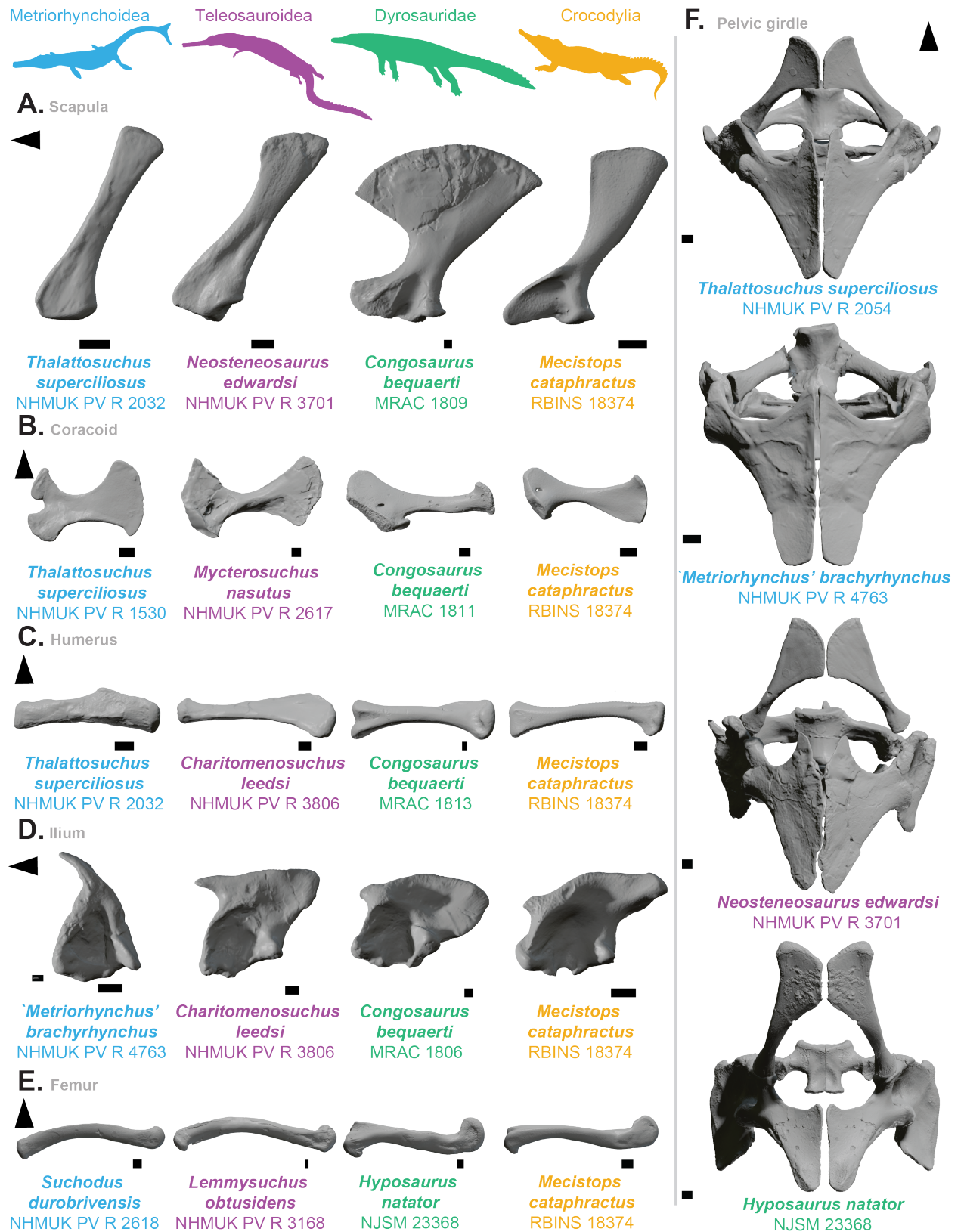
FIGURE 1. 3D models of girdle elements used in our analyses. **A.** left scapula in lateral view ; **B.** left coracoid in dorsal view ; **C.** left humerus in dorsal view ; **D.** left ilium in lateral view ; **E.** left femur in dorsal view ; **F.** Pelvic girdle reconstruction in ventral view. Arrow points anteriorly. All scale bars represent 1cm. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c) Thesupermart – License CC BY-SA 3.0.

high interspecific variance of Teleosauroidea and Metriorhynchoidea respectively, and that shape disparity is not only carried by the humerus. Indeed, the mantel test recovers a relatively significant correlation between phylogenetic distance and phenotypic distance for each dataset (thoracic dataset r=0.6299 & p=0.007; pelvic dataset r=0.755 & p=0.004; thoracic+pelvic dataset r=0.845 & p=0.036).

Yet, the K_{mult} tests performed on isolated and combined girdle elements (see supplementary table 3) exhibited relatively weak phylogenetic signal ($K_{mult} < 1$ with significant p-values p<0.005; Adams (2014)) for our phylogenetic tree comprising Thalattosuchia, Dyrosauridea and Crocodylia. However, strongly diverging branches between the clades on the phylomorphospaces implies the absence of any kind of intersuperfamily convergent evolution. Solely within Thalattosuchia, the ilium (K_{mult}=0.7648 & p<0.005) and scapula (K_{mult}=0.6319 & p<0.005) showed a stronger phylogenetic influence meaning that closely related taxa resemble each other slightly more than distantly related taxa (and potentially reflecting some degree of evolutionary conservatism), although still less than expected under Brownian motion (see supplementary table 4). The low K_{mult} values (*i.e.* $K_{mult} < 0.5$) obtained for both the isolated (with the exception of the ilium, scapula, and almost coracoid) and combined dataset note the presence of intraclade convergence within Thalattosuchia (see supplementary tables 3 and 4).

We investigated the latter by performing the updated Stayton distance-based convergence tests (Ct metrics; see supplementary table 5). Our results (p<0.05) show the presence of limited convergence between few thalattosuchian pairs for all isolated bones (*i.e. Thalattosuchus superciliosus* and *Tyrannoneustes lythrodectikos* humeri ; *Neosteneosaurus edwardsi* and *Thalattosuchus superciliosus* pubes). In comparison, a singular intersuperfamily pair showed significant results (p<0.05) of divergence: the teleosauroid *Mycterosuchus nasutus* and extant crocodylian *Mecistops cataphractus* scapulae. The remaining intraclade and intersuperfamily pairs are overall divergent (yet not significant; see supplementary table 5).

All clades differ in a number of traits. For the thoracic girdle (see Figure 2 A), Dyrosauridea displays both the sturdiest scapula, with its enlarged scapular blade, and robust humerus, with its well-developed distal condyles and thick shaft, resulting in positive values of the first axis. In contrast, the dyrosaurid coracoid is the most gracile: it has a strongly developed proximal head but a reduced coracoid blade and a slender shaft (resulting in positive values of the first and second axis respectively). Comparatively, Teleosauroidea displays a gradually shorter (proximodistal) and twisted (retroversion) humerus (see Figure 2 E), along with a slender scapula and more developed coracoid, all resulting in (increasing) negative values of both axes. The proximal region of the humerus is also enlarged and its deltopectoral crest positioned more proximally than in Crocodylia and Dyrosauridea. Teleosauroidea shows a posterior deflection of the humeral proximal head like Crocodylia, but its three proximal tuberosities are less marked. The teleosauroid scapula is slender but possesses a relatively greater scapulocoracoid synchondrosis, glenoid surface, and scapular blade which distinguishes it from Metriorhynchoidea. Basal teleosauroids show a more developed and ventrally deflected scapulocoracoid synchondrosis, whereas the orientation of the glenoid surface has a stronger lateral component among derived teleosauroids. The teleosauroid coracoid bears both a large proximal head and coracoid blade with a medium to short shaft, resulting in negative values of each axis. Metriorhynchoidea shows the most slender scapula (short scapular blade, short scapulocoracoid synchondrosis, and reduced glenoid surface) as well as the most gracile and reduced humerus, resulting in negative values of the first axis. The metriorhynchoid humerus is short and rod-like, with reduced proximal and distal articular facets. As in Teleosauroidea, the deltopectoral crest of metriorhynchoids is set more proximally than in Crocodylia or Dyrosauridea. Metriorhynchoidea also stands out with its peculiar coracoid showing: a large and perforated proximal head, a broad coracoid blade, a short shaft, and a reduced dorsoventral thickness. The overall expansion of the perforated proximal coracoid head results in positive values of the second axis like in Dyrosauridea. Metriorhynchoidea displays a wide array of shape, ranging from slender to sturdy humeri (see Figure 2 C, and see supplementary figures 20 & 24). Within Metriorhynchoidea, *Geosaurus lapparenti* stands out with its

protruding posterior capitular tuberosity and absence of distinct distal capitula. Crocodylia shows proportionally well-developed humerus, coracoid and scapula, resulting in positive values of the first axis. The crocodylian coracoid shows relatively large and similarly sized proximal head and coracoid blade for a shortened shaft. Overall, the scapulocoracoid synchondrosis of the crocodylian coracoid is proportionally smaller than the glenoid surface resulting in negative values on the second axis. Crocodylia has a less extensive scapular blade but a larger coracoid blade than Dyrosauridea, resembling teleosauroids. The crocodylian humerus shows well-formed proximal tuberosities and distal condyles as in Dyrosauridea but is more gracile.
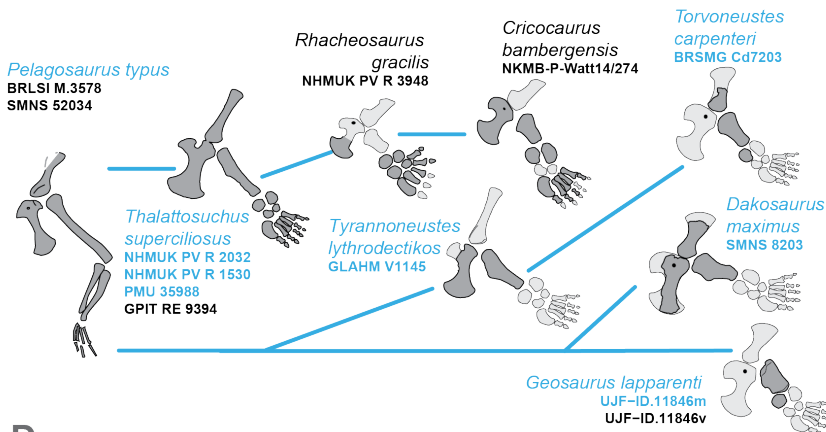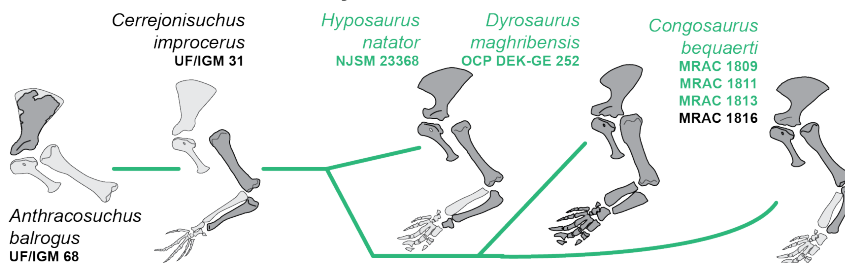
A. Thoracic combined morphospace
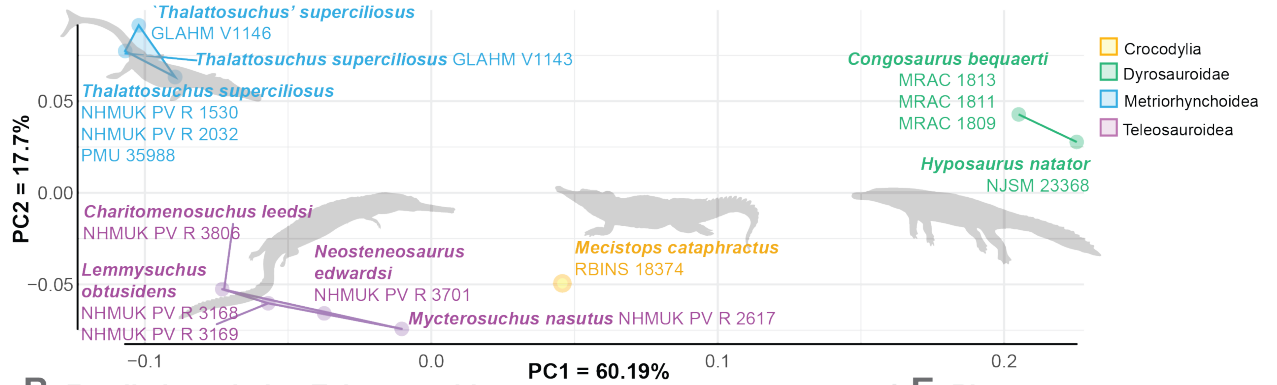
B. Forelimb evolution Teleosauroidea
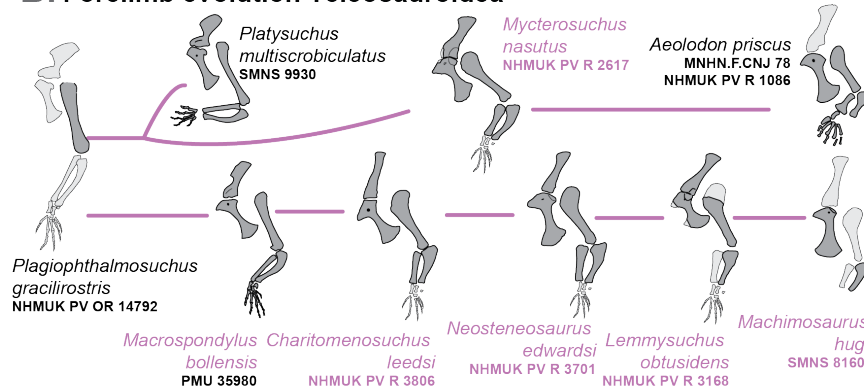
C. Forelimb evolution Metriorhynchoidea

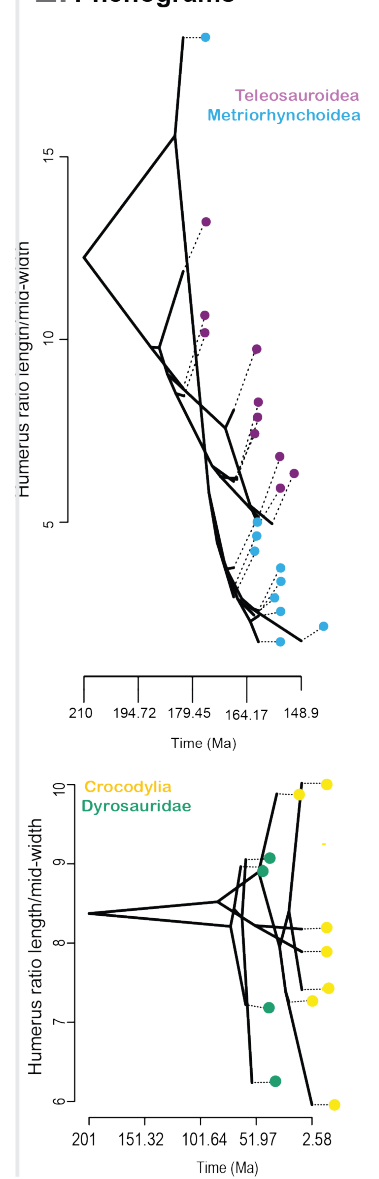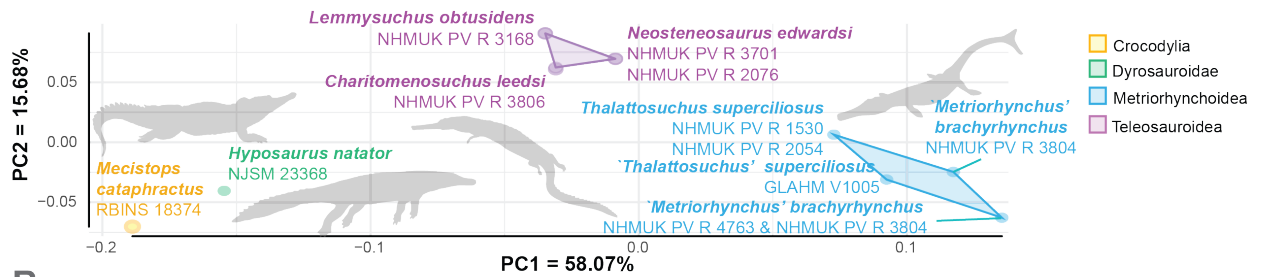## D. Forelimb evolution Dyrosauroidea

E. Phenograms

FIGURE 2. **A.** morphospace based on the combination of thoracic landmarks; **B – D** forelimb evolution within: **B.** Teleosauroidea, *Aeolodon priscus* MNHN.F.CNJ 78 modified from Foffa et al. (2019); **C.** Metriorhynchoidea, *Cricocaurus bambergensis* NKMB-P-Watt14/274 modified from Sachs et al. (2019); **D.** Dyrosauridea, *Dyrosaurus maghribensis* OCP DEK-GE 252 adapted from pictures courtesy of Stéphane Jouve. **E.** Phenograms based on the humeral ratio. Light grey colored bones are reconstructed. Colored specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c) Thesupermart – License CC BY-SA 3.0.

Crocodylomorpha also differ in pelvic morphology (see Figure 3 A). Crocodylia and Dyrosauridea possess relatively stout and twisted femora, ilia with large postacetabular processes and acetabular perforations, and proportionally anteroposteriorly limited ischia (all of which result in negative values of both axes). Crocodylia also shows a strongly reduced pubic diaphysis and a thinner ischial shaft. Dyrosauridea displays a broad ilium with the largest and widest postacetabular process, but a relatively short and stout preacetabular process and supraacetabular crest. The bony acetabulum appears relatively reduced whereas it is mediolaterally deep (as opposed to Teleosauroidea). The dyrosaurid ilium also bears the strongest ventral indentation – the acetabular perforation – separating its peduncles. The dyrosaurid ischium possesses a larger ischial blade than Crocodylia (with a short anterior process) but still less developed than Thalattosuchia. In Dyrosauridea, the anterior peduncle (with the so-called 'pubic knob') and acetabular perforation of the ischium are the largest (and second largest in Crocodylia). Dyrosauridea displays a slender pubis, with a well-developed pubic diaphysis and a greater inclination of the shaft compared to Crocodylia. In addition, the pubic peduncle of Dyrosauridea is overall small with a relatively circular outline. Dyrosauridea and Crocodylia show a double torsion of the femur (dorsoventrally and anteroposteriorly), a marked fourth trochanter (stronger in Dyrosauridea), and display well-developed distal condyles (separated by an intercondylar fossa). Teleosauroidea also displays a broad ilium but a relatively short postacetabular process and long preacetabular process compared to Dyrosauridea and Crocodylia. The teleosauroid bony acetabulum is the largest and is bordered by a relatively long supraacetabular crest (resulting in positive values of the second axis). In Teleosauroidea, the acetabular perforation is less marked than in Crocodylia and Dyrosauridea but still separates the peduncles (*contra* Metriorhynchoidea). Teleosauroidea possesses a wide ischial blade with a pointed anterior process and large posterior process (the latter resulting in positive values of the second axis). Its acetabular perforation is mainly poorly developed and its anterior peduncle is strongly reduced (but larger than in Metriorhynchoidea). The pubis of Teleosauroidea is closer to that of Metriorhynchoidea with its relatively large pubic diaphysis and oval peduncle, along with the marked inclination of the shaft laterally. Compared to Metriorhynchoidea, Teleosauroidea shows a stronger anterodorsal curvature of its femur and well-developed distal condyles. Metriorhynchoidea possesses a reduced ilium with the lack of a postacetabular process, a strongly reduced acetabular perforation and a continuous surface uniting the pubic and ischial peduncles (resulting in positive values of the first axis). Basal metriorhynchoid ilia (see supplementary figures 21 & 25) are strongly similar to Teleosauroidea. The ischium of Metriorhynchoidea also possesses an enlarged ischial blade but shows the most reduced anterior peduncle and acetabular perforation (see supplementary figures 21 & 26). However, the pubis of Metriorhynchoidea possesses the greatest pubic diaphysis and lateral inclination of the shaft (see supplementary figures 21 & 27). Like Teleosauroidea, the pubic shaft of Metriorhynchoidea is shorter than Crocodylia and Dyrosauridea, but its peduncle is proportionally larger and ovoid.
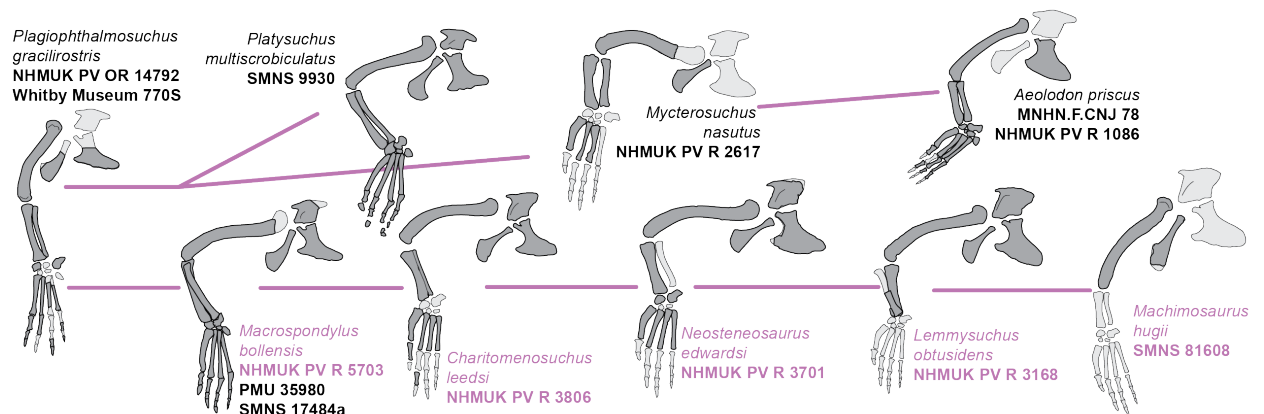
5. Discussion

5.1. **Phylogenetic implications.** In the most recent phylogenetic datasets, postcranial characters only represent about 27% of the total (Young et al., 2020b; Johnson et al., 2020). This number reaches 9% in the goniopholidid+tethysuchian matrix of Jouve and Jalil (2020a). The preponderance of cranial characters brings several issues, especially since craniodental morphology is known to be malleable (Pierce et al., 2009) and convergent in crocodylomorpha (Young et al., 2010; Godoy et al., 2016; Martin et al., 2016; McCurry et al., 2017; Martin et al., 2019a; Young et al., 2020b; Stubbs et al., 2021). This widespread craniodental convergence has obscured the global positioning of Thalattosuchia in Crocodylomorpha (Jouve, 2009; Wilberg, 2015b, 2017) a well as the interrelationships of Thalattosuchia (Martin et al., 2019a; Johnson et al., 2020). These issues were partially resolved with a better outgroup choice (Wilberg, 2015b). Increasing the dataset (quantity of characters and thalattosuchian OTUs) and character reassessment (Young et al., 2016; Ősi et al., 2018; Johnson et al., 2020; Young et al., 2020b) has been met with
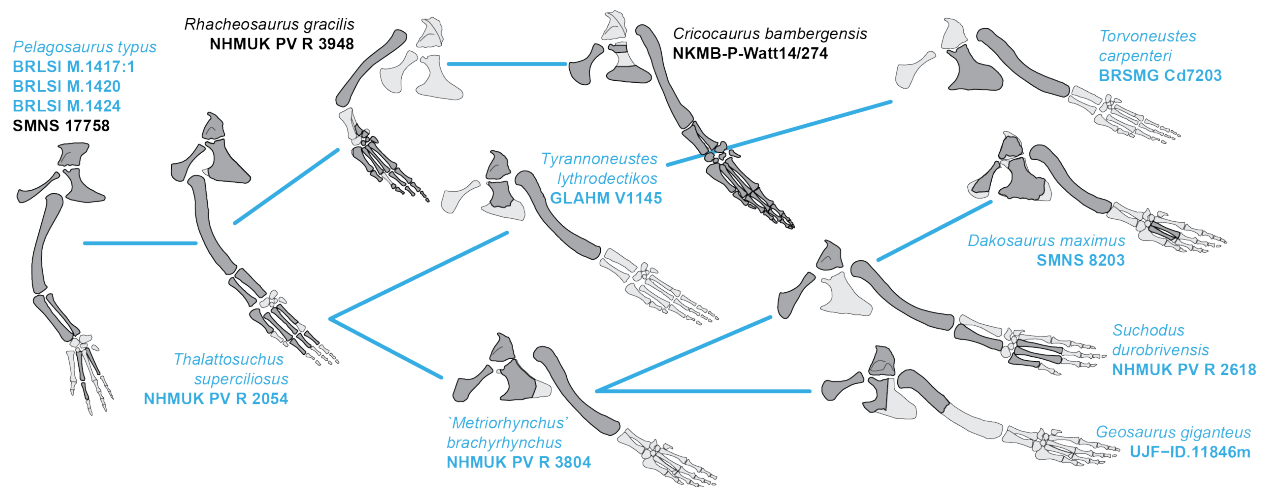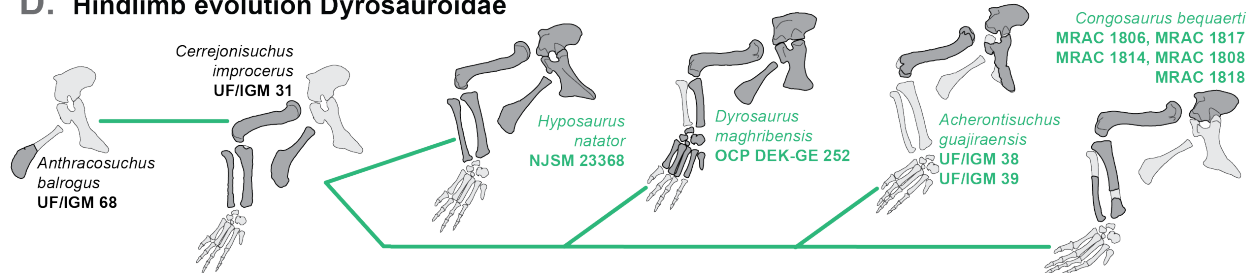
FIGURE 3. **A.** morphospace based on the combination of pelvic landmarks; **B–D** hindlimb evolution within: **B.** Teleosauroidea, *Aeolodon priscus* MNHN.F.CNJ 78 modified from Foffa et al. (2019); **C.** Metriorhynchoidea, *Cricocaurus bambergensis* NKMB-P-Watt14/274 modified from Sachs et al. (2019); **D.** Dyrosauridea, *Dyrosaurus maghribensis* OCP DEK-GE 252 adapted from pictures courtesy of Stéphane Jouve. Light grey colored bones are reconstructed. Colored specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c) Thesupermart – License CC BY-SA 3.0.

limited success (Ősi et al., 2018; Johnson et al., 2020).

The scarcity of postcranial phylogenetic characters actually concerns Crocodylomorpha in its entirety (Godoy et al., 2016; Martin et al., 2016; Mannion et al., 2019; Blanco, 2021). This issue is emphasized as postcranial anatomy is poorly presented and illustrated in publications, whether it is a matter of historically missing materials or general contempt (Godoy et al., 2016; Martin et al., 2016; Mannion et al., 2019; Scavezzoni and Fischer, 2021). Fortunately, recent works have started to incorporate more postcranial anatomy in both descriptive works and character building, which has brought to light the rich morphological disparity of Crocodylomorpha (Pol et al., 2012; Godoy et al., 2016; Martin et al., 2016, 2019b; Jouve and Jalil, 2020a; Jouve et al., 2021; Scavezzoni and Fischer, 2021), and its significance in understanding crocodylomorph relationships (Pol et al., 2012; Godoy et al., 2016; Martin et al., 2016; Jouve and Jalil, 2020a; Blanco, 2021).

In this context, it is clear that new data are in dire need to better constrain the phylogenetic evolution of crocodylomorphs (Godoy et al., 2016; Mannion et al., 2019). Our convergence analyses show that appendicular convergence amongst Crocodylomorpha is very rare. Despite showing a range of morphologies in each bone, (semi-)aquatic crocodylomorphe groups are weakly convergent, highlighting the existence of several clade-specific postcranial traits such as scapula's acromion process development, scapulocoracoid synchondrosis size, coracoid proximal head perforation, iliac acetabular perforation size, ischial acetabular perforation size and shape, ischial shaft shape, pubic diaphysis size, pubic apron lateral protuberance, etc. As a result, postcranial anatomy likely is an abundant source of phylogenetic and taxonomic characters to assess the relationships within Crocodylomorpha.

5.2. **The multiple ways of being an aquatic crocodylomorph.** Both isolated and combined analyses reveal the clear postcranial dissimilarity between Crocodylia, Thalattosuchia and Dyrosauridea, regardless of the thanatocoenosis, hinting at the presence of conservatism in the postcranium of Crocodylomorphs. Among postcranial elements, the scapula, the coracoid and the ilium prove to be most distinctive for the three clades. The humerus, ischium and pubis are mostly affected by the intraspecific variation of *'Thalattosuchus' superciliosus*, which putatively holds at least two morphotypes. Regarding the pubis, the semi-aquatic teleosauroids have only evolved a limited range of morphologies compared to metriorhynchoids. The metriorhynchoid and teleosauroid ischia appear overall similar for a wide range of thanatoceonose, echoing the weight of conservatism in crocodylomorpha. Still, metriorhynchoid and teleosauroid ischia bear distinct anatomical features (*e.g.* acetabular perforation, anterior peduncle shape, shaft thickness, posterior process shape, etc.). In parallel, the wide variety of shape of both Teleosauroidea and Metriorhynchoidea humeri reflects the various and extensive modifications undergone in each lineage. Indeed, the humerus shows progressive modifications in shape through time, gradually departing from the plesiomorphic crocodylomorph configuration to pursue different trends following the lineage. The most recent phylogenetic hypotheses for Thalattosuchia (Johnson et al., 2020; Young et al., 2020b) suggest that humeral reduction appeared independently thrice in Teleosauroidea and more than thrice in Metriorhynchoidea (see Figure 2 E, and see supplementary figure 30) (*contra* (Wilberg, 2015a; Young and de Andrade, 2009)). Furthermore, the coracoid also undergoes two evolutionary changes with a proximal opening of the foramen in basal metriorhynchids and then reverts back to enclosed foramen in more derived members. Therefore, the strong dissimilarity between Metriorhynchoidea and Teleosauroidea mirrors the existence of specific evolutionary trends within Thalattosuchia. The thalattosuchian, and more spectacularly metriorhynchoid, thoracic and pelvic girdles show a reduction of dorsal elements along with an increase of ventral ones, similarly to other pelagic marine reptiles (*e.g.* nothosaurs and plesiosaurs; Krahl (2021)). This trend is not recovered within marine dyrosaurids which were presumably as comfortable on land as at sea (Schwarz-Wings et al., 2009; Jouve, 2021). The overall reduction of the forelimb and lengthening of the hindlimb in metriorhynchoids is a pattern found in other lineages of

aquatic archosaurs like thalattosaurs (Liu et al., 2013) and hesperornithiformes (Bell et al., 2018), hinting at the existence of another type of evolutionary trajectory for pelagic taxa differing from the development of foreflippers among Archosauria.

Despite this conservatism, the diverging morphologies observed among aquatic to semi-aquatic crocodylomorphs likely mirror differences in their ecology, such as fully pelagic taxa reducing their dorsal girdle elements as opposed to load-bearing semi-aquatic taxa. Furthermore, differences in feeding behaviours (see Foffa et al. (2018)) required certain locomotor capabilities or constraint resistance, which appear to be reflected in the postcranium (*e.g.* humeral shape variation). For example, *Torvoneustes*, *Dakosaurus*, and *Geosaurus* evolved short and robust humeri that still markedly differ from on another in their overal shape, so does their inferred feeding ecology (durophageous and cutting macrophages, respectively) (Foffa et al., 2018)).

Another fascinating point concerns the location of the scapular glenoid facet of teleosauroids, which changed several times across the teleosauroid evolutionary history regardless of their habitat. In teleosauroids, the change in position of the glenoid facet on the scapula between more laterally and more posteriorly oriented implies slightly differing orientations of the humerus in relation to thoracic girdle. Posteriorly oriented glenoid facets on the scapula have occurred several times across the teleosauroid evolutionary history, with examples in at least *Indosinosuchus potamosiamensis* (Martin et al., 2019a), *Neosteneosaurus edwardsi*, and *Platysuchus multiscrobiculatus* whose habitats range from freshwater (Martin et al., 2019a), to semi-aquatic and semi-terrestrial (Johnson et al., 2022) respectively. Although relatively more elongated, the humerus of *Platysuchus multiscrobiculatus* resembles that of extant crocodylians, namely in the shape and orientation of the proximal head, distal condyles, and position of the deltopectoral crest. Due to the orientation of the glenoid facet on both scapula and coracoid and their overall shape, it is possible that the shoulder architecture of *Platysuchus multiscrobiculatus* in terms of soft tissues (muscles and cartilage) could possess certain similarities with that of extant crocodylians, especially when compared to more derived teleosauroids. Comparatively, in *Indosinosuchus potamosiamensis* and *Neosteneosaurus edwardsi*, the proximal head displays a greater posterior deflection and has less marked capitula and the condyles are anterodorsally twisted, which also impacts the orientation of the deltopectoral crest. In comparison, teleosauroids that display a laterally positioned glenoid facet on the scapula also have a relatively straighter humerus, either due to a lesser angle of the posterior deflection or by a proportionally shorter deflected head (distance between the tip deltopectoral crest and tip of proximal head). Presumably, the change in position of the glenoid facet on the scapula reflects iterative changes in the forelimb posture.

Thereby, it appears to exist multiple ways to be an aquatic crocodylomorph, not unlike what is observed for the aquatic lizards *Anolis* (Leal et al., 2002). Indeed, geographically distinct aquatic *Anolis* species are strongly dissimilar although their terrestrial counterparts – separated islanders – constitute the emblem of convergence. Furthermore, some of those aquatic lineages seem to show convergence although solely among themselves (Leal et al., 2002); a similar outcome was also found for Thalattosuchia. Hence, postcranial anatomy seems to define clade-wide functional capabilities and should be taken into account when discussing the palaeoecology of crocodylomorpha.

6. CONCLUSION

Similarly to aquatic anoles, our new dataset of crocodylomorph postcranial anatomy reveals that the extinct marine clades Thalattosuchia and Dyrosauridea are strongly dissimilar in postcranial anatomy (both in overall structure and in the morphological detail of individual bones), even though colonizing similar environments. Extant crocodylians are markedly divergent from extinct crocodylomorphs; comparatively to Dyrosauridea and Thalattosuchia, extant crocodylians likely evolved a limited range

of morphologies. Consequently, extant crocodylians do not represent flawless functional analogues for extinct crocodylomorpha.

Thalattosuchia shows some degree of intragroup convergence for the pubis and humerus, whereas the ilium and scapula appear more conservative. In comparison, the extinct crocodylomorphs appear overall divergent throughout their postcranium. Postcranial elements manifest a high, previously unsuspected potential as a source of taxonomic and phylogenetic characters to precise the relationships between crocodylomorph groups. In addition, a better understanding of the ecology and disparity of extinct crocodylomorphs appears only achievable through the inclusion of more postcranial elements, which we show are more diversified than previously thought.

7. Acknowledgements

8. List of figure captions

Figure 1:

3D models of girdle elements used in our analyses. **A.** left scapula in lateral view ; **B.** left coracoid in dorsal view ; **C.** left humerus in dorsal view ; **D.** left ilium in lateral view ; **E.** left femur in dorsal view ; **F.** Pelvic girdle reconstruction in ventral view. Arrow points anteriorly. All scale bars represent 1cm. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c) Thesupermart – License CC BY-SA 3.0.

Figure 2:

A. morphospace based on the combination of thoracic landmarks; **B – D** forelimb evolution within: **B.** Teleosauroidea, *Aeolodon priscus* MNHN.F.CNJ 78 modified from Foffa et al. (2019); **C.** Metriorhynchoidea, *Cricocaurus bambergensis* NKMB-P-Watt14/274 modified from Sachs et al. (2019); **D.** Dyrosauridea, *Dyrosaurus maghribensis* OCP DEK-GE 252 adapted from pictures courtesy of Stéphane Jouve. **E.** Phenograms based on the humeral ratio. Light grey colored bones are reconstructed. Colored specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c)

Thesupermart – License CC BY-SA 3.0.

Figure 3:

A. morphospace based on the combination of pelvic landmarks; **B–D** hindlimb evolution within: **B.** Teleosauroidea, *Aeolodon priscus* MNHN.F.CNJ 78 modified from Foffa et al. (2019); **C.** Metriorhynchoidea, *Cricocaurus bambergensis* NKMB-P-Watt14/274 modified from Sachs et al. (2019); **D.** Dyrosauridea, *Dyrosaurus maghribensis* OCP DEK-GE 252 adapted from pictures courtesy of Stéphane Jouve. Light grey colored bones are reconstructed. Colored specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorphs silhouettes: Metriorhynchoidea & Teleosauroidea (c) Gareth Monger – Licence CC BY 3.0; Dyrosauridae (c) Nobu Tamura, vectorized by Zimices – Licence CC BY-SA 3.0; Crocodylia original picture (c) Thesupermart – License CC BY-SA 3.0.

AUTHOR CONTRIBUTION

DATA ARCHIVING STATEMENT

All reconstructed models and their landmark coordinates, as well as the R scripts and phylogenetic data (nexus files and time periods) are available on ORBi `https://hdl.handle.net/2268/305703,`and the Dryad Digital Repository `https://doi.org/10.5061/dryad.qfttdz0p5.` Original raw models are available on MorphoSource (see Appendix S1 for DOIs).

SUPPORTING INFORMATION

Additional Supporting Information can be found online (`https://doi.org/10.1111/pala.12678`):
Appendix S1. List of MorphoSource DOIs for raw mesh data.
Table S1. List of taxa used in the landmark analysis.
Table S2. List of repaired taxa with references.
Table S3. Values of K$_{mult}$ for each bone of the entire dataset (Thalattosuchia–Dyrosauridea–Crocodylia).
Table S4. Values of K$_{mult}$ for each bone for Thalattosuchia.
Table S5. Pairs of crocodylomorph taxa employed in the Stayton distance-based convergence tests (Ct metrics).
Tables S6–S7. List of type II landmarks.
Table S8. List of semi-landmarks.
Table S9. List of taxa and their measurements used in the phenogram analyses.
Figs S1–S18. 3D models of individual bones before and after repair.
Figs S19–S21. Positioning of type II landmarks and semilandmarks.
Figs S22–S31. Morphospaces representing dissimilarity between Dyrosauridea, Crocodylia, Metriorhynchoidea (Thalattosuchia) and Teleosauroidea (Thalattosuchia) using the first two PCA axes.
Fig. S32. Crocodyliformes phenograms representing the evolution of the humeral ratio.

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