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Limited convergence in the postcranium of aquatic Crocodylomorpha

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Abstract: Thalattosuchia (Early Jurassic to Early Cretaceous) and Dyrosauridea (Late Cretaceous to Early Eocene) are crocodylomorph archosaurs which diversified in fluvial and marine environments and endured extinction events (i.e. Jurassic–Cretaceous boundary for Thalattosuchia; Cretaceous–Palaeogene 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.

Key words: Archosauria, postcranium, phylogenetic signal, Thalattosuchia, Dyrosauroidea, appendicular morphology.

Crocodylomorpha is currently restricted to 28 species of semiaquatic ambush predators (Rasmussen *et al.* 2011; Grigg & 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 (Toljagić & Butler 2013; Bronzati *et al.* 2015; Tennant *et al.* 2016; Mannion *et al.* 2019; Wilberg *et al.* 2019; Johnson *et al.* 2020; Jouve & Jalil 2020a; Young *et al.* 2020a; Stubbs *et al.* 2021). Thalattosuchia represents the most remarkable and diverse marine radiation within Crocodylomorpha (Fanti *et al.* 2015; Wilberg 2015a; Johnson *et al.* 2020; Young *et al.* 2020a), distinguishing itself with its wide range of postcranial morphologies, and representing several approaches to aquatic life within the clade. Dyrosauridea is another lineage that colonized the aquatic realm. The two clades do not overlap in time, with Thalattosuchia crossing the Jurassic–Cretaceous boundary and disappearing in the Early Cretaceous (Young *et al.* 2012; Chiarenza *et al.* 2015; Fanti *et al.* 2015) while Dyrosauridea radiated in the late Cretaceous and crossed the Cretaceous–Palaeogene boundary (Jouve *et al.* 2006; Hastings *et al.* 2014; Bronzati *et al.* 2015; Jouve & Jalil 2020a). Both clades initially evolved in non-marine settings before transitioning to marine environments (Wilberg *et al.* 2019; Johnson *et al.* 2020; Young *et al.* 2020a; 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 (Toljagić & Butler 2013; Bronzati *et al.* 2015; Tennant *et al.* 2016; Mannion *et al.* 2019; Wilberg *et al.* 2019; Godoy 2020; Johnson *et al.* 2020; Jouve & Jalil 2020a; Young *et al.* 2020a; Stubbs *et al.* 2021), as revealed by extensive modification of their postcranium. Yet, attention has historically been focused on craniodential anatomy, resulting in the depreciation of postcranial anatomy in diagnoses, anatomical descriptions, phylogenetic analyses and palaeoecological inferences. Recent studies of different groups of Crocodyliformes have started to shed light on the importance of postcranial anatomy in understanding the lifestyle but also the 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 & Jalil 2020a; Blanco 2021; Jouve *et al.* 2021). Withal, the postcranial anatomy of Thalattosuchia and Dyrosauridae remains profoundly overlooked despite an evident disparity. In this study we investigate

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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.

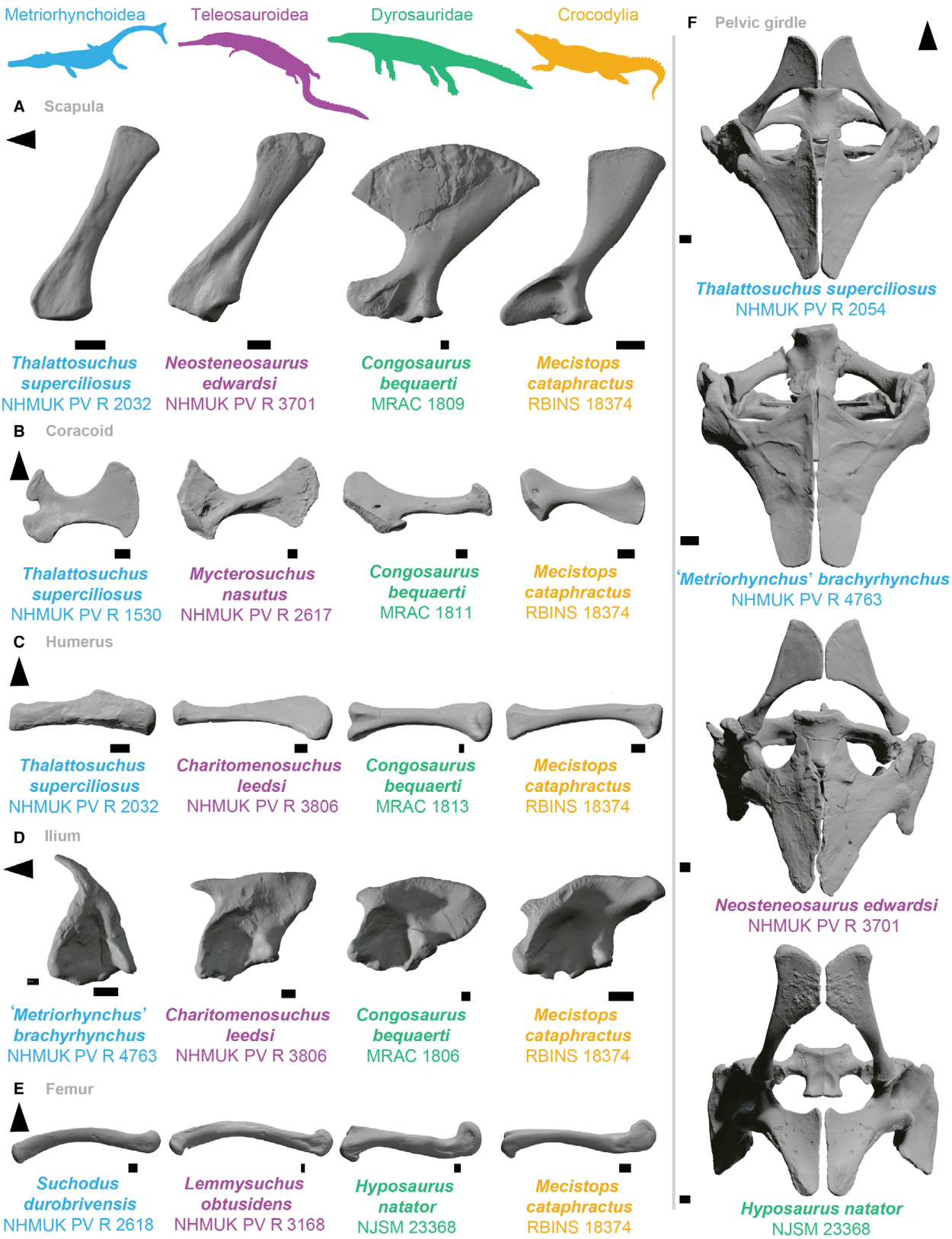
Institutional abbreviations. BRLSI, Bath Royal Literary and Scientific Institute, Bath, UK; BRSMG, Bristol City Museum and Art Gallery, UK; GLAHM, Hunterian Museum and Art Gallery, Glasgow, UK; GPIT, Geologisch–Paläontologisches Institut Tübingen, Germany; MLP, Museo de La Plata, Buenos Aires, Argentina;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

MATERIAL AND METHOD

We created 3D models of the best preserved specimens of key species of Thalattosuchia and Dyrosauridea using high precision surface scanning (Fig. 1). We sampled specimens possessing both postcranial and cranial materials, and some missing cranial remains but with outstanding postcrania (Table S1; total specimens: 1 Crocodylia, 36 Thalattosuchia, 5 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 (MM Johnson, pers. comm. 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 v2021.1.0) and assembled using Artec Studio 16. Blender (v3.1.2) was used to mirror bones into the preferred left polarity, and also to repair obvious defects (Table S2; Figs S1–S16). Our entire data set of 3D models comprises a total of: 10 scapulae, 14 coracoids, 17 humeri, 22 ilia, 19 ischia, 17 pubes and 23 femora. On each model, we placed a series of type-II landmarks (Bookstein 1997) and sliding semi-landmarks (Tables S6–S8; Figs S17–S19) using the software Stratovan Checkpoint (v2020.10.13.0859): 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: 7 crocodylians, 4 dyrosaurids, 11 metriorhynchoids and 9 teleosauroids (see Table S9 for the complete list).

All subsequent analyses were run in the R statistical environment v4.1.2 (R Core Team 2013). Landmark coordinates were saved as .pts files and imported in R using the read.pts function of the Morpho package (v2.9; Schlager *et al.* 2021). The isolated bone morphospaces were performed to allow the inclusion of a greater portion of specimens (Figs S20–S28). To analyse the distribution of landmarks of each bone, we performed a generalized Procrustes 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 Table S1). Landmark coordinates were grouped after performing separate GPA using the combine.subsets function of the Geomorph package (Adams *et al.* 2022). Each new set was then subjected to a PCA using the

FIG. 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. Arrows points anteriorly. All scale bars represent 1 cm. Crocodylomorph silhouette images from Phylopic (http://phylopic.org: Gareth Monger (Metriorhynchoidea & Teleosauroidea) CC BY 3.0; Nobu Tamura, vectorized by Zimices (Dyrosauridae) and Thesupermart (Crocodylia), both CC BY-SA 3.0).


Metriorhynchoidea
Teleosauroidea
Dyrosauridae
Crocodylia
A Scapula
Thalattosuchus superciliosus NHMUK PV R 2032
Neosteneosaurus edwardsi NHMUK PV R 3701
Congosaurus bequaerti MRAC 1809
Mecistops cataphractus RBINS 18374
B Coracoid
Thalattosuchus superciliosus NHMUK PV R 1530
Mycterosuchus nasutus NHMUK PV R 2617
Congosaurus bequaerti MRAC 1811
Mecistops cataphractus RBINS 18374
C Humerus
Thalattosuchus superciliosus NHMUK PV R 2032
Charitomenosuchus leedsi NHMUK PV R 3806
Congosaurus bequaerti MRAC 1813
Mecistops cataphractus RBINS 18374
D Ilium
'Metriorhynchus' brachyrhynchus NHMUK PV R 4763
Charitomenosuchus leedsi NHMUK PV R 3806
Congosaurus bequaerti MRAC 1806
Mecistops cataphractus RBINS 18374
E Femur
Suchodus durobrivensis NHMUK PV R 2618
Lemmysuchus obtusidens NHMUK PV R 3168
Hyposaurus natator NJSM 23368
Mecistops cataphractus RBINS 18374
F Pelvic girdle
Thalattosuchus superciliosus NHMUK PV R 2054
'Metriorhynchus' brachyrhynchus NHMUK PV R 4763
Neosteneosaurus edwardsi NHMUK PV R 3701
Hyposaurus natator NJSM 23368

gm.prcomp function of the Geomorph package (Adams *et al.* 2022) (Figs 2, 3). Again, the differences between the clades for the new sets were assessed using a Procrustes ANOVA (Adams *et al.* 2022).

We created a supertree based on the dataset from Jouve & Jalil (2020a, 2020b), with additional phylogenetic relations for Teleosauroidea obtained from Johnson *et al.* (2020) and for Metriorhynchoidea from Young *et al.* (2020a). We re-analysed this dataset using our parsimony protocol (TNT v1.5; 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 (v1.8.0; 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 (v4.1.3; Bapst 2012) based on taxon occurrences obtained from the Paleobiology Database (https://paleobiodb.org).

The estimations for Dyrosauridea–Thalattosuchia and Dyrosauridea–Crocodylia roots were taken from Jouve & Jalil (2020a). These dates were combined with morphological data to produce phylomorphospaces (Fig. S29) 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 a 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 package v2.5-6; Oksanen *et al.* 2019).

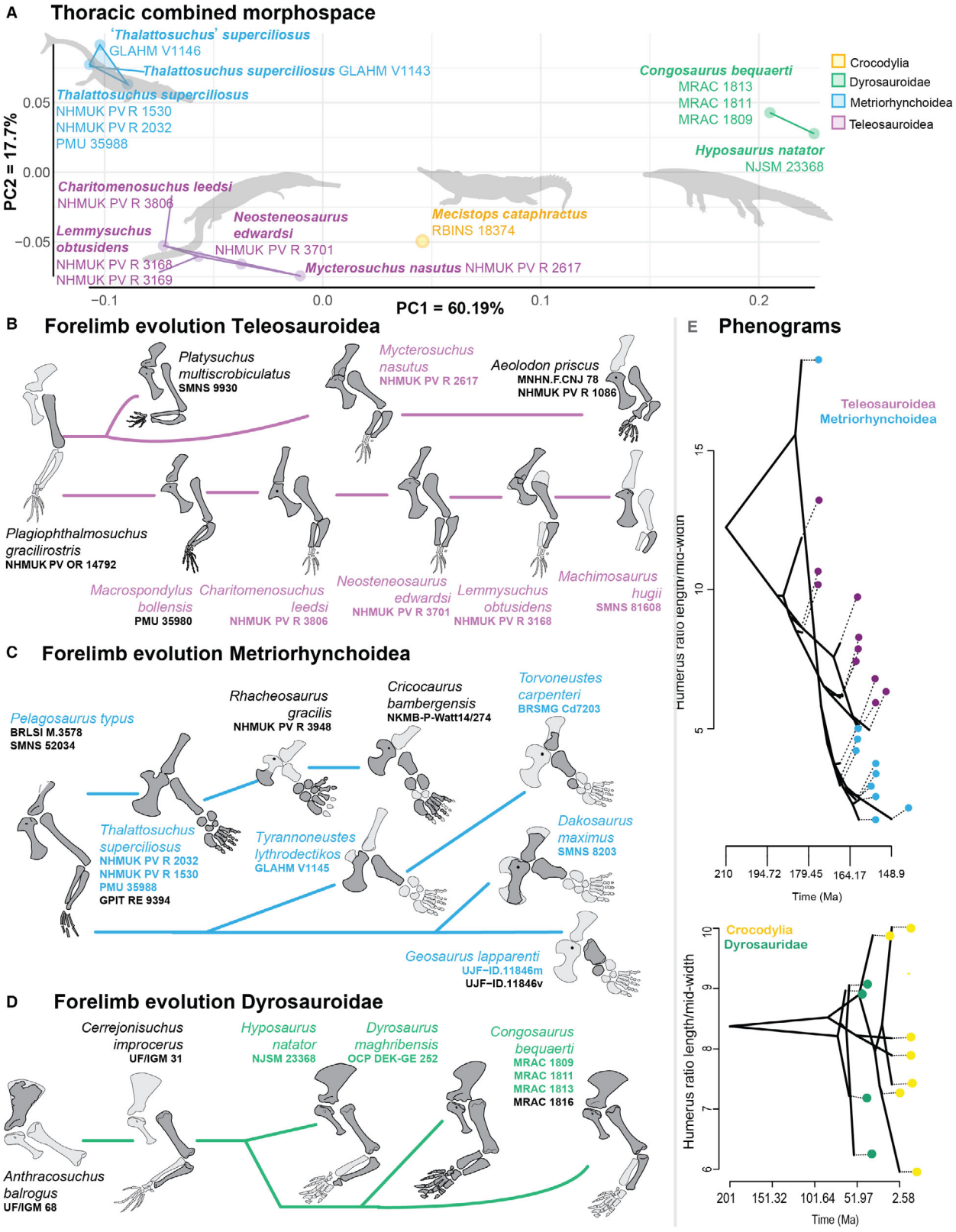
RESULTS

Morphospace occupation

Thalattosuchia, Dyrosauridea and Crocodylia cover clearly distinct portions of the morphospace for both girdles (Figs 2, 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 (Figs S20–S28). In all 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 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 $r = 0.845$, $p = 0.036$).

However, the K_{mult} tests performed on isolated and combined girdle elements (Table S3) exhibited a 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 imply 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 (Table S4). The low K_{mult} values (i.e. $K_{mult} < 0.5$) obtained for both the isolated (with the exception of the ilium, scapula and coracoid) and

FIG. 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 Stephane Jouve). E, phenograms based on the humeral ratio. Light grey coloured bones are reconstructed. Coloured specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorph silhouette images from Phylopic (http://phylopic.org: Gareth Monger (Metriorhynchoidea & Teleosauroidea) CC BY 3.0; Nobu Tamura, vectorized by Zimices (Dyrosauridae) and Thesupermart (Crocodylia), both CC BY-SA 3.0).


A
Thoracic combined morphospace
'Thalattosuchus' superciliosus GLAHM V1146
Thalattosuchus superciliosus GLAHM V1143
Thalattosuchus superciliosus NHMUK PV R 1530 NHMUK PV R 2032 PMU 35988
Congosaurus bequaerti MRAC 1813 MRAC 1811 MRAC 1809
Hyposaurus natator NJSM 23368
Charitomenosuchus leedsi NHMUK PV R 3806
Neosteneosaurus edwardsi NHMUK PV R 3701
Mecistops cataphractus RBINS 18374
Lemmysuchus obtusidens NHMUK PV R 3168 NHMUK PV R 3169
Mycterosuchus nasutus NHMUK PV R 2617
Crocodylia
Dyrosauroidae
Metriorhynchoidea
Teleosauroidea
PC2 = 17.7%
PC1 = 60.19%
B
Forelimb evolution Teleosauroidea
Platysuchus multiscrobiculatus SMNS 9930
Mycterosuchus nasutus NHMUK PV R 2617
Aeolodon priscus MNHN.F.CNJ 78 NHMUK PV R 1086
Plagiophthalmosuchus gracilirostris NHMUK PV OR 14792
Macrospondylus bollensis PMU 35980
Charitomenosuchus leedsi NHMUK PV R 3806
Neosteneosaurus edwardsi NHMUK PV R 3701
Lemmysuchus obtusidens NHMUK PV R 3168
Machimosaurus hugii SMNS 81608
C
Forelimb evolution Metriorhynchoidea
Pelagosaurus typus BRLSI M.3578 SMNS 52034
Rhacheosaurus gracilis NHMUK PV R 3948
Cricocaurus bambergensis NKMB-P-Watt14/274
Torvoneustes carpenteri BRSMG Cd7203
Thalattosuchus superciliosus NHMUK PV R 2032 NHMUK PV R 1530 PMU 35988 GPIT RE 9394
Tyrannoneustes lythrodectikos GLAHM V1145
Dakosaurus maximus SMNS 8203
Geosaurus lapparenti UJF-ID.11846m UJF-ID.11846v
D
Forelimb evolution Dyrosauroidae
Cerrejonisuchus improcerus UF/IGM 31
Hyposaurus natator NJSM 23368
Dyrosaurus maghribensis OCP DEK-GE 252
Congosaurus bequaerti MRAC 1809 MRAC 1811 MRAC 1813 MRAC 1816
Anthracosuchus balrogus UF/IGM 68
E
Phenograms
Teleosauroidea
Metriorhynchoidea
Humerus ratio length/mid-width
15
10
5
210
194.72
179.45
164.17
148.9
Time (Ma)
Crocodylia
Dyrosauridae
Humerus ratio length/mid-width
10
9
8
7
6
201
151.32
101.64
51.97
2.58
Time (Ma)

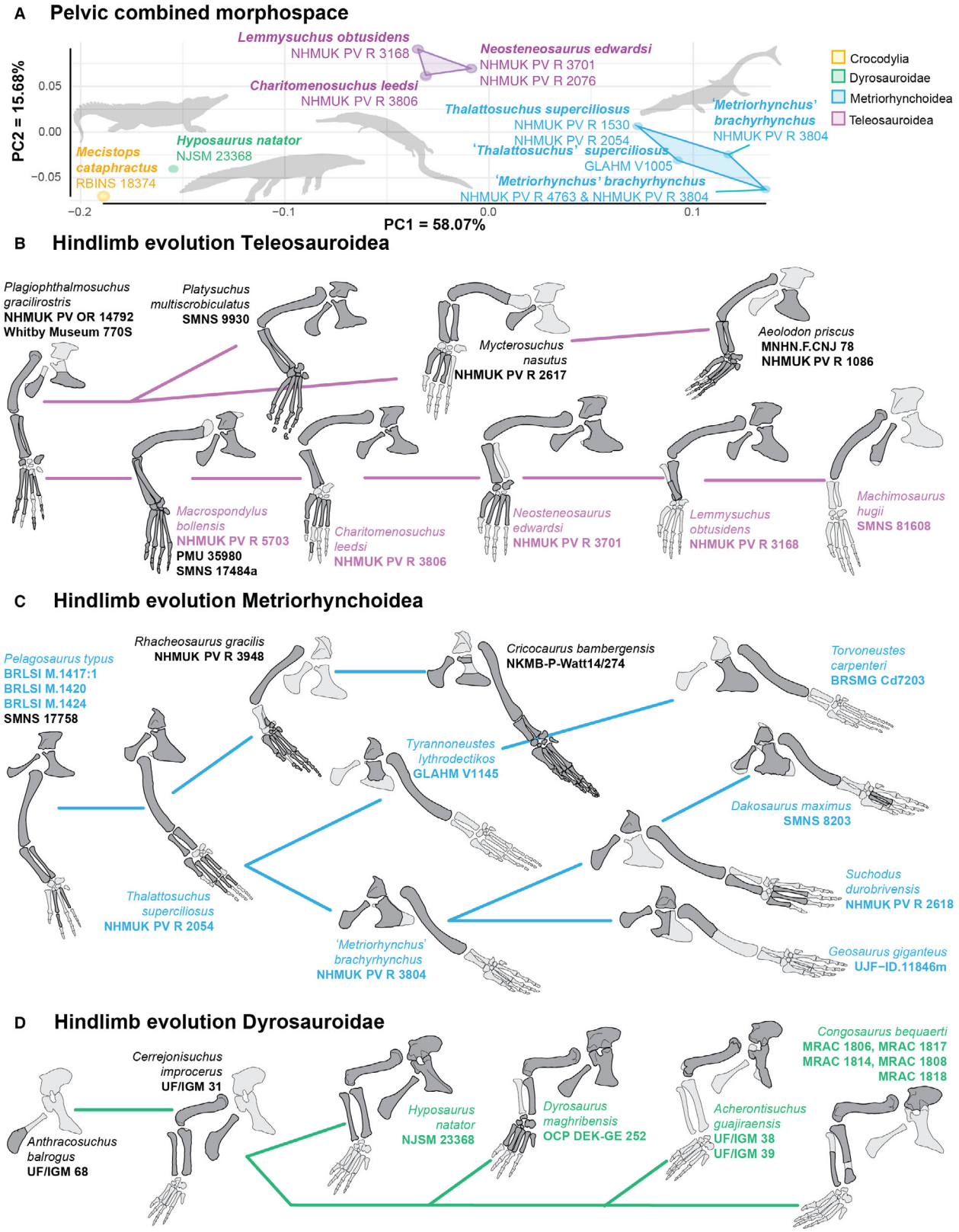

A Pelvic combined morphospace
Lemmysuchus obtusidens
NHMUK PV R 3168
Neosteneosaurus edwardsi
NHMUK PV R 3701
NHMUK PV R 2076
Charitomenosuchus leedsi
NHMUK PV R 3806
Thalattosuchus superciliosus
NHMUK PV R 1530
NHMUK PV R 2054
'Metriorhynchus' brachyrhynchus
NHMUK PV R 3804
Hyposaurus natator
NJSM 23368
Mecistops cataphractus
RBINS 18374
'Thalattosuchus' superciliosus
GLAHM V1005
'Metriorhynchus' brachyrhynchus
NHMUK PV R 4763 & NHMUK PV R 3804
Crocodylia
Dyrosauroidae
Metriorhynchoidea
Teleosauroidea
PC2 = 15.68%
PC1 = 58.07%
B Hindlimb evolution Teleosauroidea
Plagiophthalmosuchus gracilirostris
NHMUK PV OR 14792
Whitby Museum 770S
Platysuchus multiscrobiculatus
SMNS 9930
Mycterosuchus nasutus
NHMUK PV R 2617
Aeolodon priscus
MNHN.F.CNJ 78
NHMUK PV R 1086
Macrospondylus bollensis
NHMUK PV R 5703
PMU 35980
SMNS 17484a
Charitomenosuchus leedsi
NHMUK PV R 3806
Neosteneosaurus edwardsi
NHMUK PV R 3701
Lemmysuchus obtusidens
NHMUK PV R 3168
Machimosaurus hugii
SMNS 81608
C Hindlimb evolution Metriorhynchoidea
Pelagosaurus typus
BRLSI M.1417:1
BRLSI M.1420
BRLSI M.1424
SMNS 17758
Rhacheosaurus gracilis
NHMUK PV R 3948
Cricocaurus bambergensis
NKMB-P-Watt14/274
Torvoneustes carpenteri
BRSMG Cd7203
Tyrannoneustes lythrodectikos
GLAHM V1145
Dakosaurus maximus
SMNS 8203
Thalattosuchus superciliosus
NHMUK PV R 2054
Suchodus durobrivensis
NHMUK PV R 2618
'Metriorhynchus' brachyrhynchus
NHMUK PV R 3804
Geosaurus giganteus
UJF-ID.11846m
D Hindlimb evolution Dyrosauroidae
Cerrejonisuchus improcerus
UF/IGM 31
Congosaurus bequaerti
MRAC 1806, MRAC 1817
MRAC 1814, MRAC 1808
MRAC 1818
Anthracosuchus balrogus
UF/IGM 68
Hyposaurus natator
NJSM 23368
Dyrosaurus maghribensis
OCP DEK-GE 252
Acherontisuchus guajiraensis
UF/IGM 38
UF/IGM 39

FIG. 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 Stephane Jouve). Light grey coloured bones are reconstructed. Coloured specimen numbers and names are used in this work. Bones not in anatomical position. Crocodylomorph silhouette images from Phylopic (http://phylopic.org: Gareth Monger (Metriorhynchoidea & Teleosauroidea) CC BY 3.0; Nobu Tamura, vectorized by Zimices (Dyrosauridae) and Thesupermart (Crocodylia), both CC BY-SA 3.0).

combined dataset note the presence of intraclade convergence within Thalattosuchia (Tables S3, S4).

We investigated the latter by performing updated Stayton distance-based convergence tests (Ct metrics; see Table S5). 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 Table S5).

All clades differ in a number of traits. For the thoracic girdle (Fig. 2A), Dyrosauridea displays both the sturdiest scapula, with its enlarged scapular blade, and robust humerus, 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 (Fig. 2E), 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 (Fig. 2C, Figs S20, S24). Within Metriorhynchoidea, *Geosaurus lapparenti* stands out with its protruding posterior capitular tuberosity and absence of distinct distal capitula. Crocodylia show a 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 have 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.

Crocodylomorpha also differ in pelvic morphology (Fig. 3A). Crocodylia and Dyrosauridea possess relatively stout and twisted femora, ilia with large post-acetabular processes and acetabular perforations, and proportionally anteroposteriorly limited ischia (all of which result in negative values of both axes). Crocodylia also show a strongly reduced pubic diaphysis and a thinner ischial shaft. Dyrosauridea display a broad ilium with the largest and widest post-acetabular process, but a relatively short and stout pre-acetabular process and supra-acetabular 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 it is still less developed than that of 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 display 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 display a broad ilium but a relatively short post-acetabular process and long pre-acetabular process compared to Dyrosauridea and Crocodylia. The teleosauroid bony acetabulum is the largest and is bordered by a relatively long supra-acetabular 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 possess 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 show a stronger anterodorsal curvature of its femur and well-developed distal condyles. The ilium of Metriorhynchoidea does not possess a postacetabular process, its acetabular perforation is strongly reduced, and it has a continuous surface uniting the pubic and ischial peduncles (resulting in positive values of the first axis). Basal metriorhynchoid ilia (Figs S21, S25) are strongly similar to those of Teleosauroidea. The ischium of Metriorhynchoidea also possess an enlarged ischial blade but shows the most reduced anterior peduncle and acetabular perforation (Figs S21, S26). However, the pubis of Metriorhynchoidea possesses the greatest pubic diaphysis and lateral inclination of the shaft (Figs S21, S27). As in Teleosauroidea, the pubic shaft of Metriorhynchoidea is shorter than that of Crocodylia and Dyrosauridea, but the peduncle is proportionally larger and ovoid.

DISCUSSION

Phylogenetic implications

In the most recent phylogenetic datasets, postcranial characters only represent about 27% of the total (Johnson *et al.* 2020; Young *et al.* 2020b). This number is only 9% in the goniopholidid+tethysuchian matrix of Jouve & Jalil (2020a). The preponderance of cranial characters brings several issues, especially since craniodential 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 size of the dataset (quantity of characters and thalattosuchian operational taxonomic units (OTU)) and character reassessment (Young *et al.* 2016; Ősi *et al.* 2018; Johnson *et al.* 2020; Young *et al.* 2020b) has been met with 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 magnified as postcranial anatomy is poorly presented and illustrated in publications, whether it is a matter of historically missing material or general contempt (Godoy *et al.* 2016; Martin *et al.* 2016; Mannion *et al.* 2019; Scavezzoni & Fischer 2021). Fortunately, recent works have started to incorporate more postcranial anatomy in both descriptions 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 & Jalil 2020a; Jouve *et al.* 2021; Scavezzoni & Fischer 2021) and its significance in understanding crocodylomorph relationships (Pol *et al.* 2012; Godoy *et al.* 2016; Martin *et al.* 2016; Jouve & Jalil 2020a; Blanco 2021).

In this context, it is clear that new data are urgently needed to better constrain the phylogenetic evolution of crocodylomorphs (Godoy *et al.* 2016; Mannion *et al.* 2019). Our convergence analysis shows that appendicular convergence amongst Crocodylomorpha is very rare. Despite showing a range of morphologies in each bone, (semi)aquatic crocodylomorph 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 is an abundant source of phylogenetic and taxonomic characters with which to assess the relationships within Crocodylomorpha.

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, coracoid and 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 includes at least two morphotypes. Regarding the pubis, the semiaquatic teleosauroids have evolved only a limited range of morphologies compared to metriorhynchoids. The metriorhynchoid and teleosauroid ischia appear overall similar for a wide range of thanatoceonoses, 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). 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 (Fig. 2E, Fig. S30) (*contra* Young & de Andrade 2009; Wilberg 2015a). 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 semiaquatic crocodylomorphs probably mirror differences in their ecology, such as fully pelagic taxa reducing their dorsal girdle elements as opposed to load-bearing semiaquatic taxa. Furthermore, differences in feeding behaviours (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 overall shape, as does their inferred feeding ecology (durophagous 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 the 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 semiaquatic and semiterrestrial (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, in terms of soft tissues (muscles and cartilage), the shoulder architecture of *Platysuchus multiscrobiculatus* 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 with a 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 to 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.

Therefore, it appears that there 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 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.

CONCLUSION

As for 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 they colonized similar environments. Extant crocodylians are markedly divergent from extinct crocodylomorphs; compared with Dyrosauridea and Thalattosuchia, extant crocodylians have 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 only appears achievable by the inclusion of more postcranial elements, which we show are more diversified than previously thought.

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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).

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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 (halattosuchia–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 semi-landmarks.
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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