geodiversitas

2024 • 46 • 6

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art. 46 (6) — Published on 2 May 2024
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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

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Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

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Submitted on 17 January 2023 | accepted on 2 October 2023 | published on 2 May 2024

urn:lsid:zoobank.org:pub:6ACF6A79-9149-4781-808D-478668673EB6

Scavezzoni I., Fischer V., Johnson M. M. & Jouve S. 2024. — Form and function of the pelvic girdle of Thalattosuchia and Dyrosauridae (Crocodyliformes). *Geodiversitas* 46 (6): 135-326. https://doi.org/10.5252/geodiversitas2024v46a6. http://geodiversitas.com/46/6

ABSTRACT

Crocodyliformes Hay, 1930 represents an important group of archosaurs that is currently restricted to twenty-eight species of semi-aquatic ambush predators. However, the extensive fossil record of Crocodyliformes indicates this group was much more diverse in the past and had a complex evolutionary history, rhythmed by a series of extinction events. An iconic expression of this past diversity is the colonization of the marine realm by several crocodyliform lineages, most notably by Thalattosuchia Fraas, 1901 during the Early Jurassic-Early Cretaceous and by Dyrosauridae de Stefano, 1903 during the Late Cretaceous-Early Eocene. Thalattosuchia constitutes by far the most spectacular and speciose marine radiation of Crocodyliformes, colonizing several ecological niches, before mysteriously going extinct during the Early Cretaceous. Dyrosauridae is well known for massively surviving the end-Cretaceous mass extinction, but disappearing soon afterwards. How crocodyliformes evolved to occupy marine niches and why they went extinct outside the marine extinction events of the Mesozoic is a mystery. Indeed, despite a good fossil record, postcranial elements of thalattosuchians and dyrosaurids have long been disregarded, withal several modern works during the past century. Attention has been focused, for years, on craniodental adaptations and feeding styles only, overlooking the swimming-related adaptations recorded in the postcranial skeleton that permitted these radiations. This work consists of a new thorough comparative description of the pelvic girdle of the most representative members of two extinct clades of aquatic crocodyliforms: Thalattosuchia and Dyrosauridae. This work also provides a standardize terminology and orientated of pelvic elements in those clades. This works does not aim at refining the taxonomy or cladistics of Thalattosuchia and Dyrosauridae, but will certainly clear the way for such future more specific endeavors. This work focuses on the postcranial morphology of Thalattosuchia and Dyrosauridae and aspires to shed light on pelvic evolution throughout their histories. Lastly, this work intends to highlight the relations between form and function within the postcranium of Thalattosuchia and Dyrosauridae, in order to better understand the locomotor habits or limitations present among the members of those extinct groups.

KEY WORDS
Archosauria,
postcranium,
anatomy,
locomotion,
appendicular
morphology,
ilium,
ischium,
pubis.

RÉSUMÉ

Forme et fonction de la ceinture pelvienne des thalattosuchiens et des dyrosauridés (Crocodyliformes).

Les crocodyliformes Hay, 1930 constituent un groupe majeur d'archosaures actuellement restreint à vingt-huit espèces semi-aquatiques de prédateurs en embuscade. Cependant, le vaste enregistrement fossile de Crocodyliformes révèle une plus grande diversité passée ainsi qu'une histoire évolutive complexe, rythmée par une série d'extinctions. Une représentation emblématique de cette diversité passée se trouve dans la colonisation du milieu marin par plusieurs lignées de crocodyliformes, et plus précisément par les thalattosuchiens (Thalattosuchia Fraas, 1901) pour l'intervalle Jurassique inférieur-Crétacé inférieur, et par les dyrosauridés (Dyrosauridae de Stefano, 1903) pour l'intervalle Crétacé supérieur-Éocène inférieur. Les thalattosuchiens constituent de loin la plus spectaculaire et diverse radiation marine de Crocodyliformes ayant colonisé plusieurs niches écologiques, avant de s'éteindre mystérieusement durant le Crétacé inférieur. Les dyrosauridés sont bien connus pour avoir survécu massivement à l'extinction de la fin du Crétacé, mais disparaissent peu de temps après. La façon dont les crocodyliformes ont évolué pour coloniser les niches marines et les raisons de leur disparition en dehors des épisodes d'extinction marine du Mésozoique constituent un mystère. En effet, malgré un bon enregistrement fossile, les éléments postcraniens des thalattosuchiens et des dyrosauridés ont longtemps été mis de côté, en dépit de plusieurs travaux plus modernes au cours du siècle passé. L'attention s'est principalement concentrée, pendant des années, sur leurs adaptations craniodentaires et sur leurs régimes alimentaires, masquant les adaptations liées au mode de nage enregistrée dans le squelette postcrânien, qui ont permis ces radiations. Ce travail consiste en une nouvelle description minutieuse de la ceinture pelvienne des membres les plus représentatifs de deux clades éteints de crocodyliformes aquatiques : les thalattosuchiens et les dyrosauridés. Ce travail fournit également une terminologie standardisée et orientée des éléments pelviens pour ces clades. Ce travail ne vise pas à affiner la taxonomie ou la cladistique de Thalattosuchia et Dyrosauridae, mais facilitera ce type de travail futur beaucoup plus spécifique. Ce travail se concentre sur l'anatomie postcranienne de Thalattosuchia et Dyrosauridae et aspire à clarifier les étapes de leur évolution pelvienne à travers leurs histoires. Enfin, ce travail a pour objectif de mettre en évidence les relations entre la forme et la fonction au sein du squelette postcrânien des thalattosuchiens et des dyrosauridés, dans le but d'obtenir une meilleure compréhension des habitudes ou limitations locomotrices présentes au sein des membres de ces groupes disparus.

MOTS CLÉS
Archosauria,
postcranien,
anatomie,
locomotion,
morphologie
appendiculaire,
ilium,
ischium,
pubis.

INTRODUCTION

Two clades with radically distinct evolutionary histories are nested within Thalattosuchia Fraas, 1901: Metriorhynchoidea Fitzinger, 1843 which evolved several highly pelagic forms (Fernández & Gasparini 2008; Young *et al.* 2010; Herrera *et al.* 2013, 2017; Wilberg 2015a), and Teleosauroidea Geoffroy Saint-Hilaire, 1831 which is mainly represented by semi-aquatic forms (Buffetaut 1981; Massare 1987; Hua & Buffetaut 1997; Wilberg 2015a; Johnson *et al.* 2018, 2020, 2022; Foffa *et al.* 2019). Derived metriorhynchoids (i.e. metriorhynchids) markedly depart from the crocodyliform Bauplan by showing a series of unusual features related to a fully aquatic lifestyle, such as laterally oriented orbits, pre-orbital salt glands, forelimb reduction and paddle-like hindlimbs (Fraas 1901, 1902; Ammon 1905; Arthaber 1906; Auer 1907; Andrews 1913, 1915), loss of dermal ossification, and presence of a hypocercal tail (as in merriamosaurian ichthyosaurians and some derived mosasaurs) (Von Meyer 1831; Fraas 1901, 1902; Andrews 1913; Hua 1994; Fernández & Gasparini 2008; Herrera *et al.* 2013; Molnar *et al.* 2015; Wilberg 2015a; Young *et al.* 2010, 2020a, b). However, the posterior retraction of the external nares, a key feature to sustained swimmers, is adopted relatively late in some metriorhynchids (Hua *et al.* 2000; Young *et al.* 2020b). The evolutionary history of basal Metriorhynchoidea is not well known due to fragmentary taxa (Wilberg 2015a; Ősi *et al.* 2018; Aiglstorfer *et al.* 2019), shrouding the timing of these aquatic acquisitions which appear to follow a mosaic pattern (Wilberg 2015b; Ősi *et al.* 2018; Aiglstorfer *et al.* 2019). In contrast, teleosauroids (Early-Late Jurassic) and the basal metriorhynchoid *Pelagosaurus typus* Bronn, 1841 (Early Jurassic) are mainly known from proximal deposits (Duffin 1979a, b;

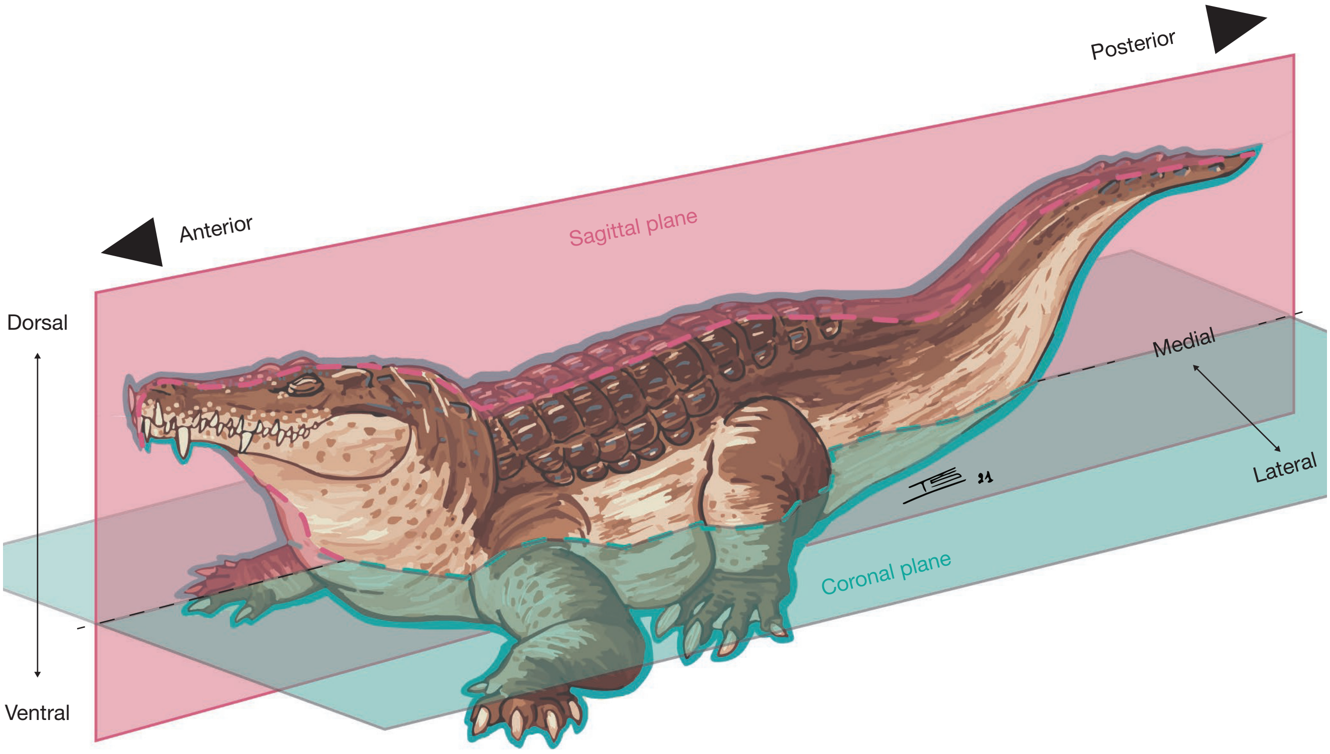


Fig. 1. — Schematic representation of a dyrosaurid, *Cerrejonisuchus improcerus* Hastings, Bloch, Cadena & Jaramillo, 2010, illustrating the conventions of bone orientation based on the presumed resting pose of said taxa. **Anterior-Posterior**: anterior relates to any part closer to the front of the animal than the rear, and posterior relates to any part closer to the rear of the animal than its front; **Dorsal-Ventral**: dorsal relates to any part closer to the back of the animal than to the abdomen, and ventral relates to any part closer to the abdominal side of the animal than to its vertebra; **Medial-Lateral**: medial relates to any part closer to the centre of the animal (*i.e.* the sagittal or bilateral plane) than to its flanks, and lateral relates to any part situated further away from the centre of the animal. Artwork by I.S.

Pierce & Benton 2006; Jouve 2009; Young *et al.* 2016), but share some marine specializations with more derived metriorhynchoids such as a streamlined body and skull, and reduced forelimbs (Young *et al.* 2011b; Chiarenza *et al.* 2015; Ősi *et al.* 2018; Johnson *et al.* 2020). Teleosauroidea also shows at least two pelagic transitions with *Aeolodon* + *Bathysuchus* (Foffa *et al.* 2019) and Machimosaurus (Martin & Vincent 2013; Young *et al.* 2014b), as well as a possible case of semi-terrestriality *with Platysuchus* + *Teleosaurus* (Johnson *et al.* 2020, 2022) and expansion into freshwater environments (southeast Asian taxa) (Martin *et al.* 2019a; Johnson *et al.* 2022). Teleosauroids and *Pelagosaurus typus* probably employed axial subundulatory swimming, while metriorhynchids are hypothesized to have a more efficient swimming mode (Duffin 1979a, b; Pierce *et al.* 2009; Young *et al.* 2010; Molnar *et al.* 2015). In parallel, many studies have compared generalised thalattosuchian morphology with that of other crocodyliformes (Hua 1994; Hua & De Buffrenil 1996; Wilberg 2015a; Wilbert *et al.* 2019; Molnar *et al.* 2015) because of a global lack of data on the postcranial anatomy of thalattosuchians, notably in cladistic datasets (where they reach 27% in the most recent datasets). This lack of data prevents computation of reliable estimates of the disparity of the group through time. As a result, the influence of the debated Jurassic-Cretaceous boundary extinction (see Fischer *et al.* 2012; Benson & Druckenmiller 2014; Tennant *et al.* 2016) on the ecological disparity of marine crocodyliforms cannot be unambiguously assessed at the present time. Dyrosauridae belongs to the extinct crocodyliform clade of Tethysuchia (along with Pholidosauridae) which spans the Late Jurassic-Middle Eocene (Jouve & Jalil 2020; Jouve 2021). Dyrosauroids have initially developed in non-marine settings (Hastings *et al.* 2010, 2011, 2014; Jouve 2021) before transitioning to the marine habitat with more derived members (Schwarz *et al.* 2006; Schwarz-Wings *et al.* 2009; Jouve *et al.* 2008a, 2020; Jouve & Jalil 2020; Jouve 2021). Dyrosaurid morphology differs from the pelagic transformations observed in metriorhynchoids: dyrosaurids are namely comprised of a highly flexible tail (Schwarz-Wings *et al.* 2009), stout girdles and limbs, ventral and dorsal osteodermal shields, large neural spines, and thoracic hypapophyses (Langston 1995; Jouve & Schwarz 2004; Jouve *et al.* 2006; Schwarz *et al.* 2006; Schwarz-Wings *et al.* 2009). Dyrosaurids are thought to initially originate from Africa (Barbosa *et al.* 2008; Jouve *et al.* 2008b, 2020; Hastings *et al.* 2014), they are first reported from the Turonian-Early Campanian of Lapur Sandstone in northern Kenya (J. J. Sertich *et al.* 2006; Tiercelin *et al.* 2012) and from the Campanian-Maastrichtian Shendi Formation of Sudan (Buffetaut *et al.* 1990; Salih *et al.* 2015). Dyrosaurids spread out several times from their craddle with notably three episodes of exchange with America during the Late Cretaceous (Jouve *et al.* 2020; Hastings *et al.* 2014). The group crossed the Cretaceous-Paleogene mass extinction event (Bronzati *et al.* 2012, 2015; Hastings *et al.* 2014; Martin *et al.* 2019b; Wilberg *et al.* 2019; Jouve & Jalil 2020; Jouve 2021), and went extinct

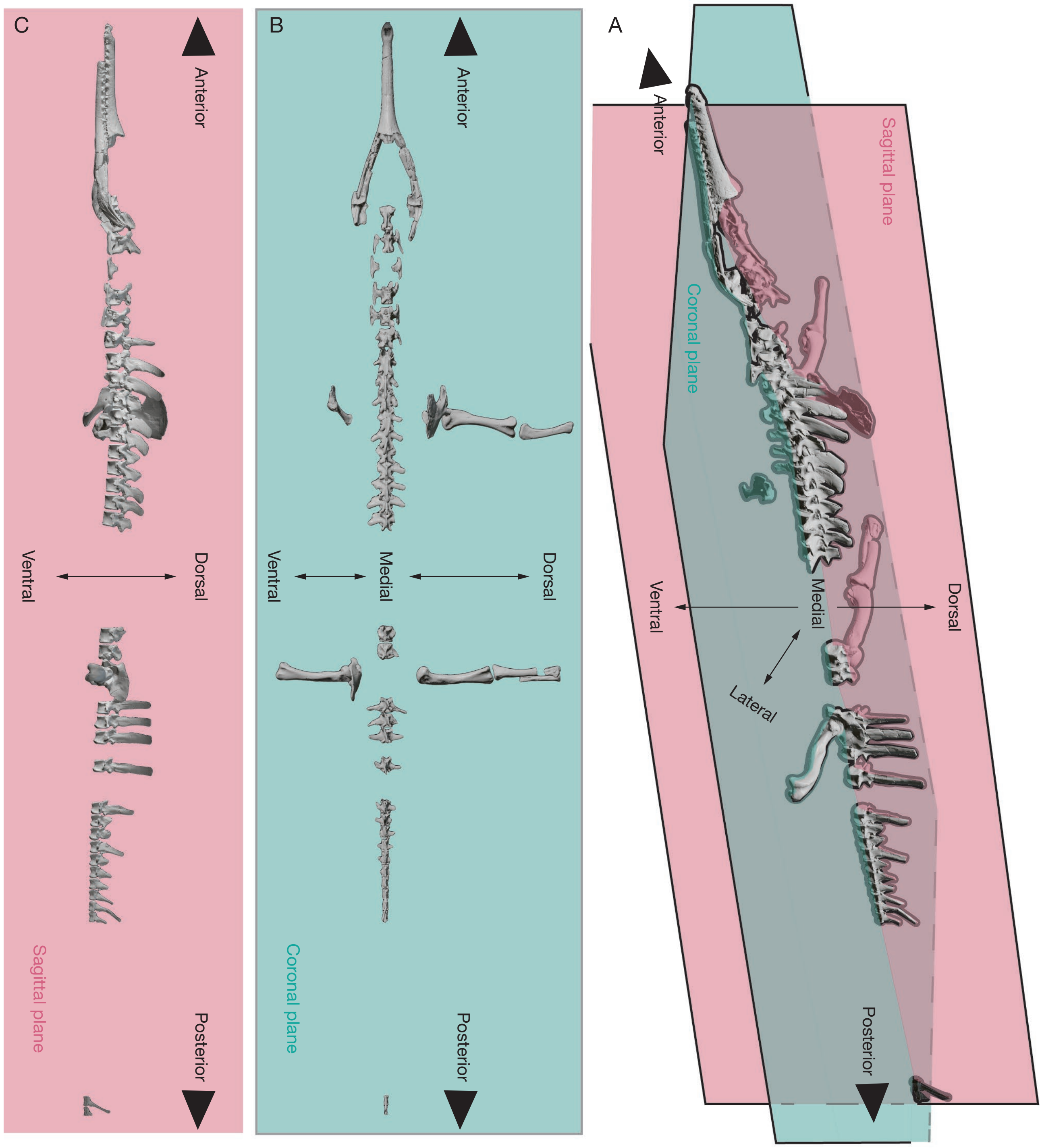


FIG. 2. — 3D model of the skeleton of the holotype *Congosaurus bequaerti* Dollo, 1914 illustrating the conventions of bone orientation used in the following text: **A**, diagonally oriented to illustrate both the sagittal and coronal plane; **B**, in dorsal view to illustrate the coronal plane; **C**, in lateral view to illustrate the sagittal plane.

seemingly at the Ypresian-Lutecian boundary (Buffetaut 1978; Jouve *et al.* 2006; Jouve 2007, 2021; Martin *et al.* 2019b). The group has recently been brought into the spotlight with new, in-depth studies evaluating its evolution (Jouve & Jalil 2020; Jouve *et al.* 2020; Jouve 2021) and ecological diversity (Jouve 2021). In parallel, the dyrosaurid postcranium remains globally undervalued (Godoy *et al.* 2016) and would benefit from a fresh comprehensive, detailed investigation (Martin *et al.* 2019b) as it has been done in some recent works (Jouve & Jalil 2020; Jouve 2021).

Our main goal is to describe the morphological disparity of the pelvic girdle of both Thalattosuchia and Dyrosauridae throughout their histories. For this reason, descriptions are arranged following phylogenetic lineages originating from recent phylogenetic works (Johnson *et al.* 2020; Jouve & Jalil 2020; Young *et al.* 2020a; Sachs *et al.* 2021).

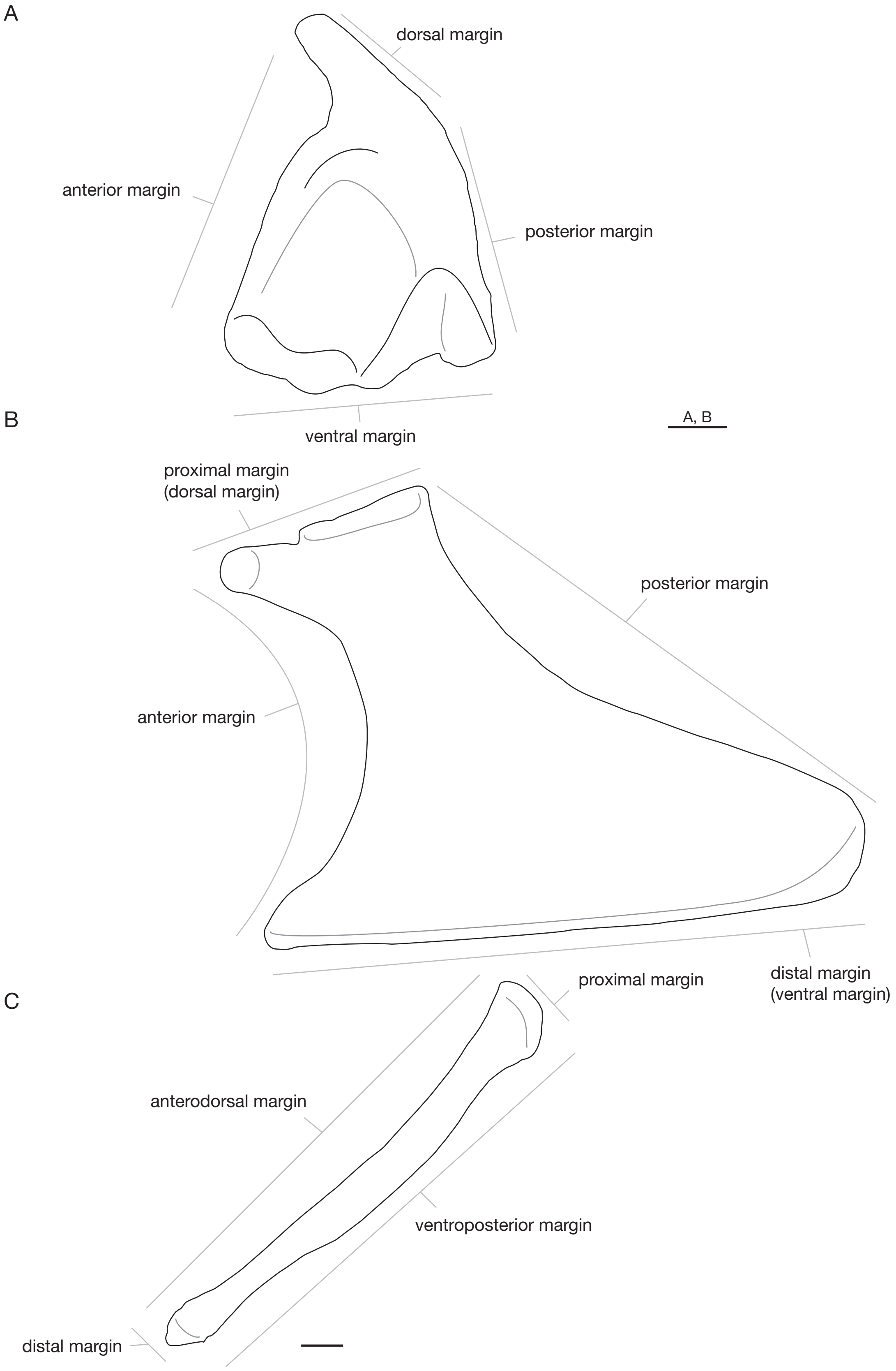


FIG. 3. — Schematic left metriorhynchoid pelvic girdle in lateral view as laying on a flat surface (based on the reconstruction of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867) [specimen NHMUK PV R 3804, holotype of '*Metriorhynchus*' *cultridens* & NHMUK PV R 4763] from below) illustrating the orientation of each bone: **A**, ilium; **B**, ischium; **C**, pubis. Scale bars: 1 cm.

MATERIAL AND METHODS

Orientation and terminology

To orientate the different bones composing the postcranium, we decided to depart from the approach based on the putative resting posture of the extinct animal (Fig. 1). Instead, in our convention, we take the orientation of the bones from the body of the animal laid flat, and its limbs perpendicular to the body within the coronal plane (Fig. 2). We chose this method of orientation for its facility of execution and its rigorous repeatability, leading to more accurate correlations across groups. A schematic drawing of a metriorhynchoid pelvic girdle in lateral view has been added on Fig. 3 to represent the impact of our conventions.

The pubic shaft and neck both correspond to the transition between the pubic peduncle and the pubic plate or apron (Fig. 4). The pubic neck shifts to the pubic plate or apron when its dorsal and ventral surfaces thin down following a maximum in thickness (visible in lateral and medial views). This phenomenon is sometimes paired with the flaring of its medial and lateral margins (visible in anterior and posterior views). The pubic shaft ends at the minimum width, before the widening of the medial and lateral margins.

The 'pubic rod' corresponds to the rod-like structure connecting the pubic peduncle proximally and the pubic plate distally. The exact transition from the rod to the pubic apron is more subject to estimation errors than the definition of the shaft and is therefore not used in the description. In general, the combination of the mediolateral flaring and dorsoventral thinning of the pubis marks the transition between thenpubic rod and the pubic apron.

Sampling

The most representative specimens have been elected based on the completeness of their materials and/or the presence of an associated skull for further taxonomical identification (Tables 1-3).

For the majority of the specimens, measurements were taken using digital calipers (approximate error of 0.1 mm). Additional measurements were recorded on 3D scans using the free license of the software for analysing and 3D measuring data: GOM Inspect 2018 (GOM Inspect 2018-2019).

The majority of surface scan data were obtained using the surface laser scanner Creaform HandySCAN 300 (accuracy of 0.2 mm). The surface model of *Acherontisuchus guajiraensis* Hastings, Bloch & Jaramillo, 2011 was modelled using photogrammetry (Meshroom version 2021.1.0) and assembled using Artec Studio 16 (Artec Studio 16, 2021). Blender (version 3.6.2) (Community 2018) was used to mirror bones into the preferred left polarity, and also to repair obvious defects portions.

The models of the NJSM 23368 specimen of *Hyposaurus natator* (Troxell, 1925) were shared and scanned by Candice Stefanic using the structured light scanner Artec Space Spider (accuracy up to 0.05 mm).

Taxonomic practice

Dyrosaurids tend to show a greater intraspecific variability than thalattosuchians (Jouve & Jalil 2020). Inherently, the concept of intraspecific variability is anchored in taxonomic attributions, and thalattosuchians have met with a splitting trend for the past few years (Johnson *et al.* 2020; Young *et al.* 2020a). These different taxonomic practices thus result in varying degrees of intraspecific variability. Still, Thalattosuchia bears many specimens with unresolved affinities such as the waste-basket taxon '*Metriorhynchus*'.

Institutional abbreviations

AMNH	American Museum of Natural History, New York, United States;
ANSP	Academy of Natural Sciences, Drexel University, Philadelphia, United States;
BRLSI	Bath Royal Literary and Scientific Institute, Bath, United Kingdom;
BHN	Muséum d'Histoire naturelle de Boulogne-sur-Mer, Boulogne-sur-Mer, France;
BRSMG	Bristol City Museum and Art Gallery, Bristol, United Kingdom;
CAMSM	Sedgwick Museum of Earth Science, Cambridge, United Kingdom;
DGM	Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Brazil;
GLAHM	Hunterian Museum and Art Gallery, Glasgow, United Kingdom;
MJSN	Musée jurassien des sciences naturelles, Porrentruy, Switzerland (Jurassica Museum [JURASSICA]);
MLP	Museo de La Plata, Buenos Aires, La Plata, Argentina;
MRAC	Musée royal de l'Afrique centrale, Tervuren, Belgium;
NHM	Natural History Museum, London, United Kingdom;
NJSM	New Jersey State Museum, Trenton, United States;
NMI	Natural History Museum of Ireland, Dublin, Republic of Ireland;
OCP DEK-GE	Office Chérifien des Phosphates, Direction de l'Exploitation de Khouribga, Géologie-Exploitation, Khouribga, Morocco;
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom;
PETGM	Peterborough Museum and Art Gallery, Peterborough, United Kingdom;
PMU	Evolutionsmuseet, Uppsala Universitet, Uppsala, Sweden;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RVC	Royal Veterinary College, University of London, London, United Kingdom;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
SCR	'Sur Combe Ronde', specimens housed at the Jurassica Museum (JURASSICA), Porrentruy, Switzerland;
UF/IGM UF	Florida Museum of Natural History (FLMNH), University of Florida, Gainesville, United States;
IGM	Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, Minería y Quimica, Bogotá, Colombia;
YPM	Yale Peabody Museum, New Haven, United States.

THE EXTANT CROCODYLIAN HIP ARTICULATION AND RESPIRATION

The pelvic girdle of extant crocodylians is composed of three bones: the ilium, the ischium, the pubis (Figs 7-9). However, only the ilium and ischium are involved in the acetabulum, which is the articular socket that receives the femoral head

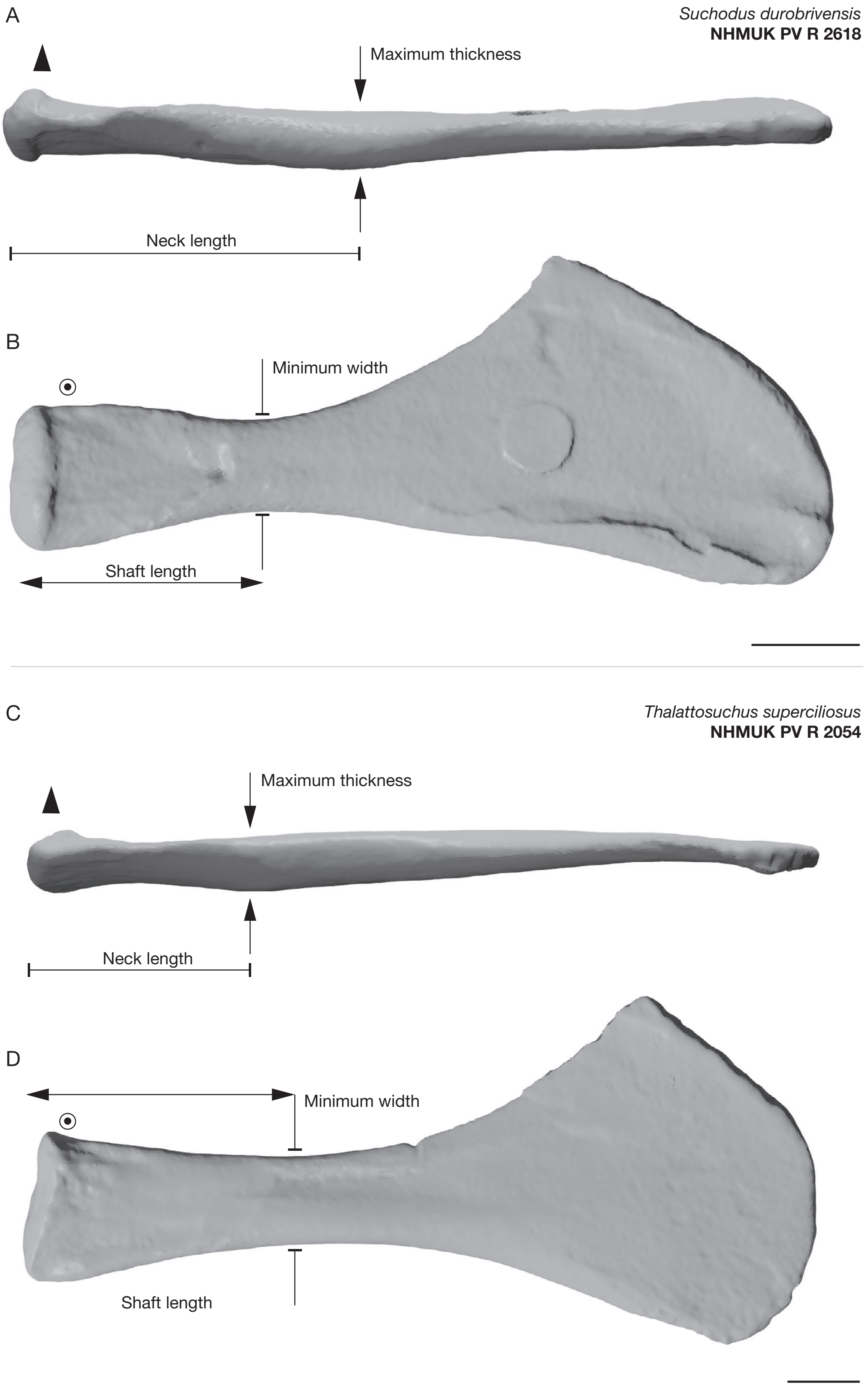


FIG. 4. — 3D models of thalattosuchian pubes illustrating the difference between shaft and neck: **A, B**, right pubis of *Suchodus durobrivensis* Lydekker, 1890, NHMUK PV R 2618; **C, D,** right pubis of *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852), NHMUK PV R 2054. Scale bars: 1 cm.

TABLE 1. — List of dyrosaurid specimens.

Species	Inventory number	Age	Formation	Location	Hypodigm	Completeness	References
Anthracosuchus balrogus Hastings, Bloch & Jaramillo, 2015	UF/IGM 68	Middle Paleocene	Cerrejon Fm	Colombia	Paratype	Partial cranium and postcranium	Hastings *et al.* 2014
Cerrejonisuchus improcerus Hastings, Bloch, Cadena & Jaramillo, 2010	UF/IGM 31	Middle-late Paleocene	Cerrejon Fm	Colombia	Referred	Partial cranium and postcranium	Hastings *et al.* 2010
Hyposaurus natator (Troxell, 1925)	YPM VP.000985	Danian	Hornerstown Fm	Monmouth Co., NJ (United States)	Referred	Partial cranium and postcranium	Troxell 1925
	YPM VP.000753	Danian	Unkown (probably New Egypt Fm or Hornerstown Fm)	Gloucester Co., NJ (United States)	Holotype of '*H. natator oweni*'	Partial postcranium	Troxell 1925
	NJSM 23368	Danian	Hornerstown Fm	Gloucester Co., NJ (United States)	Referred	Almost complete skeleton	Dr David Parris (pers. comm. August 2019)
Dyrosaurus maghribensis Jouve, Iarochène, Bouya & Amaghzaz, 2006	OCP DEK-GE 255	Lower Eocene (Ypresian)	Phosphate mine of Mera el Arech (Oulad Abdoun Basin)	Morocco	Holotype	Partial cranium and postcranium	Jouve *et al.* 2006
	OCP DEK-GE 252	Lower Eocene (Ypresian)	Phosphate mine of Mera el Arech (Oulad Abdoun Basin)	Morocco	Referred	Partial cranium and postcranium	Jouve *et al.* 2006
Acherontisuchus guajiraensis Hastings, Bloch & Jaramillo, 2011	UF/IGM 38	Middle-late Paleocene	Cerrejon Fm	Colombia	Referred	Nearly complete ilium and ischium	Hastings *et al.* 2011
Congosaurus bequaerti Dollo, 1914	MRAC 1806, 1809, 1811, 1813, 1815	Selandian	–	Landana, Angola	Holotype	Partial cranium and postcranium	Jouve & Schwarz (2004)

(Farmer & Carrier 2000a; Claessens & Vickaryous 2012). Instead, the pubis directly connects to the ischium through movable joints (Romer 1956) and is therefore relatively mobile (Farmer & Carrier 2000a; Claessens & Vickaryous 2012). *In vivo*, the three pelvic bones are united by the acetabular hyaline cartilage (part of the acetabulum), and the mobile portion merging the pubis and ischium is called the puboischial synchondrosis (Claessens & Vickaryous 2012; Tsai & Holliday 2015). The acetabulum comprises a relatively smooth area, the acetabular surface, as well as a prominent crescent shaped region, the lunate surface. The acetabular surface is covered by hyaline cartilage and fibrocartilage. The lunate surface is composed of two distinct portions: the acetabular labrum anteriorly, and the antitrochanter posteriorly. The acetabular labrum is borne on the ilium where it originates on the ventral surface of the supraacetabular crest, and spreads over a great portion of the hollow region of the ilium also called acetabulum. The volume taken by those soft tissue help reduce the wide space of the bony acetabulum of the ilium, so that the femoral head and the acetabulum are congruent (i.e. fit closely together) (Tsai & Holliday 2015). However, the smooth surface of the bony acetabulum and the overall shape of the femoral head do not form a perfect ball and socket pair (as opposed to birds), and therefore crocodylians need thick strata of soft tissues in compensation (Tsai & Holliday 2015; Tsai *et al.* 2019). The acetabular labrum is formed by loose connective tissue while the antitrochanter is composed of fibrocartilage. The antitrochanter stems from the puboischial synchondrosis, and takes the shape of two overlapping menisci: the superficial meniscus and the deep meniscus. The latter extends further from the acetabulum to form the posterior portion of the *ligamentum capitis femoris*, one of the intrinsic ligaments. The deep meniscus also merges partially with the *M. ischiotrochantericus* tendon dorsally. The anterior portion of the *ligamentum capitis femoris* stems from the pubic peduncle of the ischium, near the rim where the inner acetabular membrane starts (Tsai & Holliday 2015). The main function of ligaments in the hip articulation is to prevent the articular cartilage and muscles from damage (Reilly & Elias 1998), notably by limiting excessive joint excursion (Girgis *et al.* 1975; Kuznetsov & Sennikov 2000). The involvement of a muscle in the joint capsule (*M. ischiotrochantericus*) suggests that the ligaments may be correlated to the loading environment (Jenkins & Camazine 1977).

The acetabular labrum and antitochanter, are flexible and relatively mobile structures respectively. The composition of the acetabular labrum renders it quite malleable, whereas it is the type of attachment (i.e. intracapsular ligamentous) of

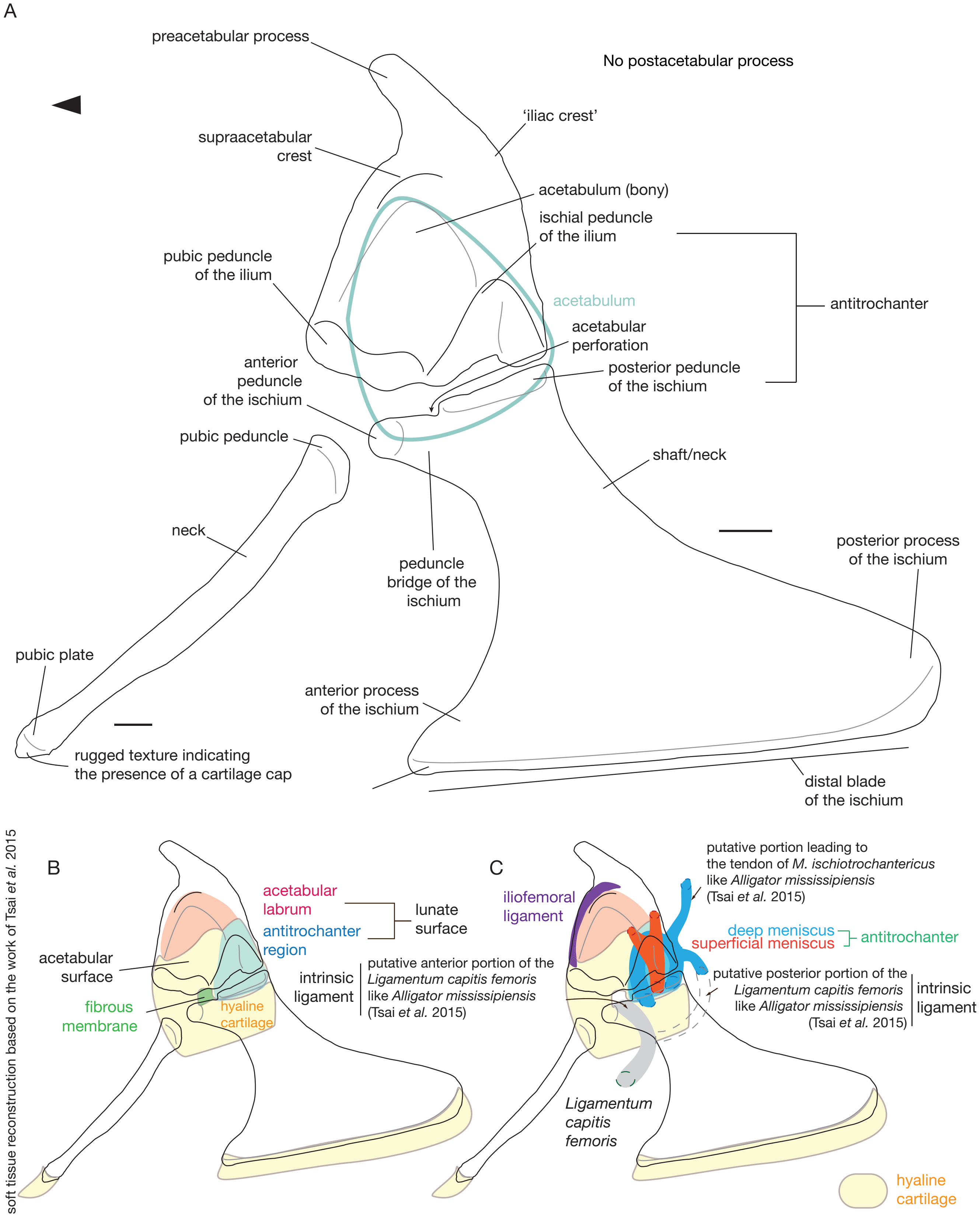


FIG. 5. — A metriorhynchoid schematic pelvic girdle in lateral view, based on '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867) (NHMUK PV R 3804, holotype of '*Metriorhynchus*' *cultridens* & NHMUK PV R 4763): **A**, pelvic girdle with associated vocabulary; **B**, **C**, reconstruction of the soft tissues, based on the work of Tsai & Holliday (2015). Scale bars: 1 cm.

Table 2. — List of metriorhynchoid specimens. Abbreviation: **Compl.**, Completeness.

Species	Inventory number	Data source	Age	Formation	Location	Hypodigm	Compl.	References
Pelagosaurus typus Bronn, 1841	BRLSI M.1417.1	–	Jurassic (Toarcian)	Upper Lias Group	Strawberry Bank (England)	Referred	Partial ilium	Pierce & Benton 2006
	BRLSI M.1410	–	Jurassic (Toarcian)	Upper Lias Group	Strawberry Bank (England)	Referred	Partial ischium	Pierce & Benton 2006
	BRLSI M.1411	–	Jurassic (Toarcian)	Upper Lias Group	Strawberry Bank (England)	Referred	Partial ischium	Pierce & Benton 2006
	BRLSI M.1420	–	Jurassic (Toarcian)	Upper Lias Group	Strawberry Bank (England)	Referred	Partial pubis	Pierce & Benton 2006
	NHMUK PV OR 32604	–	Jurassic (Toarcian)	Upper Lias Group	Curcy (France)	Referred	Partial pubis	NHMUK Data Portal
	NHMUK PV OR 32605	–	Jurassic (Toarcian)	Upper Lias Group	Curcy (France)	Referred	Partial ischium	NHMUK Data Portal
	SMNS 17758	–	Jurassic (Toarcian)	Posidonia Shale	Holzmaden (Germany)	Referred	Partial skeleton in 2D	
Thalattosuchus superciliosus (Blainville *in* Eudes-Deslongchamps & Blainville, 1852)	NHMUK PV R 2054	–	Middle or Upper Jurassic (Callovian or Oxfordian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Young *et al.* 2020a
	NHMUK PV R 1530	–	Middle or Upper Jurassic (Callovian or Oxfordian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Young *et al.* 2020a
	SMNS 10116	–	Middle or Upper Jurassic (Callovian or Oxfordian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Young *et al.* 2020a
	NMI F21731	–	Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	
‘*Metriorhynchus*’ sp.	GLAHM V1146	–	Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Referred	Partial postcranium	GLAHM data portal
‘*Metriorhynchus*’ *brachyrhynchus* (Eudes-Deslongchamps, 1867)	NHMUK PV R 3804	–	Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Holotype of ‘*Metriorhynchus*’ *cultridens*	Partial cranium and postcranium	Andrews 1913; Young *et al.* 2010, 2011a, 2012, 2020a, b
	NHMUK PV R 4763	–	Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Young 2014; Young *et al.* 2010, 2012
	LEICT G.418.1956.13.5 and G.418.1956.13.6		Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Skull identified by Dr Mark Young (19 sept. 2012)

the antitrochanter that are responsible for its mobility. Both structures accommodate the movements of the femur during the different phases of the step cycle (Tsai *et al.* 2019).

The crocodylian ilium and ischium both present a gap separating their two peduncles; called the acetabular perforation (Romer 1956) or foramen. This opening is covered by a fibrous membrane (the inner acetabular membrane) *in vivo* against which lies the *ligamentum capitis femoris*. The presence of a membrane rather than of an ossified inner wall protects the femoral ligament (*ligamentum capitis femoris*) against compression, and helps accommodate its movements within the joint cavity (Tsai & Holliday 2015). Moreover, the fibrous membrane covering the acetabular perforation allows crocodylians to perform postures which overcome the mechanical constraints inherent to the configuration of their pelvic girdle (more specifically inherited from the shape of their articular surfaces) (Kuznetsov & Sennikov 2000). When the femur lies horizontally (i.e. parallel to the coronal plane; abduction), its femoral head is congruent with the hip capsule, whereas when it is held upright in a parasagittal posture (i.e. during the high-walk; adduction), the femoral head looses contact with the hip capsule and becomes dislocated from the acetabulum (Kuznetsov & Sennikov 2000; Tsai *et al.* 2019). When

Table 2. — Continuation.

Species	Inventory number	Data source	Age	Formation	Location	Hypodigm	Compl.	References
Tyrannoneustes lythrodectikos Young, de Andrade, Brusatte, Sakamoto & Liston, 2012	GLAHM V972		Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Holotype	Partial cranium and postcranium	Young *et al.* 2012
	GLAHM V1145		Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Holotype	Partial postcranium and teeth	Young *et al.* 2012
Suchodus durobrivensis	NHMUK PV R 2618		Jurassic (Middle Callovian)	Oxford Clay Fm	United Kingdom	Referred	Partial cranium and postcranium	Andrews 1913; Young *et al.* 2010
Cricosaurus araucanensis (Gasparini & Dellapé, 1976)	MLP 72-IV-7-1	2D and 3D data courtesy of Dr Herrera	Upper Jurassic (lower Tithonian)	Vaca Muerta Fm	Cerro Lotena and Bosque Petrificado (Argentina)	Holotype	Complete ilium and partial ischium	Herrera *et al.* 2013
	MLP 73-II-27-6	2D data courtesy of Dr Herrera	Upper Jurassic (lower Tithonian)	Vaca Muerta Fm	Cerro Lotena and Bosque Petrificado (Argentina)	Referred	2D ischium and pubis	Herrera *et al.* 2013
Cricosaurus suevicus (Fraas, 1901)	SMNS 9808		Jurassic (Late Kimmeridgian)	Nusplingen Plattenkalk	Nusplingen (Germany)	Lectotype	Nearly complete skeleton in 2D	Fraas 1902
Cricosaurus albersdoerferi (Sachs, Young, Abel & Mallison, 2021)	BMMS-BK 1-2	Sachs *et al.* 2021	Jurassic (Late Kimmeridgian)	Torleite Fm	Bavaria (Germany)	Holotype	Nearly complete skeleton in 2D	Sachs *et al.* 2021
Cricosaurus bambergensis (Sachs, Young, Abel & Mallison, 2019)	NKMB-P-Watt14/274	Sachs *et al.* 2019	Jurassic (Late Kimmeridgian)	Torleite Fm	Bavaria (Germany)	Holotype	Nearly complete skeleton in 2D	Sachs *et al.* 2019
Geosaurus giganteus (Von Sömmerring, 1816)	NHMUK PV R 1230		Jurassic (Tithonian)	Mornsheim Fm	Daiting (Germany)	Referred	Partial cranium and postcranium	Young & De Andrade 2009
Dakosaurus maximus (Plieninger, 1846)	SMNS 8203	SMNS 8203	Jurassic (Upper Kimmeridgian)	Nusplingen Limestone?	Staufen near Gingen (Germany)	Neotype	Partial cranium and postcranium	Fraas 1902; Young *et al.* 2020b
Torvoneustes carpenteri (Wilkinson, Young & Benton, 2008)	BRSMG Cd7203	BRSMG Cd7203	Jurassic (Upper Kimmeridgian)	Kimmeridge Clay Formation	Westbury (United Kingdom)	Paratype	Partial cranium and postcranium	Wilkinson *et al.* 2008

existing the acetabulum, the femoral head is held by the *ligamentum iliofemorale* which tightly covers the femoral head. This position also places the intertrochanteric fossa of the femur (area under the fourth trochanter) against the acetabulum, which improves both the precision and facility of the parasagittal (i.e. anteroposterior) movements of the femur in spite of its excursion. Indeed, the existence of an extra synovial pad covering the intertrochanteric fossa (formed by the exfoliated periosteum of the intertrochanteric fossa) helps smoothen the movements between the femur and the acetabulum. Yet, the major issue with the parasagittal position of the femur is the gap created between the femur and the acetabulum, in which a spacing is created in the hip articulation but the whole system is closed: the quantity of synovial fluid is constant and therefore the movements of the femur in the parasagittal posture are more tense during the excursion. This tension could cause the articular capsule to collapse, be sucked inside the gap and be crushed in between the femur and the ilium. Fortunately, the presence of a fibrous membrane over

TABLE 3. — List of teleosauroid specimens.

Species	Inventory number	Data source	Age	Formation	Location	Hypodigm	Completeness	References
Plagiophthalmosuchus gracilirostris (Westphal, 1961)	NHMUK PV OR 14792		Jurassic (Toarcian)	Whitby Mudstone Fm	Whitby (United Kingdom)	Holotype	Nearly complete skeleton in 2D	Johnson *et al.* 2020
Aeolodon priscus (Von Sömmerring, 1814)	NHMUK PV R 1086		Jurassic (Tithonian)	Mornsheim Fm	Daiting (Germany)	Holotype	Nearly complete skeleton in 2D	Johnson *et al.* 2020
	MNHN.F. CNJ78		Jurassic (Tithonian)	Canjuers lagerstätte (France)	Neotype	Nearly complete skeleton in 2D	Johnson *et al.* 2020	–
Sericodon jugleri Von Meyer, 1845	SCR010-312	3D data courtesy of Dr Anquetin	Jurassic (late Kimmeridgian)	Reuchenette Fm	Courtedoux-sur-Combe Ronde (Switzerland)	Referred	Partial cranium and postcranium in 3D	Schaefer *et al.* 2018
Mycterosuchus nasutus (Andrews, 1909)	NHMUK PV R 2617		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Holotype	Partial cranium and postcranium	Johnson *et al.* 2020
	CAMSM J.1420		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Nearly complete skeleton	Johnson *et al.* 2020
Teleosaurus sp.	NHMUK PV R 238		Jurassic (Bathonian)	Taynton Limestone Fm	Stonesfield (United Kingdom)	Referred	Ischium encased in matrix	NHMUK Data Portal
	OUMNH. J1638		Jurassic (Bathonian)	Great Oolite Gp	Enslow Bridge, Oxfordshire (United Kingdom)	Referred	Ischium and pubis	Phillips 1871
Platysuchus multiscrobiculatus (Berckhemer, 1929)	SMNS 9930		Jurassic (Toarcian)	Posidonia Shale Fm	Baden-Wurttemberg (Germany)	Holotype	Nearly complete skeleton in 2D	Westphal 1961
Macrospondylus bollensis (Jäger, 1828)	NHMUK PV R 5703		Jurassic (Toarcian)	Whitby Mudstone Fm	Yorkshire (United Kingdom)	Referred	Partial skeleton encased in matrix	Johnson *et al.* 2020
	SMNS 17484a		Jurassic (Toarcian)	Posidonia Shale Fm	Baden-Wurttemberg (Germany)	Referred	Pelvic girdle in 2D	SMNS data
	SMNS 16848		Jurassic (Toarcian)	Posidonia Shale Fm	Baden-Wurttemberg (Germany)	Referred	Ischium	SMNS data
	PMU 35980					Referred	Nearly complete skeleton in 2D	–

the acetabular perforation acts like a buffer and prevents the destruction of the articular capsule: when the femur switches to a parasagittal posture, the fibrous membrane is drawn towards the newly created gap which preserves the articular capsule (Kuznetsov & Sennikov 2000). For Tsai & Holliday (2015), the acetabular perforation is an osteological correlate hinting at the existence of intrinsic ligaments in the pelvic articulation. Intrinsic and capsular ligaments are all involved the hip joint, with intrinsic ligaments positioned within the synovial cavity rather than the joint capsule. Extant crocodylians possess two intrinsic ligaments, the anterior and posterior *ligamentum capitis* (which converge into the *ligamentum capitis femoris*), and one extrinsic (or capsular) ligament: the iliofemoral ligament (i.e. *ligamentum iliofemorale*, which originates on the acetabular labrum) (Tsai & Holliday 2015).

The flexible joint of the pubis has several repercussions on the crocodylian lifestyle, as it notably impacts buoyancy, aquatic locomotion (Gans & Clark 1976; Uriona & Farmer 2008), terrestrial locomotion (Gans & Clark 1976; Carrier 1987; Farmer & Carrier 2000b; Munns *et al.* 2012), and lung ventilation (i.e. aspiration breathing) (Rathke 1866; Gans & Clark 1976; Farmer & Carrier 2000a; Claessens 2004; Claessens & Vickaryous 2012; Munns *et al.* 2012; Reichert*et al.* 2019). For tetrapods that use lateral bending of the trunk for locomotion (e.g. such as a sprawling gait or axial swimming), possessing an alternate mean of lung ventilation allows sustained loco-

Table 3. — Continuation.

Species	Inventory number	Data source	Age	Formation	Location	Hypodigm	Completeness	References
Charitomenosuchus leedsi (Andrews, 1909)	NHMUK PV R 3806		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Nearly complete skeleton	Johnson *et al.* 2020
Proexochokefalos cf. *bouchardi* (Sauvage, 1872)	SCR010-374	3D data courtesy of Dr Anquetin	Jurassic (late Kimmeridgian)	Reuchenette Fm	Courtedoux-sur-Combe Ronde (Switzerland)	Referred	Partial cranium and postcranium in 3D	Schaefer *et al.* 2018
Neosteneosaurus edwardsi (Eudes-Deslongchamps, 1868)	PETMG R178		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Nearly complete skeleton	Johnson *et al.* 2020
	NHMUK PV R 3701		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Partial cranium and postcranium	Johnson *et al.* 2020
	NHMUK PV R 2076		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Partial cranium and postcranium	Johnson *et al.* 2020
	NHMUK PV R 3898		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Femur, ilium and ischium	Johnson *et al.* 2020
Neosteneosaurus edwardsi (continuation)	NHMUK PV R 2865		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Referred	Complete skull and partial postcranium	Johnson *et al.* 2020
Lemmysuchus obtusidens (Andrews, 1909)	NHMUK PV R 3168		Jurassic (Middle Callovian)	Oxford Clay Fm	Peterborough (United Kingdom)	Holotype	Partial cranium and postcranium	Johnson *et al.* 2017
Machimosaurus sp.	SMNS 81608		Jurassic (Middle Callovian)		Portland (United Kingdom)	Referred	Partial postcranium	–
	BHN2R 1100		–	–	–	Lost Neotype of *Machimosaurus mosae*	Partial cranium and postcranium	Hua *et al.* 1993

motor activity. In contrast, the musculoskeletal *Bauplan* of lepidosaurs prevents them from breathing and walking simultaneously (Carrier 1987).

On land, extant crocodylians can achieve lung ventilation through the action of the coastal muscles (ribs adjustments; coastal muscles shorten to bring the ribs together (Gans & Clark 1976)), the abdominal muscles (rotation of the pubis), and the *diaphragmaticus* muscle (both of which are involved in the hepatic piston pump) (Gans & Clark 1976; Carrier 1987; Farmer & Carrier 2000a; Munns *et al.* 2012). All three types of muscles are active during terrestrial locomotion, either to shift viscera or hold the trunk during the visceral displacement (Gans & Clark 1976).

The coastal and abdominal muscles are active during both inspiration and expiration (Gans & Clark 1976; Munns *et al.* 2012). At rest, the *diaphragmaticus* muscle doesn't make a significant contribution (Uriona & Farmer 2006; Munns *et al.* 2012), unlike episodes of locomotion (such as galloping or running) or high metabolic demands (such as digestion) (Gans & Clark 1976; Munns *et al.* 2012; Reichert *et al.* 2019). The latter is especially true for younger individuals (Uriona & Farmer 2006; Munns *et al.* 2012; Reichert *et al.* 2019), whereas older individuals rely comparatively more on the hepatic piston pump (Gans & Clark 1976; Reichert *et al.* 2019). Older crocodylians display a more muscular and keratinized body wall, which presumably induces a loss of flexibility compared to younger individuals (Reichert *et al.* 2019). Moreover, the relative importance of the *diaphragmaticus* muscle in the lung ventilation appears to vary between extant crocodylians families and subfamilies (Farmer & Carrier 2000a; Munns *et al.* 2012), rendering the extent of its contribution difficult to assess in extinct forms. Following immersion in the caiman, an important part of coastal muscle activity is allocated to holding the ribs to stiffen the ribcage (Gans & Clark 1976; Grigg & Kirshner 2015), for the optimization of the hepatic piston (i.e. induced changes in pressure are maximum) (Gans & Clark 1976). Therefore, lung ventilation is almost exclusively achieved through the actions of the hepatic piston and expiration becomes passive as the hydrostatic pressure suffices to shift the liver anteriorly (Gans & Clark 1976; Grigg & Kirshner 2015). In addition, when immersed the hepatic piston can help manage buoyancy as well as regulate the position of the

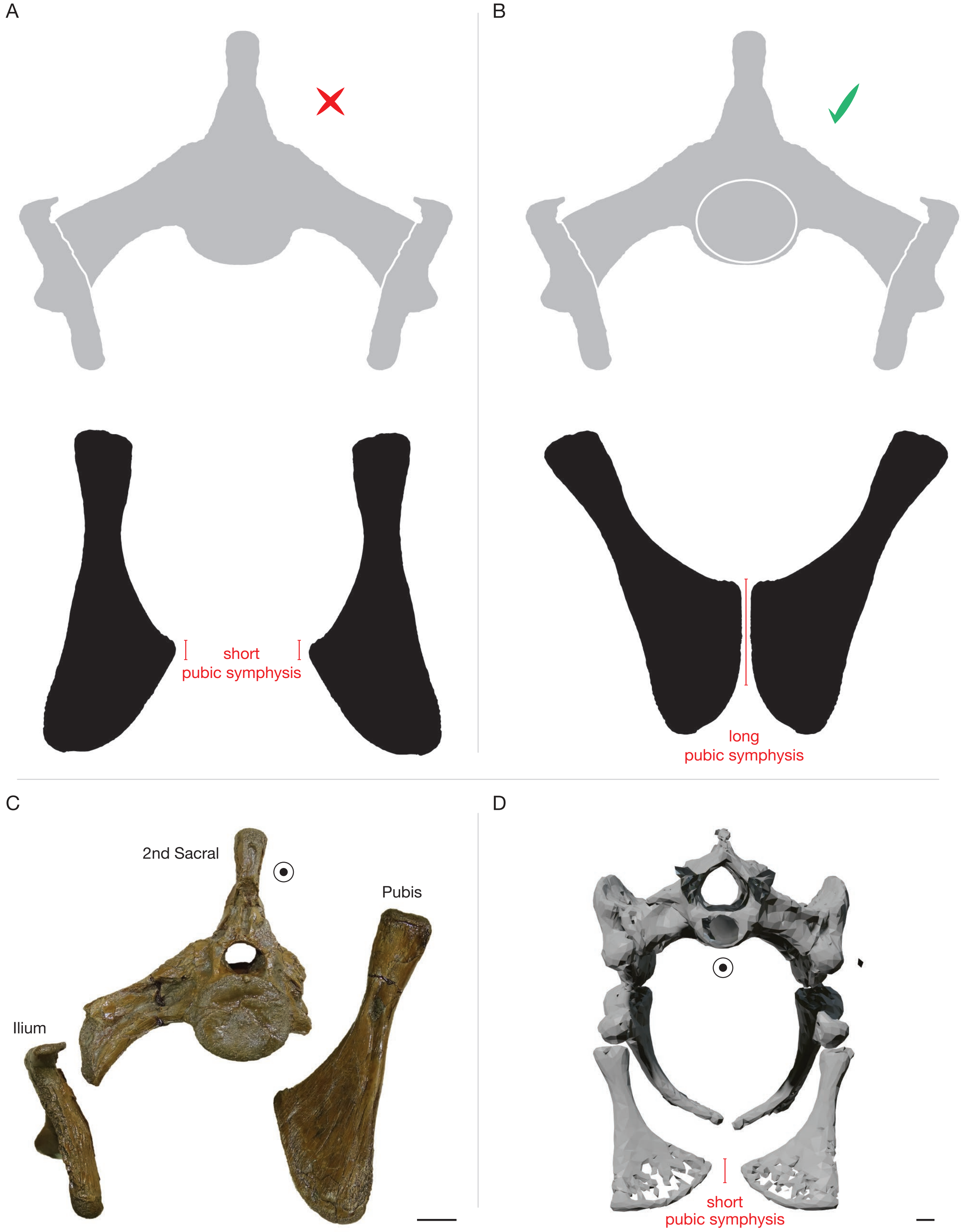


Fig. 6. — Reconstruction of the pelvic girdle in anterior view of *Suchodus durobrivensis* Lydekker, 1890, NHMUK PV R 2618: **A**, erroneous reconstruction based on the hypothesis of a short pubic symphysis (**orange**) similar to extant crocodylians; **B**, legitimate reconstruction based on the hypothesis of a long pubic symphysis (**orange**) as opposed to extant crocodylians; **C**, right ilium, second sacral, and left pubis in anterior view; **D**, snapshot in anterior view of the pelvic girdle of the alligatoroid *Palaeosuchus palpebrosus* Cuvier, 1807 (RVC-JRH-PP1, Fig. 7). Pubes are colored in black. CT scan courtesy of Professor John Hutchinson (see https://skfb.ly/6ByyV). Target indicates anterior. Scale bars: 1 cm.

centre of mass, which is important for aquatic locomotion (Uriona & Farmer 2008).

In alligators, the *diaphragmaticus* muscle stems from the ischium and last gastralia, and encompasses the liver anteriorly (Farmer & Carrier 2000a). In crocodiles (Munns *et al.* 2012) and caiman (Gans & Clark 1976), the *diaphragmaticus* muscle embraces the pubis and ischium (Gans & Clark 1976; Munns *et al.* 2012). It is also reported that the *diaphragmaticus* muscle originates on the ilium (Reese 1915). When the *diaphragmaticus* and abdominal muscles shorten, the liver translates anteroposteriorly and acts like a piston increasing or reducing the volume in the pleural cavities (Gans & Clark 1976; Farmer & Carrier 2000a; Munns *et al.* 2012). During inspiration, the *diaphragmaticus* muscle is contracted and the liver is propelled posteriorly provoking an increase of volume for the lungs (Gans & Clark 1976; Carrier 1987; Farmer & Carrier 2000a; Munns *et al.* 2012); the ischiopubis and ischiotruncus muscles (pelvic muscles) have also been correlated with inspiration as their action rotate the pubis ventrally, thus augmenting the abdominal volume (Farmer & Carrier 2000a). The anterior displacement of the liver is then achieved through the contraction of the abdominal muscles (*rectus abdominis* and *transversus abdominis*), inducing the expiration by reducing the volume in the pleural cavities (Gans & Clark 1976; Farmer & Carrier 2000a). Simultaneously, the activity of the abdominal and pelvic muscles during the episodes of expiration and inspiration respectively, also provoke the rotation of the pubis which is being rotated dorsally and ventrally alternating (Farmer & Carrier 2000a). In return, these movements of the pubis induce the displacement of viscera anteroposteriorly and thereby assist the diaphragmatic ventilation (Gans & Clark 1976; Farmer & Carrier 2000a; Claessens & Vickaryous 2012).

In summary, the movement of the pubis aids lung ventilation through the hepatic piston pump (combined works of abdominal and 'diaphragmatic' muscles [Gans & Clark 1976]). Thereby, it grants crocodylians an alternative to perform respiration during terrestrial locomotion, especially at times of high metabolic needs such as running or galloping (during which it helps stymie Carrier's constraint), or even digestion (Gans & Clark 1976; Carrier 1987; Farmer & Carrier 2000b; Munns *et al.* 2012). The hepatic piston pump can take over the ventilation of the lung when the bending of the trunk, which is actually not capable of ventilating the lungs, requires lateral and dorsal muscles during locomotion (Carrier 1987).

EXTANT CROCODYLIAN HIP MUSCLES

Ilium

The lateral surface of the ilium of extant crocodylians (see Table 4) mainly comprises extensors and flexors for the hip and knee (Romer 1923; Otero *et al.* 2010; Allen *et al.* 2014). Medially, the area extending from the tip of the preacetabular process to the extremity of the postacetabular process above the sacral rib attachment sites for the sacral ribs is anchored with (origins and insertions of) dorsal muscles connecting the ilium and sacral ribs to the thoracic and caudal vertebra (i.e. *M. dorsalis trunci, M. dorsalis caudae*, Romer [1923]).

Table 4. — List of pelvic muscles of the ilium of extant crocodylians (Romer 1923; Otero *et al.* 2010; Allen *et al.* 2014).

Abbreviation	Full name	Approximated function
CFB	*M. coccygeo-femoralis/ caudofemoralis brevis*	Hip extensors & knee flexors (Allen *et al.* 2014; Otero *et al.* 2010)
IT 3	*M. iliotibialis* 3	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
ILFB	*M. iliofibularis*	Hip extensors & knee flexors (Allen *et al.* 2014; Otero *et al.* 2010)
FMTE	*M. femorotibialis externus*	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
FTI 2	*M. flexor tibialis internus* 2	Hip extensors & knee flexors (Allen *et al.* 2014; Otero *et al.* 2010)
ISC	*M. ilioischiocaudalis/ iliococcydeus*	Connects ilium and ischium to ventral part of tail in *Alligator mississippiensis* (Romer 1923)
IF	*M. iliofemoralis*	Hip abductors; this muscle also extends over the postacetabular process (Allen *et al.* 2014; Otero *et al.* 2010)
IT 1	*M. iliotibialis* 1	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
IT 2	*M. iliotibialis* 2	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
IC	*M. ilio-costalis*	Segmental tendons connecting the ilium to ribs in *Alligator mississippiensis* (Romer 1923; Tsuihiji 2007)
PIFI 1 (medially)	*Pubo-ischio-femoralis internus* 1	Hip flexors, connects ilium to proximomedial surface of femur, protracts leg and help in adduction (Allen *et al.* 2014; Otero *et al.* 2010; Romer 1923)

Ischium

Laterally, most of the surface of the ischium of extant crocodylians is occupied by adductors muscles. Medially, the ischium displays mainly hip extensors and knee flexors (see Table 5, Reese (1915); Romer (1923); Farmer & Carrier (2000a); Otero *et al.* (2010); Munns *et al.* (2012); Allen *et al.* (2014)).

Pubis

Anterodorsally and posteroventrally, most of the surface of the pubis of extant crocodylians is occupied by hip adductors and muscles involved in the respiration (see Table 6; Reese 1915; Romer 1923; Farmer & Carrier 2000a; Otero *et al.* 2010; Munns *et al.* 2012; Allen *et al.* 2014).

Table 5. — List of soft tissues anchored on the ischium of extant crocodylians (Reese 1915; Romer 1923; Farmer & Carrier 2000a; Otero *et al.* 2010; Munns *et al.* 2012; Allen *et al.* 2014).

Abbreviation	Full name	Approximated function
PIFE 3	*M. Pubo-ischio-femoralis externus* 3	Hip adductors, contribute to the adduction of the leg with PIFE 1 and PIFE 2 (Allen *et al.* 2014; Otero *et al.* 2010); rotates pubis ventrally during inspiration (Farmer & Carrier 2000a)
FTI 3	*M. flexor tibialis internus* 3	Hip extensors & knee flexors (Allen *et al.* 2014; Otero *et al.* 2010)
ADD 1	*M. adductor femoris* 1/ *Adductor* 1	Hip adductors, contribute to the retraction of the limb (Allen *et al.* 2014; Otero *et al.* 2010)
ADD 2	*M. adductor femoris* 2/ *Adductor* 2	Hip adductors, contribute to the retraction of the limb (Allen *et al.* 2014; Otero *et al.* 2010)
ISC	*M. ilioischiocaudalis/ ilio-coccydeus*	Connects ilium and ischium to ventral part of tail in Alligator mississippiensis (Romer 1923)
PIT	*M. pubo-ischio-tibialis*	Long flexors to lower leg (Romer 1923); contribute to the adduction of the leg (Otero *et al.* 2010); Hip extensors & knee flexors (Allen *et al.* 2014)
RABD (insertion)	*M. rectus abdominis*	Connects last abdominal rib to the pubis Alligator mississippiensis (Romer 1923); rotates the pubis craniodorsally during expiration (Farmer & Carrier 2000a)
FTI 1 (medially)	*M. flexor tibialis internus* 1	Hip extensors & knee flexors (Allen *et al.* 2014; Otero *et al.* 2010)
ISTR (medially)	*M. ischiotro-chantericus*	Hip extensors & knee flexors; the muscle extends to rotate the femur laterally (Allen *et al.* 2014; Otero *et al.* 2010)
AMB 1 (medially)	*Ambiens* 1	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
–	*Diaphragmaticus*	In alligators it is connected to the ischia and last gastralia (Farmer & Carrier 2000a); in crocodiles and caimans it is connected to the ischia and pubes (Munns *et al.* 2012). There also appears to be a connection to the ilium (Reese 1915). Contraction pulls the liver caudally (Munns *et al.* 2012).

Table 6. — List of soft tissues anchored on the pubis of extant crocodylians (Reese 1915; Romer 1923; Farmer & Carrier 2000a; Otero *et al.* 2010; Munns *et al.* 2012; Allen *et al.* 2014).

Abbreviation	Full name	Approximated function
PIFE 1	*M. Pubo-ischio-femoralis externus* 1	Hip adductors (Allen *et al.* 2014; Otero *et al.* 2010); rotates pubis ventrally during inspiration (Farmer & Carrier 2000a)
PIFE 2	*M. Pubo-ischio-femoralis externus* 2	Hip adductors (Allen *et al.* 2014; Otero *et al.* 2010); rotates pubis ventrally during inspiration (Farmer & Carrier 2000a)
AMB 1	*Ambiens* 1	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
AMB 2	*Ambiens* 2	Knee extensors (Allen *et al.* 2014; Otero *et al.* 2010)
RABD	*M. rectus abdominis*	Connects last abdominal rib to the pubis Alligator mississippiensis (Romer 1923); rotates the pubis craniodorsally during expiration (Farmer & Carrier 2000a)
–	*Diaphragmaticus*	In alligators it is connected to the ischia and last gastralia (Farmer & Carrier 2000a); in crocodiles and caimans it is connected to the ischia and pubes (Munns *et al.* 2012). There also appears to be a connection to the ilium (Reese 1915). Contraction pulls the liver caudally (Munns *et al.* 2012)

THE PELVIC GIRDLE SKELETON OF THALATTOSUCHIANS: METRIORHYNCHOIDS

Pelagosaurus typus Bronn, 1841

For measurements, see Tables 7-9.

Ilium

Overall, the ilium of *Pelagosaurus typus* (Figs 10; 11) appears more similar to that of extant crocodylians (e.g. *Palaeosuchus palpebrosus* Cuvier, 1807 [Fig. 7], *Mecistops cataphractus* Cuvier, 1824 [Fig. 8], *Caiman crocodilus* [Fig. 9]) than other thalattosuchians. The ilium of *Pelagosaurus typus* differs from that of metriorhynchoids (e.g. *Tyrannoneustes lythrodectikos* Young, de Andrade, Brusatte, Sakamoto & Liston, 2012, *Suchodus durobrivensis* Lydekker, 1890, *Dakosaurus maximus* (Plieninger, 1846)) in possessing a developed postacetabular process and a protruding pubic peduncle (anteriorly and ventrally). Moreover, the ilium of *Pelagosaurus typus* further differs from that of teleosauroids in displaying a protruding pubic peduncle. In SMNS 17758, the ventral margin of the pubic peduncle is not parallel to that of the ischial peduncle, unlike in BRLSI M.1417.1, *Sericodon jugleri* Von Meyer, 1845, *Charitomenosuchus leedsi* (Andrews, 1909), *Proexochokefalos* cf. *bouchardi* (Sauvage, 1872), *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), and *Lemmysuchus obtusidens* (Andrews, 1909). In comparison, extant crocodylians possess both a developed postacetabular process as well as a protruding and leaning pubic peduncle whose ventral margin is not parallel to neither the ventral margin of the ischial peduncle nor the dorsal margin of the iliac crest. There are at least two dyrosaurids which display non-parallel peduncles on their ilia, *Congosaurus bequaerti* Dollo, 1914 and *Acherontisuchus guajiraensis*, but only the latter shows an angular relation between their peduncles similar to *Pelagosaurus typus* (Fig. 10D).

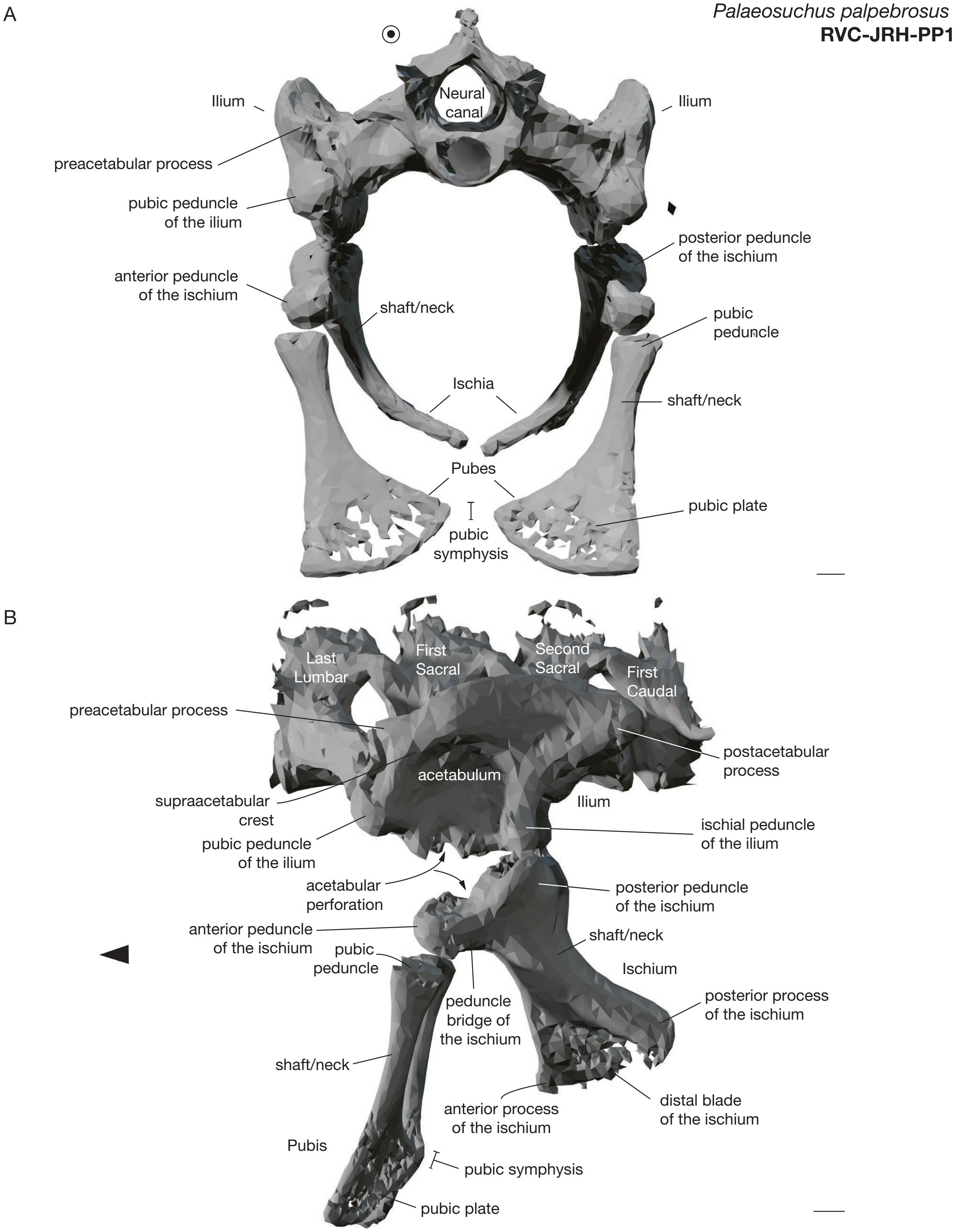


FIG. 7. — Snapshot of the pelvic girdle of the alligatoroid *Palaeosuchus palpebrosus* (Cuvier, 1807), RVC-JRH-PP1: **A**, in anterior view; **B**, in lateral view. Note the orientation of the pubes. Cross indicates posterior view. Arrow points anteriorly. CT scan courtesy of Professor John Hutchinson (see https://skfb.ly/6ByyV). Scale bars: 1 mm.

TABLE 7. — List of measurements in mm of crocodyliformes ilia. Abbreviations: **Ha**, anterior height; **Hv**, ventral length; **Hd**, dorsal length; **PST.l**, postacetabular process anteroposterior length; **PST.h**, postacetabular process dorsoventral height; **PRE.l**, preacetabular process anteroposterior length; **PRE.h**, preacetabular process dorsoventral height; **ACE.h**, acetabulum dorsoventral height; **ACE.w**, acetabulum width at mid-height; **GAP.w**, base length of acetabular perforation; **GAP.h**, max height of acetabular perforation; **PUB.l**, pubic peduncle anteroposterior length; **PUB.h**, pubic peduncle dorsoventral height; **ISC.l**, ischial peduncle anteroposterior length; **ISC.h**, Ischial peduncle dorsoventral height.

	Taxon	Inventory number	Ha	Hv	Hd	PST.l	PST.h	PRE.l	PRE.h	ACE.h	ACE.w	GAP.w	GAP.h	PUB.l	PUB.h	ISC.l	ISC.h
1	*Mecistops cataphractus*	RBINS 18374	30.22	–	57.96	23.80	22.91	7.51	9.66	26.54	27.58	6.98	2.49	20.28	6.39	17.85	9.69
2	*Alligator sinensis*	NHMW 37966	38.33	–	66.19	–	–	11.10	22.90	23.57	28.00	8.05	3.45	18.62	10.82	18.43	10.08
3	*Caiman crocodilus*	NHMW 30900	23.61	–	53.87	–	–	5.46	12.79	23.27	20.69	10.27	2.18	17.27	5.09	18.53	9.83
4	*Crocodylus niloticus*	NHMW 31.137	50.88	–	93.23	–	–	22.41	32.70	35.61	46.18	5.96	2.91	35.28	9.97	34.57	12.25
5	*Crocodylus rhombifer*	AMNH FARB 16708-10-25-26	98.39	–	188.00	79.24	88.58	29.25	56.25	87.90	72.73	28.34	4.40	58.96	34.30	57.16	32.00
6	*Crocodylus rhombifer*	AMNH FARB 16688	104.00	–	210.69	86.10	82.54	61.48	26.44	65.91	95.63	14.61	4.39	67.02	29.71	56.97	26.00
7	*Mecistops cataphractus*	RBINS 18374	30.22	–	57.96	23.80	22.91	7.51	9.66	26.54	27.58	6.98	2.49	20.28	6.39	17.85	9.69
8	*Thoracosaurus neocesariensis*	NJSM 15437	30.45	–	–	–	23.11	–	–	23.27	24.18	8.53	2.50	–	–	14.88	6.30
9	*Acherontisuchus guajiraensis*	UF/IGM 38	97.07	–	195.00	–	–	51.40	60.83	82.36	61.32	29.30	20.38	79.11	26.63	47.20	29.01
10	*Congosaurus bequaerti*	MRAC 1741	87.29	–	155.00	78.86	88.57	40.14	47.30	72.28	63.41	24.01	5.60	–	15.48	–	21.23
11	*Dyrosaurus maghribensis*	OCP DEK-GE 252	116.46	140.89	197.40	57.93	99.57	38.75	71.18	89.25	108.79	36.92	9.91	53.05	28.82	57.34	38.76
12	*Dyrosaurus maghribensis*	OCP DEK-GE 255	122.57	139.49	222.33	82.98	102.24	–	–	–	–	42.09	11.49	49.70	–	55.21	–
13	*Hyposaurus natator*	YPM VP.000985	55.90	–	–	36.57	45.74	18.76	11.01	37.25	37.48	15.63	7.50	26.97	14.40	22.67	18.74
14	*Hyposaurus natator*	YPM VP.000753	79.88	–	134.00	62.63	60.62	35.16	39.81	40.25	54.60	29.51	13.59	30.50	15.60	29.00	25.56
15	*Hyposaurus natator*	NJSM 23368	63.65	68.99	102.52	53.13	54.93	14.13	21.27	43.26	39.45	20.11	10.96	37.78	17.28	30.76	23.67
16	*Pelagosaurus typus*	SMNS 17758	7.46	7.98	10.53	–	–	1.97	1.22	–	–	–	–	–	–	–	–
17	*Pelagosaurus typus*	SMNS 80065	20.42	23.95	28.02	–	–	6.23	6.77	–	–	–	–	–	–	–	–
18	*Pelagosaurus typus*	BRLSI M.1417.1	30.92	30.99	–	18.47	23.26	–	11.24	21.57	21.23	6.85	1.73	11.97	8.01	15.43	5.47
19	*Pelagosaurus typus*	BRLSI M.1421	–	–	–	16.58	19.47	–	–	23.13	25.11	7.45	1.61	–	8.78	14.52	6.06
20	*Thalattosuchus superciliosus*	SMNS 10116	55.04	49.33	40.66	–	–	12.96	15.66	17.40	20.15	12.79	2.01	18.17	13.09	27.92	18.97
21	*Thalattosuchus superciliosus*	PMU 35988	53.66	46.83	40.83	0.00	0.00	11.47	6.57	32.40	25.00	10.35	2.24	18.28	–	23.74	18.05
22	*Thalattosuchus superciliosus*	NHMUK PV R 2054	65.60	55.27	46.94	0.00	0.00	18.93	14.10	25.02	31.94	11.71	2.03	21.61	14.50	28.00	16.68
23	*Thalattosuchus superciliosus*	NHMUK PV R 2032	59.56	61.13	35.36	0.00	0.00	6.43	8.27	35.45	29.18	5.65	0.77	21.99	–	34.80	20.80
24	*Thalattosuchus superciliosus*	GLAHM V1005	63.05	50.83	51.62	0.00	0.00	21.20	13.43	33.91	25.52	8.18	0.83	28.18	13.22	23.25	18.55
25	*Thalattosuchus superciliosus*	GLAHM V1146	54.34	46.26	42.95	0.00	0.00	15.83	9.41	31.38	25.80	6.69	0.71	20.25	8.25	29.94	15.95
26	*Cricosaurus suevicus*	SMNS9808	27.68	24.91	22.42	–	–	4.80	5.10	10.10	14.42	–	–	14.02	7.00	11.38	8.20
27	*Cricosaurus araucanensis*	MLP 72-IV-7-1	41.87	35.71	29.27	0.00	0.00	11.94	5.41	13.32	19.44	0.00	0.00	16.51	8.57	20.34	15.01
28	*Metriorhynchus brachyrhynchus*	NHMUK PV R 4763	56.00	39.90	35.00	0.00	0.00	19.30	9.75	22.60	18.14	2.70	0.40	23.00	13.30	–	18.36
29	*Metriorhynchus brachyrhynchus*	NHMUK PV R 3804	76.84	67.94	48.04	0.00	0.00	16.58	14.05	37.93	33.90	4.42	0.61	36.32	10.76	32.61	18.27
30	*Tyrannoneustes lythrodectikos*	GLAHM V1145	66.98	59.35	43.49	0.00	0.00	15.31	12.18	–	–	2.46	0.60	30.60	12.95	25.44	18.50
31	*Tyrannoneustes lythrodectikos*	GLAHM V972	–	–	41.95	–	–	–	–	34.71	32.28	–	–	–	–	26.58	15.29
32	*Suchodus durobrivensis*	NHMUK PV R 2618	42.48	38.35	26.83	0.00	0.00	9.43	7.33	21.97	16.92	0.00	0.00	20.47	6.81	18.50	9.01
33	*Geosaurus giganteus*	NHMUK PV R 1230	26.01	24.72	16.30	0.00	0.00	3.18	3.18	13.00	17.66	–	–	12.20	–	11.37	8.54
34	*Dakosaurus maximus*	SMNS 8203	–	65.80	–	–	–	–	–	–	–	–	–	35.76	13.40	30.71	–
35	*Plagiophthalmosuchus gracilirostris*	NHM PV OR 14792	–	–	–	17.21	11.51	–	–	–	–	–	–	–	–	–	–
36	*Sericodon jugleri*	MJSN SCR010-312	80.99	72.44	93.80	39.43	59.68	24.69	20.82	52.06	50.29	12.87	3.88	28.66	25.10	39.02	15.57
37	*Platysuchus multiscrobiculatus*	SMNS9930	40.96	–	74.98	24.90	19.20	18.84	12.37	–	32.29	–	–	–	–	–	–
38	*Macrospondylus bollensis*	SMNS 9428	49.53	48.21	75.15	14.65	26.00	12.80	13.90	–	–	–	–	–	–	–	–
39	*Macrospondylus bollensis*	SMNS 17484a	43.18	49.83	60.22	16.60	48.30	13.00	11.79	30.76	31.12	–	–	20.50	8.42	27.85	9.75
40	*Macrospondylus bollensis*	PMU 35980	37.52	60.58	–	–	–	12.43	13.81	22.20	38.24	–	–	–	–	–	–
41	*Charitomenosuchus leedsi*	NHMUK PV R 3806	74.82	62.45	93.86	46.58	56.03	28.10	16.40	50.26	43.48	7.16	0.96	26.70	14.01	32.64	12.38
42	*Proexochokefalos cf. bouchardi*	MJSN SCR010-374	88.87	81.12	114.57	41.65	63.93	34.49	37.91	–	–	5.76	1.10	34.23	12.53	48.75	17.23
43	*Neosteneosaurus edwardsi*	NHMUK PV R 3701	70.13	77.92	97.03	34.52	58.51	22.98	19.27	40.65	44.05	10.88	2.64	32.61	13.72	35.78	16.38
44	*Neosteneosaurus edwardsi*	NHMUK PV R 3898	148.79	146.08	184.87	68.68	103.56	47.14	37.74	–	–	20.56	2.99	58.97	42.88	–	24.87
45	*Neosteneosaurus edwardsi*	NHMUK PV R 2076	88.18	88.14	107.28	43.16	72.91	28.70	26.57	59.03	56.45	18.14	2.23	36.01	26.88	43.78	15.44
46	*Lemmysuchus obtusidens*	NHMUK PV R 3168	109.80	120.34	172.00	73.84	92.68	28.40	23.05	77.83	73.42	26.97	0.00	50.85	17.59	41.63	21.39

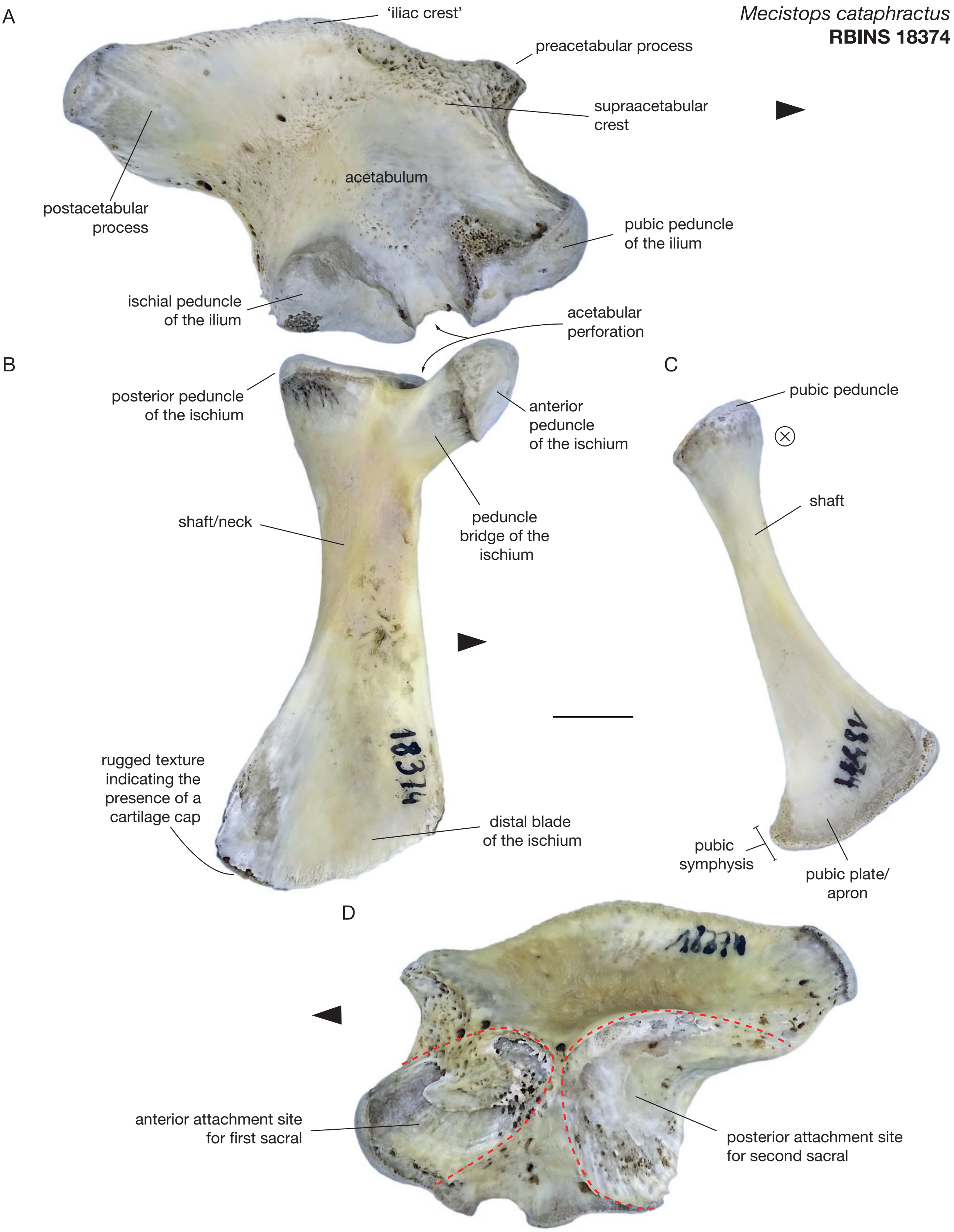


FIG. 8. — Right pelvic girdle of *Mecistops cataphractus* Cuvier, 1825, RBINS 18374: **A**, ilium in lateral view; **B**, ischium in lateral view; **C**, pubis in ventral view; **D**, ilium in medial view. Cross indicates posterior. Arrow points anteriorly. Scale bar: 1 cm.

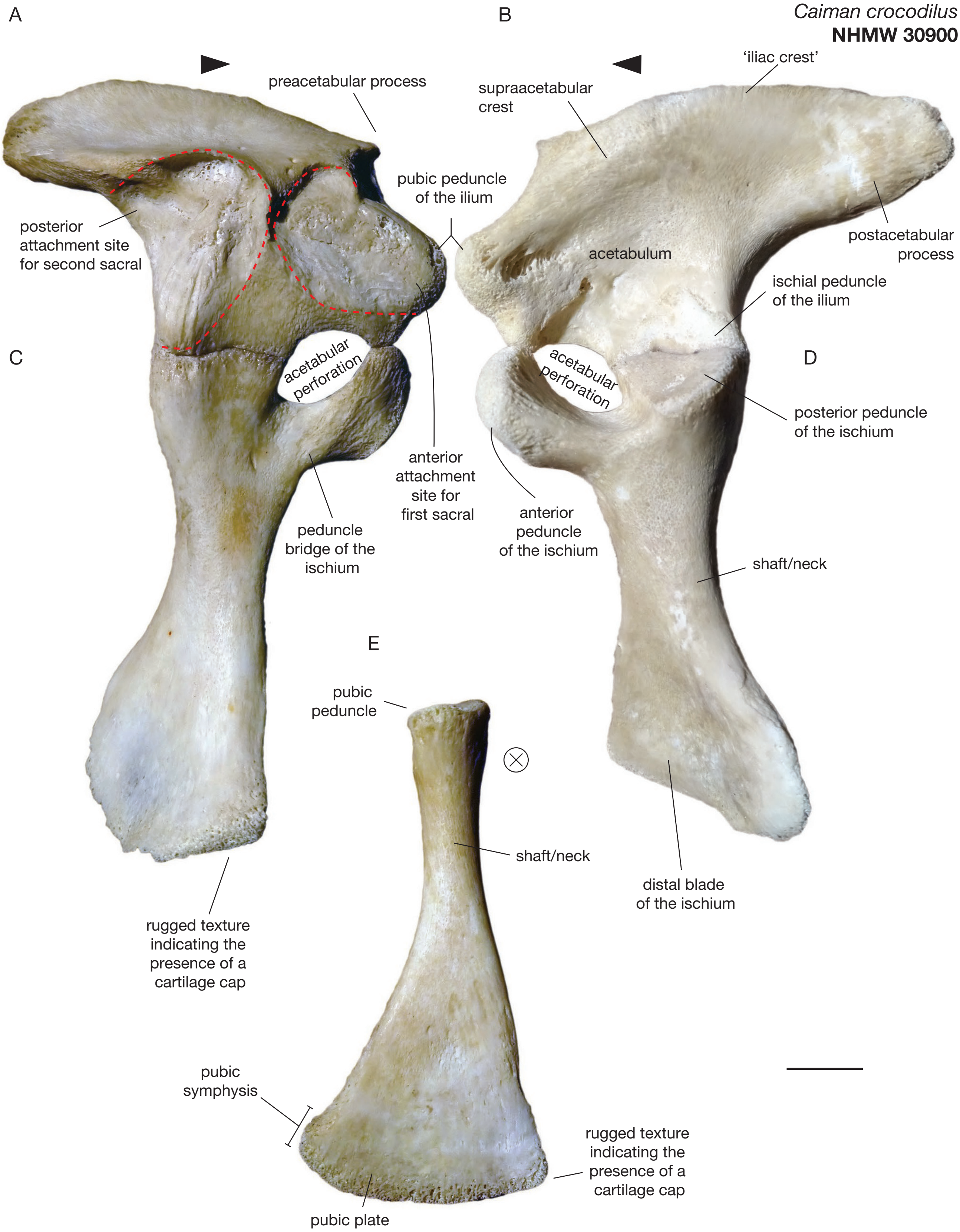


FIG. 9. — Left pelvic girdle of *Caiman crocodilus* (Linnaeus, 1758), NHMW 30900: **A**, ilium in medial view; **B**, ilium in lateral view; **C**, ischium in medial view; **D**, ischium in lateral view; **E**, pubis in posterior view. Target indicates anterior. Arrow points anteriorly. Scale bar: 1 cm.

The anterior margin of the ilium of *Pelagosaurus typus* (Fig. 10D) forms a straight surface connecting the preacetabular process to the pubic peduncle. The junction between the anterior margin and the ventral border of the preacetabular process is achieved through an acute angle, due to the relative inclination of the anterior margin of the ilium. Indeed, by prolonging both surfaces until they meet (thus ignoring the preacetabular process), the anterior margin of the ilium appears to form an angle of approximately 120° with the dorsal margin. Overall, the preacetabular process of *Pelagosaurus typus* is well developed as in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867) NHMUK PV R 4763, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, etc.) and also teleosauroids (e.g. *Macrospondylus bollensis* (Jäger, 1828), *Sericodon jugleri*, *Charitomenosuchus leedsi*, etc.) compared to extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*). The preacetabular process of *Pelagosaurus typus* reaches about half of the anteroposterior length of the pubic (or even ischial) peduncle, as in some metriorhynchoids (e.g. *Suchodus durobrivensis* or *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852)). However, several other thalattosuchian taxa display a larger preacetabular process, both proportionally and in absolute values (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus* (Fraas, 1901), *Lemmysuchus obtusidens*, etc.). The preacetabular process of *Pelagosaurus typus* is proportionally long, sharp, and in line with the iliac crest. The junction between the preacetabular process and the iliac crest is achieved through a subtle recess, and the iliac crest is faintly convex. Some teleosauroids also display a relatively straight to subtly convex dorsal margin, due to the alignment of the preacetabular and postacetabular processes without a marked depression at their junction (e.g. namely *Macrospondylus bollensis* and *Platysuchus multiscrobiculatus* (Berckhemer, 1929), but also the more derived *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*).

As mentioned, the dorsal margin of the ilium of *Pelagosaurus typus* (Fig. 10D) corresponding to the iliac crest is slightly convex over most of its surface, with only the subtle recess marking the junction with the preacetabular process. The lateral surface of the iliac crest is scarred with a series of ridges perpendicular to the margin of the bone. Posteriorly, the dorsal margin of the ilium culminates in a relatively sharp apex pointing strictly posteriorly which corresponds to the extremity of the postacetabular process. The latter takes the overall shape of a Lancet arch since its dorsal and ventral borders are slightly convex. The postacetabular process of *Pelagosaurus typus* is slender with a subtlety convex ventral margin. The latter stems from the main body of the ilium at around half of its dorsoventral height, which results in a relatively narrow postacetabular process, similar to some teleosauroids (e.g. *Macrospondylus bollensis* and *Platysuchus multiscrobiculatus*) although not as tubular. The postacetabular process of *Pelagosaurus typus* appears shorter than that of teleosauroids as its anteroposterior length does not constitute half of the total anteroposterior length of the iliac crest (unlike in *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). In addition, the anteroposterior length of the ilium at the peduncles almost equals that of the entire iliac crest dorsally in teleosauroids. The transition between the postacetabular process and the posterior margin of the ischial peduncle is achieved through a smooth obtuse angle, as in the teleosauroids *Macrospondylus bollensis* and *Platysuchus multiscrobiculatus*.

The entire ventral margin of the ilium of *Pelagosaurus typus* (Fig. 10D) is strongly undulating due to a major difference in the orientation of both peduncles. Hence, along the ventral margin of the bone, there is a small notch marking the changeover to the pubic peduncle. This small indentation corresponds to the acetabular perforation, which is usually not pronounced on the ilium of Thalattosuchia regardless of the clade (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Macrospondylus bollensis*, *Lemmysuchus obtusidens*, *Proexochokefalos* cf. *bouchardi*, etc.). In more derived metriorhynchoids, the acetabular perforation does not separate the peduncles (which form a continuous surface laterally), as a consequence of the reduction of the dorsal elements of their girdles (e.g. *Thalattosuchus superciliosus*, *Suchodus durobrivensis*, *Cricosaurus araucanensis* (Gasparini & Dellape, 1976), etc.). In *Pelagosaurus typus*, the acetabular perforation forms a concave notch, which is more than twice as long as it is deep. The corners of the ischial and pubic peduncles bordering the acetabular perforation are prominent, which increases the concave aspect of their respective ventral margins.

The pubic peduncle of the ilium of *Pelagosaurus typus* SMNS 17758 (Fig. 10) stands out from the rest of the bone as it is shaped as an anteroventrally protruding rectangle, whereas in BRLSI M.1417.1 the pubic peduncle is not as titled anteroventrally. Anteriorly, the pubic peduncle of BRLSI M.1417.1 strongly protrudes from the anterior margin of the ilium, forming a bump. In SMNS 17758, the pubic peduncle is not as prominent. Ventrally, the surface of the pubic peduncle is a slightly concave, similar to the ischial peduncle. The subtle inclination of the pubic peduncle of *Pelagosaurus typus* conveys the idea that only the posterior corner of the said peduncle was close to the anterior peduncle of the ischium (Fig. 12), as in extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) and teleosauroids (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). Comparatively, in metriorhynchoids, the anterior peduncle of the ischium extends more anteriorly proportionally to the ilium and either meets with the middle portion of the pubic peduncle of the ilium (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763) or is located underneath the anterior corner the pubic peduncle of the ilium (e.g. *Thalattosuchus superciliosus* NHMUK PV R 2054). Laterally, the facet of the pubic peduncle of BRLSI M.1417.1 forms a strong sinusoidal shape: its anterior half is dorsally concave whereas its posterior half displays an overall elliptical outline, with the apex pointing posteriorly. A similar shape of the pubic peduncle is found in the teleosauroids *Sericodon jugleri*, *Proexochokefalos* cf. *bouchardi*, and *Neosteneosaurus*

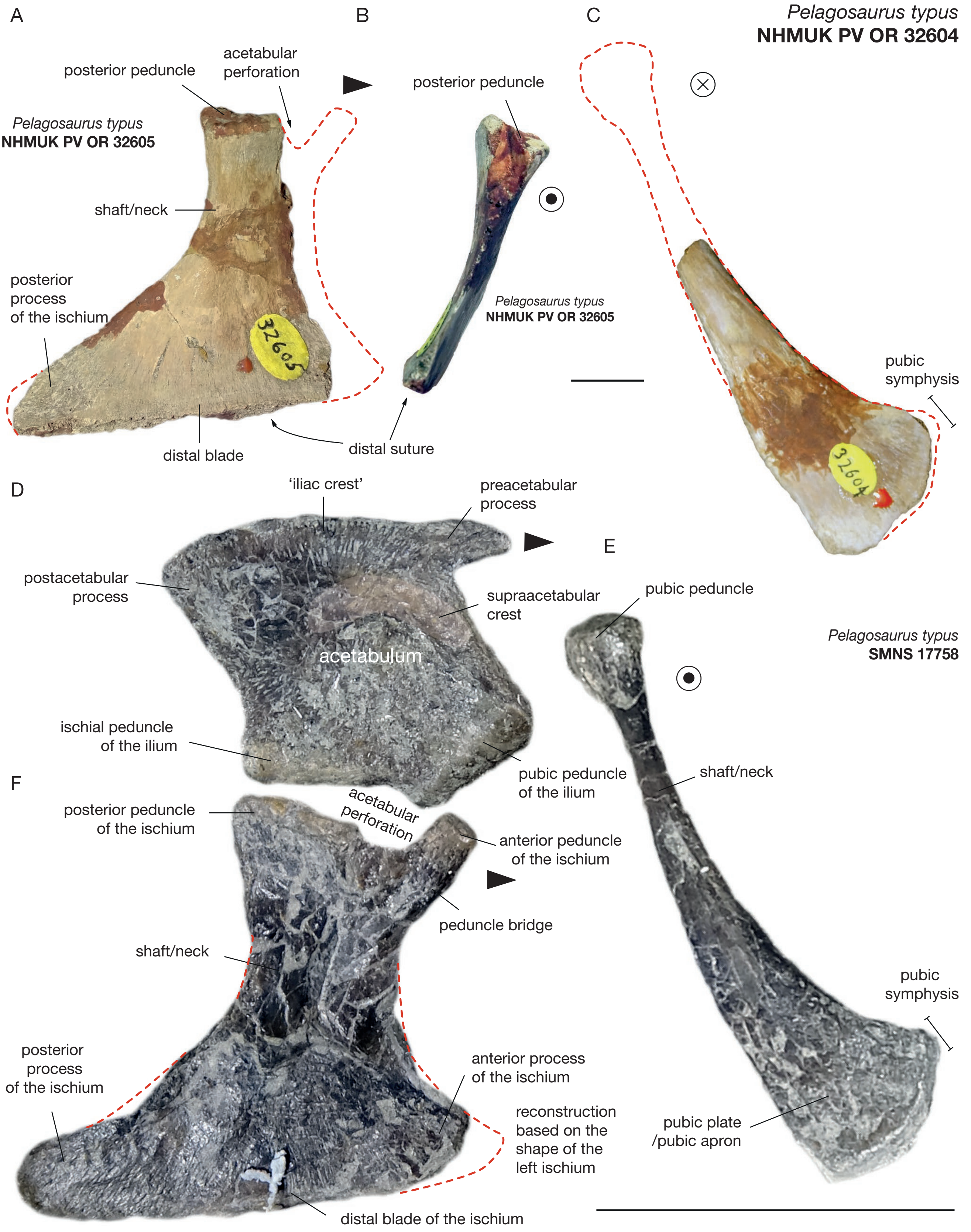


FIG. 10. — Pelvic girdle elements of *Pelagosaurus typus* Bronn, 1841: **A**, **B**, NHMUK PV OR 32605; **A**, left ischium in medial view; **B**, left ischium in anterior view; **C**, NHMUK PV OR 32604, left pubis in posterior view; **D**-**F**, SMNS 17758; **D**, right ilium in lateral view; **E**, right pubis in anterior view; **F**, right ischium in medial view. Target indicates anterior. Arrow points anteriorly. Scale bars: 1 cm.

edwardsi. Dorsally, the highest portion of the pubic peduncle of BRLSI M.1417.1 towers the ischial peduncle, whereas the ischial peduncle of *Pelagosaurus typus* SMNS 17758 shows a size and shape similar to the pubic peduncle.

On the lateral surface of the ilium, the facet of the ischial peduncle appears relatively reduced compared to other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, etc). This relation is usually inverted in extant crocodylians, metriorhynchoids and dyrosaurids (e.g. *Mecistops cataphractus* [Fig. 8], '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Congosaurus bequaerti*). In comparison, teleosauroids tend to have an ischial peduncle that is shorter or subequal to the pubic peduncle on the lateral surface of the ilium (e.g. *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Sericodon jugleri*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*), similar to *Pelagosaurus typus*. The lateral facet of the ischial peduncle is lunate-shaped and is therefore anteroposteriorly longer than it is dorsoventrally high, similar to some teleosauroids (e.g. *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Sericodon jugleri*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, etc.). The apex of the elliptic outline of the ischial peduncle is not centred but is rather posteriorly deflected. Compared to the pubic peduncle, the ischial peduncle is dorsoventrally shorter (as mentioned previously). Hence, in *Pelagosaurus typus* the ischial peduncle does not appear to form a salient posterior barrier due to its short size. It is however still markedly protruding laterally.

The bony acetabulum is located on the lateral surface of the ilium of *Pelagosaurus typus* (Fig. 10D). It is limited by the supraacetabular crest anteriorly and dorsally, and by the ischial peduncle posteriorly. The supraacetabular crest extends over about ⅔ of the entire length of the ilium. Anteriorly, the supraacetabular crest does not influence the shape of the anterior margin of the bone, similar to *Geosaurus giganteus* (Von Sommerring, 1816) *sensu* Von Quenstedt (1852), *Lemmysuchus obtusidens*, and *Platysuchus multiscrobiculatus* but unlike in more derived metriorhynchoids where the supraacetabular crest forms a more extensive rugged area encompassing the anterior margin (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, or *Thalattosuchus superciliosus*).

Pelagosaurus typus bears two distinct attachment sites for the sacral ribs on the medial side of the ilium (Fig. 11B). The sacral rib attachment sites are located around the mid-height of the bone and along its anterior and posterior margins, unlike more derived metriorhynchoids (e.g. *Thalattosuchus superciliosus*, *Cricosaurus araucanensis*, *Dakosaurus maximus*, etc.). Yet, *Pelagosaurus typus* displays the long and pendent sacral ribs characteristic of Metriorhynchoidea, as opposed to the relatively short and horizontal ones of Teleosauroidea (e.g. *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, etc.). The posterior attachment site is overall larger than the anterior one and is located more ventrally which indicates a slight dorsal orientation for the ilium (Fig. 12). The shape and position of the sacral rib attachment sites of *Pelagosaurus typus* is similar to that of other unreduced ilia which still display a postacetabular process. This reflects the impact of the girdle reduction on its position and orientation in more derived members of Metriorhynchoidea.

Ischium

The ischium of *Pelagosaurus typus* (Figs 10-12) strongly differs from that of other metriorhynchoids and teleosauroids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Geosaurus giganteus*, *Aeolodon priscus* (Von Sömmerring, 1814) Von Meyer, 1832, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Lemmysuchus obtusidens*, etc.) in displaying a thick distal suture whose surface is perpendicular to that of the distal blade. The main consequence is a different orientation of the ischium of *Pelagosaurus typus* compared to that of other thalattosuchians, where both ischia of *Pelagosaurus typus* are set at a greater angle medially (Fig. 12).

Overall, the ischium of *Pelagosaurus typus* displays a proportionally long and thick shaft. Indeed, the narrowing of the shaft (which delimits it) is located at about half of the total dorsoventral height of the bone and the anteroposterior length of this narrowing exceeds that of the posterior peduncle. Several thalattosuchians display a relatively thick shaft (e.g. *Cricosaurus suevicus*, *Dakosaurus maximus*, *Aeolodon priscus* NHMUK PV R 1086, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*), however a proportionally elongated shaft is less common (e.g. *Thalattosuchus superciliosus* NHMUK PV R 2054). In addition, the anterior and posterior margins of the shaft of *Pelagosaurus typus* (i.e. underneath the peduncles) are both markedly concave as seen in several thalattosuchians (e.g. *Cricosaurus suevicus*, *Cricosaurus araucanensis*, *Dakosaurus maximus*, *Torvoneustes carpenteri* (Wilkinson, Young & Benton, 2008), *Aeolodon priscus*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, etc.), resulting in a significant flaring of the bone proximally and distally.

The anterior peduncle of the ischium of *Pelagosaurus typus* (Fig. 10F) appears to have an ovoid shape and is located further dorsally than the posterior peduncle as in other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Geosaurus giganteus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, etc.). Indeed, the anterior peduncle is borne on the extremity of the peduncle bridge, which constitutes an elongated cylindrical structure emanating from the dorsal-most portion of the shaft. The latter is almost as long proximodistally as the posterior peduncle is anteroposteriorly long. The thickness of the peduncle bridge in lateral view seems constant throughout its length, and is equal to that of the anterior peduncle. In *Pelagosaurus typus*, the anterior and posterior peduncles are set further apart than in most thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, etc.). The junction between the anterior and posterior peduncles appears forms a wide hemispherical indentation on the dorsal margin of the ischium. This large gap constitutes the ventral border of the acetabular perforation, and thus makes up for

TABLE 8. — List of measurements in mm of crocodyliformes ischia. When measurements are missing on the first ischium, it takes measurements from next ischium. NHMUK PV R 4763 shaft reconstructed. Abbreviations: **Hd**, total height from posterior peduncle to tip of posterior process; **PP.h**, height of posterior process tip; **AP.h**, base height of anterior process; **AP.w**, total length of anterior process; **BL.l**, total length of ischial blade; **GAP.w**, base length of acetabular perforation; **GAP.h**, max height of acetabular perforation; **PPed.Ll**, anteroposterior length of posterior peduncle taken laterally; **PPed.Wa**, mediolateral width of posterior peduncle taken anteriorly; **BR.l**, total length of peduncle bridge; **APed.w**, mediolateral width of anterior peduncle; **APed.h**, dorsoventral height of anterior peduncle; **Arch.l**, anterior arch length from anterior peduncle to anterior process; **Arch.h**, maximal depth between base arch and bone margin; **S**, length from proximal extremity to maximal constriction; **C**, anteroposterior width of constriction.

	Taxon	Inventory number	Hd	PP.h	AP.h	AP.w	BL.l	GAP. w	GAP. h	PPed. Ll	PPed. Wa	BR.l	APed. w	APed. h	Arch. l	Arch. h	S	C
1	*Alligator sinensis*	NHMW 37966	67.41	–	–	–	46.58	15.89	4.21	18.52	19.19	18.52	13.33	17.99	43.61	7.76	–	–
2	*Caiman crocodilus*	NHMW 30900	66.79	–	–	–	35.59	16.74	5.30	16.27	18.84	19.38	15.04	12.69	47.33	8.30	–	–
3	*Crocodylus niloticus*	NHMW 31.137	106.13	16.56	–	–	63.55	28.60	7.17	24.37	35.74	29.64	26.64	22.79	72.65	4.25	–	–
4	*Mecistops cataphractus*	RBINS 18374	68.65	–	0.00	0.00	34.28	15.17	10.10	22.01	23.43	23.23	18.14	18.78	53.44	11.61	24.88	12.17
5	*Acherontisuchus guajiraensis*	UF/IGM 38	272.00	–	–	–	145.00	66.81	11.81	44.65	19.40	45.42	58.29	31.44	42.00	5.06	106.05	57.98
6	*Dyrosaurus maghribensis*	OCP DEK-GE 252	205.29	31.93	68.22	25.61	134.64	37.41	23.03	53.36	–	45.76	66.89	28.89	97.20	18.85	112.24	74.52
7	*Dyrosaurus maghribensis*	OCP DEK-GE 255	250.12	38.36	58.01	21.48	147.21	47.81	–	–	–	57.98	–	–	119.65	16.32	110.23	80.11
8	*Hyposaurus natator*	AMNH FARB 2390	–	–	–	–	–	37.53	6.93	–	34.89	34.54	30.03	20.60	–	–	–	–
9	*Hyposaurus natator*	YPM VP.000985	–	–	–	–	–	16.01	15.90	20.28	27.30	35.54	39.24	21.03	–	–	–	–
10	*Hyposaurus natator*	YPM VP.000753	172.00	–	–	–	–	29.36	21.92	29.81	35.07	48.10	47.40	23.15	31.61	9.04	–	–
11	*Hyposaurus natator*	NJSM 23368	137.64	12.23	34.68	20.14	86.13	34.65	21.14	23.81	30.04	34.33	43.35	34.36	57.69	16.70	56.14	33.72
12	*Pelagosaurus typus*	SMNS 17758	12.59	1.91	2.64	1.97	13.19	2.38	1.01	4.12	–	2.39	1.28	–	7.19	2.75	4.29	3.90
13	*Pelagosaurus typus*	SMNS 80065	34.87	5.58	8.55	6.58	40.15	6.20	2.51	10.51	–	9.09	2.09	–	23.80	9.65	12.01	9.75
14	*Pelagosaurus typus*	BRLSI M.1410	–	–	15.33	10.25	–	10.48	4.42	12.83	–	14.68	4.95	–	40.46	12.83	20.41	15.43
15	*Pelagosaurus typus*	BRLSI M.1424	67.18	8.52	19.06	–	–	13.58	4.13	10.74	–	16.56	3.51	–	–	–	18.65	15.10
16	*Pelagosaurus typus*	NHMUK PV OR 32605	52.32	–	–	–	–	–	–	11.70	–	–	–	–	–	–	–	–
17	*Thalattosuchus superciliosus*	PMU 35988	103.80	16.92	22.95	18.67	103.05	9.83	4.28	21.33	15.99	15.79	8.95	6.94	58.07	19.76	21.51	30.10
18	*Thalattosuchus superciliosus*	NHMUK PV R 2054	120.10	18.68	25.54	–	–	15.59	3.64	25.85	18.56	25.12	8.97	11.34	–	–	25.72	33.67
19	*Thalattosuchus superciliosus*	NHMUK PV R 1530	115.29	–	22.88	19.58	114.97	11.81	5.51	18.45	23.88	23.35	8.71	9.97	64.28	24.46	28.95	34.95
20	*Thalattosuchus superciliosus*	GLAHM V1005	15.61	17.60	25.97	22.73	108.75	–	–	25.95	23.66	–	–	–	–	–	24.31	32.51
21	*Thalattosuchus superciliosus*	GLAHM V950	–	–	26.15	20.66	–	12.31	4.01	26.79	28.94	27.76	11.60	15.89	74.07	24.67	24.68	33.15
22	*Thalattosuchus superciliosus*	GLAHM V960	–	–	20.61	10.75	–	11.29	3.20	20.17	19.74	22.35	8.32	6.52	58.76	15.53	21.47	29.48
23	*Thalattosuchus superciliosus*	GLAHM V1142	103.41	14.59	22.57	–	94.13	14.36	2.46	19.88	14.47	24.29	7.63	6.30	–	–	21.02	29.74
24	*Cricosaurus albersdoerferi*	BMMS-BK 1-2	–	–	–	–	–	–	–	17.72	–	10.84	8.13	–	–	–	14.99	18.61
25	*Cricosaurus bambergensis*	NKMB-P-Watt14/274	–	–	13.31	7.94	36.12	–	–	–	–	8.65	3.81	–	25.01	8.12	–	9.09
26	*Cricosaurus suevicus*	GPIT RE 7322	42.32	13.13	12.84	9.47	41.65	2.61	–	6.13	–	6.33	3.33	–	24.36	7.10	13.51	14.90
27	*Cricosaurus araucanensis*	MLP 72-IV-7-1	–	–	–	–	–	9.45	2.84	16.25	12.04	14.73	8.82	6.57	–	–	–	–
28	*Cricosaurus araucanensis*	MLP 72-II-27-6	–	–	–	–	–	–	–	–	–	14.20	6.50	–	–	–	14.90	15.60
29	*Metriorhynchus brachyrhynchus*	NHMUK PV R 3804	–	–	31.56	29.45	–	10.97	–	38.36	34.01	30.61	26.30	14.17	68.50	22.27	31.42	47.46
30	*Metriorhynchus brachyrhynchus*	LEICT G.418.1956-58	157.23	–	–	–	–	11.85	2.73	51.00	–	–	14.50	18.80	–	–	33.18	50.88
31	*Metriorhynchus brachyrhynchus*	NHMUK PV R 4763	88.51	17.68	18.65	15.96	96.76	13.35	4.61	22.76	17.84	13.91	6.35	8.38	57.04	19.79	19.86	25.02
32	*Tyrannoneustes lythrodectikos*	GLAHM V972	–	–	–	–	–	–	–	–	16.83	–	–	–	–	–	21.76	37.48
33	*Geosaurus giganteus*	NHMUK PV R 1230	–	–	13.25	10.76	–	–	–	–	–	12.84	5.77	–	25.00	12.16	–	–
34	*Dakosaurus maximus*	SMNS 8203	113.82	64.15	47.13	40.29	186.00	–	–	59.97	41.40	–	–	–	103.92	33.40	42.03	66.04
35	*Torvoneustes carpenteri*	Cd7203	177.40	44.93	43.83	39.27	167.16	23.25	7.04	34.40	22.21	40.49	10.02	11.23	112.35	37.03	43.34	49.03
36	*Aeolodon priscus*	NHMUK PV R 1086	26.19	6.24	7.18	6.19	28.53	3.71	0.81	6.69	–	4.55	1.74	–	15.68	6.56	6.45	9.74
37	*Sericodon jugleri*	MJSN SCR010-312	–	–	–	–	–	15.89	5.28	25.95	26.95	21.20	8.90	19.34	–	–	–	–
38	*Teleosaurus sp.*	OUMNH.J1638	148.82	26.20	–	–	–	–	–	36.16	–	–	–	–	–	–	41.00	36.71
39	*Teleosaurus sp.*	NHMUK PV R 238	–	–	28.65	15.97	–	–	–	25.12	–	27.82	9.98	–	65.24	25.61	35.05	29.58
40	*Platysuchus multiscrobiculatus*	SMNS9930	81.45	18.25	21.78	15.71	86.66	–	–	–	13.01	–	–	–	–	–	32.59	27.50
41	*Macrospondylus bollensis*	SMNS 16848	96.45	15.29	18.85	14.20	101.90	14.02	7.50	22.28	3.58	24.12	9.63	5.52	45.36	19.66	31.25	28.88
42	*Macrospondylus bollensis*	SMNS 9428	74.90	11.18	–	–	–	6.89	8.89	19.42	–	18.89	5.67	–	–	–	22.86	21.79
43	*Macrospondylus bollensis*	SMNS 17484a	91.98	12.17	24.00	13.78	94.20	17.36	8.95	19.54	11.82	20.21	6.69	7.39	53.95	16.01	22.38	29.27
44	*Macrospondylus bollensis*	PMU 35980	112.23	15.26	–	–	–	21.27	2.60	26.17	–	27.73	10.60	15.55	91.85	21.82		
45	*Macrospondylus bollensis*	NHMUK PV R 5703	–	–	–	–	–	27.20	9.81	28.29	33.32	32.95	9.93	20.76	–	–	36.03	35.53
46	*Steneosaurus bollensis*	SMNS 15712a	–	–	–	–	–	–	–	–	–	–	–	–	–	–		

Table 8. — Continuation.

	Taxon	Inventory number	Hd	PP.h	AP.h	AP.w	BL.l	GAP. w	GAP. h	PPed. Ll	PPed. Wa	BR.l	APed. w	APed. h	Arch. l	Arch. h	S	C
47	*Charitomenosuchus leedsi*	NHMUK PV R 3806	127.34	27.65	29.05	–	–	20.07	11.94	24.06	26.99	28.83	10.15	17.51	–	–	36.39	28.76
48	*Proexochokefalos cf. bouchardi*	MJSN SCR010-374	131.66	41.22	–	–	136.58	17.61	6.57	34.30	25.65	28.99	10.53	20.99	87.81	29.29	40.19	33.36
49	*Neosteneosaurus edwardsi*	NHMUK PV R 3701	125.59	16.55	–	–	–	21.57	4.86	25.66	25.68	26.88	8.81	12.69	–	–	28.26	37.73
50	*Neosteneosaurus edwardsi*	NHMUK PV R 2865	165.82	34.59	48.82	33.86	173.21	27.24	9.93	37.82	35.71	31.67	15.77	21.44	89.25	35.59	43.78	49.30
51	*Neosteneosaurus edwardsi*	NHMUK PV R 3898	234.14	27.24	60.04	–	256.40	–	–	54.43	53.94	–	–	–	–	–	53.35	66.31
52	*Lemmysuchus obtusidens*	NHMUK PV R 3168	203.00	53.22	51.91	47.02	206.50	28.73	11.30	52.17	51.67	32.70	20.41	31.33	87.00	43.53	55.26	54.59

the more reduced counterpart of the ilium. The posterior peduncle of the ischium of *Pelagosaurus typus* dorsally stands out from the acetabular perforation. Its articular surface appears slightly undulating and uneven so that the posterior-most border is located more dorsally (Fig. 10A, F). The posterior corner of the ischium connecting the posterior peduncle with the shaft is smooth and rounded.

The distal blade of the ischium (Figs 10A, F; 12) is relatively slender as in '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus bambergensis* (Sachs *et al.* 2019) Wagner, 1858, *Macrospondylus bollensis*, and *Platysuchus multiscrobiculatus*. Indeed, the dorsoventral height of the posterior process of the distal blade is smaller than the constriction of the shaft, giving it a tapered look. The dorsal margin of the posterior process is relatively straight, like the ventral margin of the distal blade. The extremity of the posterior process is hemispherical similar to '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, *Cricosaurus bambergensis*, and *Platysuchus multiscrobiculatus*. Anteriorly, the distal blade culminates in a sharp apex mainly pointing anteriorly but with a small dorsal component. The dorsoanterior margin of the anterior process follows the continuity of the anterior margin of the shaft: i.e. the margin is concave with the same degree of concavity.

Pubis

The pubis of *Pelagosaurus typus* (Figs 10-12) differs from other thalattosuchians in displaying the combination of a drastically slender pubic apron (almost three times longer than wide) with a proportionally well-developed pubic symphysis regarding the width of its pubic apron (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Lemmysuchus obtusidens*, *Machimosaurus* Von Meyer, 1837, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, etc.). Indeed, the pubic symphysis of *Pelagosaurus typus* reaches almost ⅓ of the total dimension of the distal blade, and the shaft only accounts for about 12.79% of the entire proximodistal height of the pubis. Still, the pubic symphysis of *Pelagosaurus typus* is overall shorter than in most thalattosuchians. Other thalattosuchians possessing a globally shorter pubic symphysis include notably *Geosaurus giganteus* and *Macrospondylus bollensis*.

Overall, the pubis of *Pelagosaurus typus* has a very distinctive appearance as it is strongly arched laterally, with its median margin being concave throughout and its lateral margin being entirely convex (Fig. 12). The specimens NHMUK PV OR 32605 and SMNS 17758 display a stronger curvature than in BRLSI M.1420. The outline of the distal margin of the pubic apron of *Pelagosaurus typus* (including the pubic symphysis) is also characteristic: it is slightly convex as in extant crocodylians, but with a more developed symphysis. Comparatively, few thalattosuchian taxa display a similarly curved distal margin, namely rhacheosaurines (i.e. *Rhacheosaurus gracilis* Von Meyer, 1831, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021), and *Cricosaurus bambergensis*), *Geosaurus giganteus*, and *Macrospondylus bollensis*. The latter displays the overall closest shape to *Pelagosaurus typus*, but with a wider and shorter pubic apron and thicker shaft. The pubic symphysis of *Pelagosaurus typus* is strongly reduced and corresponds to the area forming the junction between the medial and distal margins, similar to extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, etc.).

Proximally, the shaft of *Pelagosaurus typus* displays a significant widening to form the pubic peduncle. Indeed, the mediolateral width of the latter is 2.5 times greater than the constriction of the shaft. The pubis of SMNS 17758 is anteroposteriorly flattened and shows breakage proximally, which presumably emphasizes the width of its proximal extremity compared to BRLSI M.1420.

Several other thalattosuchians show a proximal flaring (e.g. *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Platysuchus multiscrobiculatus*, *Machimosaurus*, *Macrospondylus bollensis*, but few display a comparable intensity (e.g. *Cricosaurus suevicus*, *Geosaurus giganteus*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*).

The shape of the peduncle of the pubis of *Pelagosaurus typus* does not differ from what is observed in most thalattosuchians: the articular surface is oval in shape, is slightly convex, and has rounded corners laterally and medially defining the extremities of the peduncle.

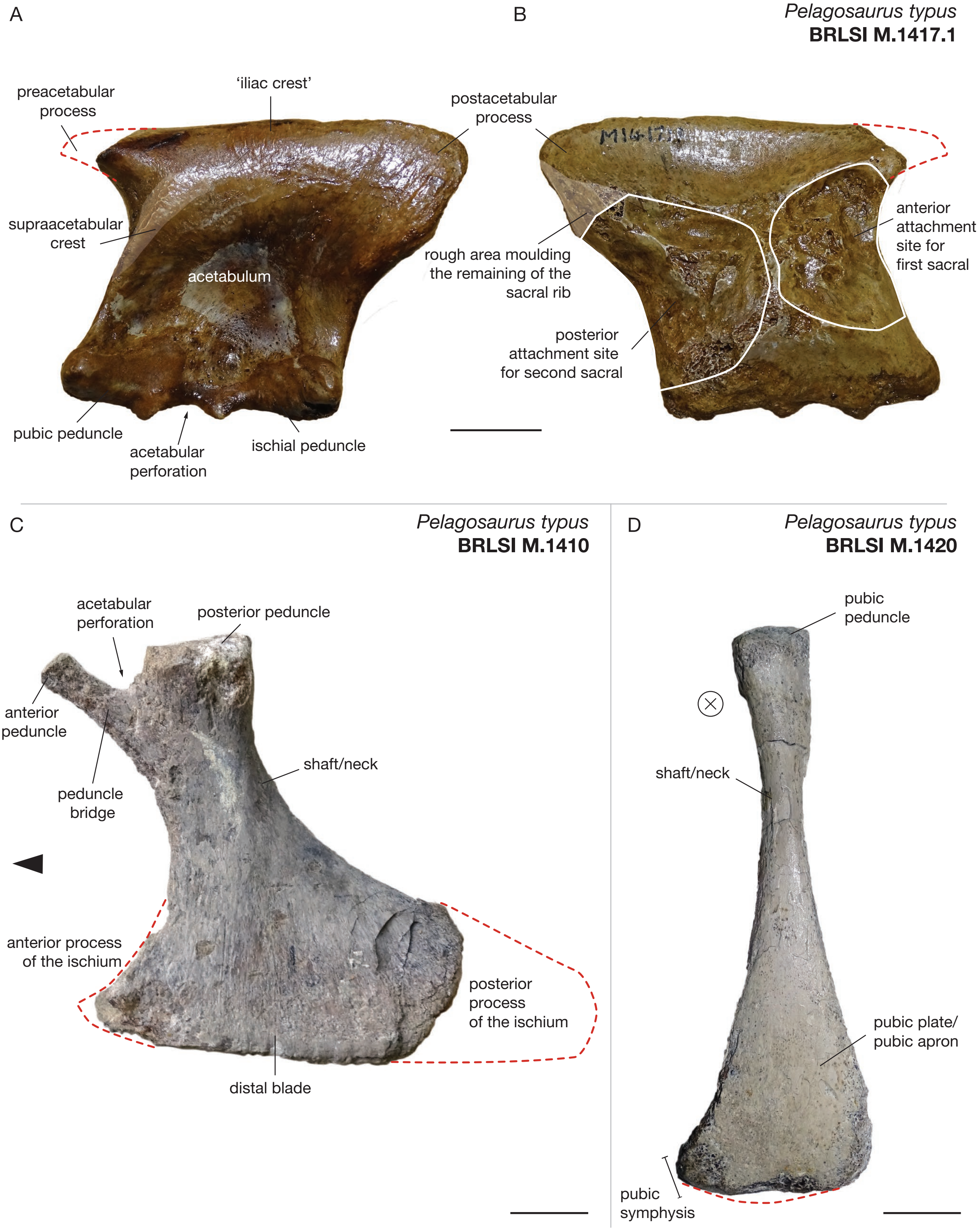


FIG. 11. — Pelvic girdle elements of *Pelagosaurus typus* Bronn, 1841: **A**, **B**, BRLSI M.1417.1; **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, BRLSI M.1410, left ischium in lateral view; **D**, BRLSI M.1420, right pubis in posterior view. Cross indicates posterior. Arrow points anteriorly. Scale bars: 1 cm.

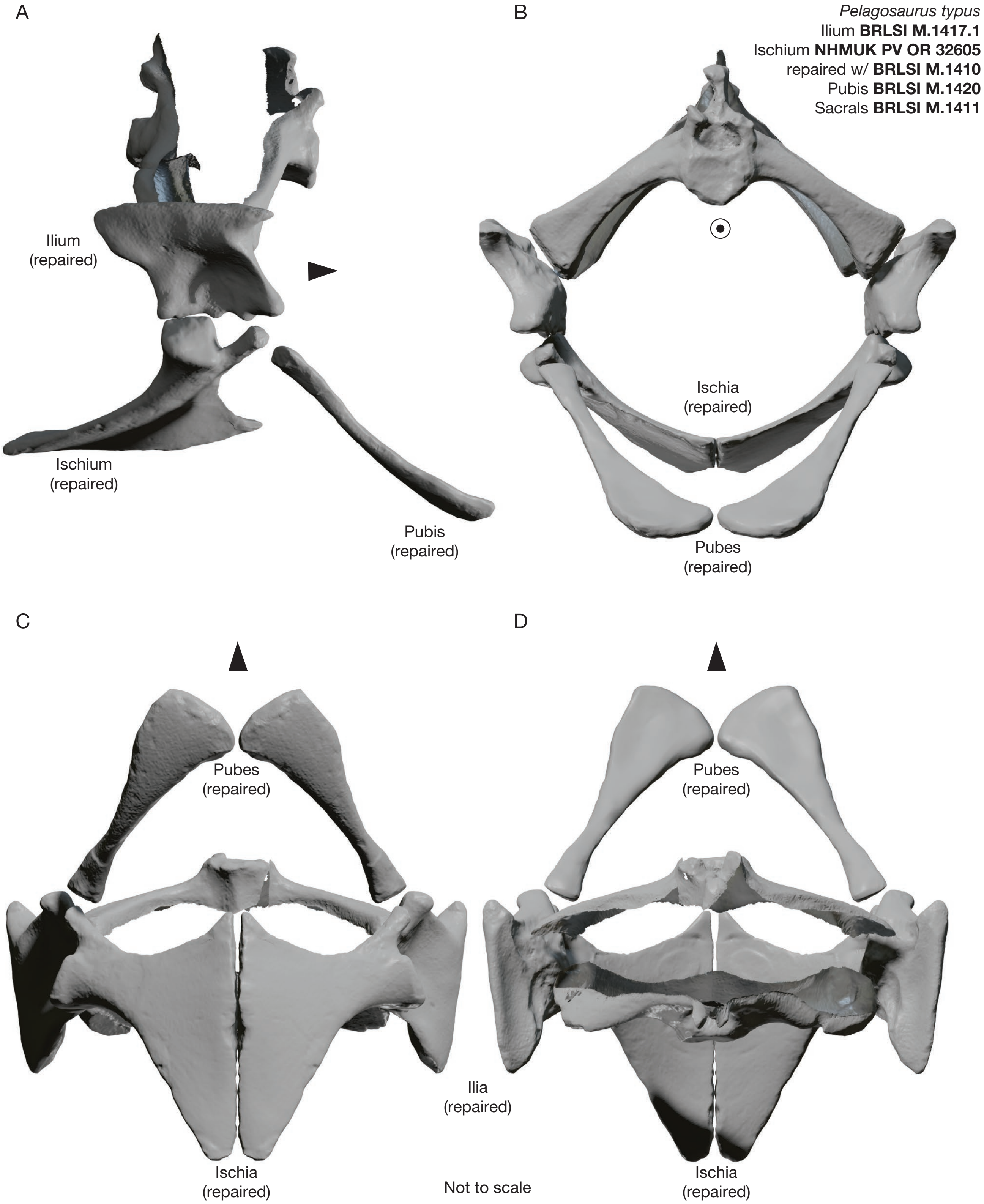


FIG. 12. — Pelvic reconstruction of *Pelagosaurus typus* Bronn, 1841: ilium corresponds to the specimen BRLSI M.1417.1, ischium to NHMUK PV OR 32605 repaired with BRLSI M.1410, pubis to BRLSI M.1420, and sacrals to BRLSI M.1411; **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. All bones are scaled to one another based on specimens from BRLSI and NHM. Arrow points anteriorly. Target indicates anterior. The right ilium and ischium, and left pubis are mirrored. Reconstructed bones only serve as a qualitative representation to better illustrate the pelvic girdle of *Pelagosaurus typus*. Not to scale.

TABLE 9. — List of measurements in mm of crocodyliformes pubes. When measurements are missing on the first bone, it takes measurements from the next one. SMNS 81608 has been reconstructed. Abbreviations: **H**, total proximodistal height; **Wh**, mediolateral width at mid length; **Ldia**, length of diaphysis; **Lbl**, freehand length of distal blade up to diaphysis; **Dbl**, distance between both medial and lateral extremities of distal blade; **Wprox**, anteroposterior width of proximal peduncle; **Lprox**, mediolateral length of proximal peduncle; **Shaft**, proximodistal length of shaft; **Neck**, proximodistal length of neck; **C**, anteroposterior width of constriction; **Arch.l**, anterior arch length from peduncle to pubic diaphysis; **Arch.h**, maximal depth between base arch and bone margin; **Arch.d**, distance between proximal base of arch and position of max depth along the arch.

–	Taxon	Inventory number	H	Wh	Ldia	Lbl	Dbl	Wprox	Lprox	Shaft	Neck	C	Arch.l	Arch.h	Arch.d
1	*Alligator sinensis*	NHMW 37966	57.54	14.00	12.90	40.14	34.11	10.58	14.21	15.27	–	–	40.06	7.02	28.14
2	*Caiman crocodilus*	NHMW 30900	70.55	12.13	5.52	32.70	34.50	8.24	11.96	25.06	29.14	–	56.53	7.78	29.05
3	*Crocodylus niloticus*	NHMW 31.137	106.98	19.66	30.72	38.41	54.30	17.40	27.10	27.04	–	–	87.27	16.94	41.42
4	*Crocodylus rhombifer*	AMNH FARB 16696	185.00	32.24	38.30	–	76.34	36.05	61.11	54.21	76.16	–	128.23	26.71	58.44
5	*Mecistops cataphractus*	RBINS 18374	54.41	6.73	7.04	23.22	24.39	8.11	12.65	19.80	18.74	–	42.06	5.91	25.62
6	*Anthracosuchus balrogus*	UF/IGM 68	–	–	76.30	94.00	130.81	–	–	–	–	–	–	–	–
7	*Cerrejonisuchus improcerus*	UF/IGM 31	158.00	28.47	65.40	39.50	75.17	11.34	24.05	38.63	56.77	–	85.59	11.98	61.00
8	*Dyrosaurus maghribensis*	OCP DEK-GE 252	268.06	51.53	–	–	–	–	36.51	86.54	–	–	188.56	11.08	108.22
9	*Dyrosaurus maghribensis*	OCP DEK-GE 254	215.79	37.44	51.46	117.04	97.94	–	36.74	47.33	–	–	145.13	13.40	64.69
10	*Hyposaurus natator*	YPM VP.000985	–	–	–	–	–	17.49	23.90	–	–	–	–	–	–
11	*Hyposaurus natator*	YPM VP.000753	210.00	26.41	38.67	55.56	60.15	21.35	28.41	55.07	76.43	–	173.00	22.04	90.00
12	*Hyposaurus natator*	NJSM 23368	161.18	19.54	38.00	32.80	61.92	19.01	24.29	39.79	62.61	11.25	118.17	13.10	70.03
13	*Pelagosaurus typus*	SMNS 17758	16.97	1.82	2.17	3.57	4.70	–	2.10	4.01	–	–	14.86	2.14	9.18
14	*Pelagosaurus typus*	NHMUK PV OR 15926	54.44	4.71	–	–	14.06	–	5.54	–	–	–	–	–	–
15	*Pelagosaurus typus*	NHMUK PV OR 32604	–	–	2.86	–	20.86	–	–	–	–	–	–	–	–
16	*Thalattosuchus superciliosus*	SMNS 10116	105.86	17.13	20.80	30.11	39.50	8.44	20.22	38.72	–	–	92.67	9.82	48.79
17	*Thalattosuchus superciliosus*	PMU 35988	93.16	11.62	24.74	20.92	42.15	–	14.68	–	42.88	–	69.81	9.27	45.80
18	*Thalattosuchus superciliosus*	NHMUK PV R 1530	94.82	21.77	36.09	35.59	56.52	7.69	24.15	29.66	34.78	14.27	66.69	12.22	33.12
19	*Thalattosuchus superciliosus*	GLAHM V960	89.68	14.90	25.60	27.96	43.14	9.73	17.47	28.78	31.88	10.37	64.31	9.05	31.31
20	*Thalattosuchus superciliosus*	GLAHM V1005	105.57	17.95	35.44	32.81	52.90	9.26	18.39	32.82	38.03	10.79	72.86	10.30	35.90
21	*Thalattosuchus superciliosus*	NHMUK PV R 2054	108.64	14.00	28.15	35.44	49.00	8.22	20.54	45.27	31.28	12.93	83.93	12.21	47.06
22	*Cricosaurus albersdoerferi*	BMMS-BK 1-2	–	–	17.61	39.46	50.30	–	–	–	–	–	–	–	–
23	*Cricosaurus bambergensis*	NKMB-P-Watt14/274	36.17	6.22	12.23	15.83	23.34	–	9.69	12.59	–	5.44	–	–	–
24	*Cricosaurus araucanensis*	MLP 72-II-27-6	69.50	14.10	20.40	–	37.80	–	12.40	23.90	–	7.50	50.60	8.54	23.10
25	*Metriorhynchus brachyrhynchus*	NHMUK PV R 3804	129.03	25.69	46.01	40.13	57.70	12.32	24.90	40.69	45.46	–	80.33	14.88	49.00
26	*Metriorhynchus brachyrhynchus*	NHMUK PV R 4763	–	–	–	–	–	10.28	18.26	29.37	26.49	8.55	–	–	–
27	*Suchodus durobrivensis*	NHMUK PV R 2618	74.03	14.08	23.50	10.86	37.84	6.36	13.74	24.70	19.79	–	46.61	8.42	26.67
28	*Geosaurus giganteus*	NHMUK PV R 1230	43.74	8.37	4.18	27.37	19.55	–	11.22	13.61	16.25	6.38	31.77	4.61	13.81
29	*Dakosaurus maximus*	SMNS 8203	169.00	42.57	49.96	–	–	14.54	26.69	51.52	56.19	–	–	–	–
30	*Aeolodon priscus*	NHMUK PV R 1086	–	–	–	–	–	–	–	–	–	–	–	–	–
31	*Mycterosuchus nasutus*	NHMUK PV R 2617	–	–	57.17	–	82.29	–	–	–	–	–	–	–	–
32	*Teleosaurus sp.*	OUMNH.J1638	143.15	17.10	46.74	–	56.85	–	27.18	48.97	–	12.20	–	–	–
33	*Platysuchus multiscrobiculatus*	SMNS9930	94.24	12.05	8.60	24.38	43.22	–	15.70	32.64	–	–	74.39	9.26	49.85
34	*Macrospondylus bollensis*	SMNS 17484a	97.05	16.99	17.25	27.57	41.14	–	–	23.23	–	–	68.01	6.20	47.18
35	*Macrospondylus bollensis*	SMNS 9428	75.07	15.65	–	–	–	–	12.25	21.12	–	–	–	–	–
36	*Macrospondylus bollensis*	PMU 35980	129.82	23.25	35.21	26.08	54.95	–	30.40	–	58.78	–	90.14	15.94	51.85
37	*Macrospondylus bollensis*	NHMUK PV R 5703	135.73	20.72	20.15	35.89	49.91	–	27.39	44.12	38.70	10.13	100.08	14.91	47.36
38	*Steneosaurus bollensis*	SMNS 9427	131.23	16.93	24.71	33.72	48.66	10.36	24.34	44.20	39.68	–	96.03	16.09	61.00
39	*Charitomenosuchus leedsi*	NHMUK PV R 3806	128.74	22.31	42.05	46.38	67.03	8.31	18.36	35.39	41.83	12.39	85.42	8.50	37.97
40	*Neosteneosaurus edwardsi*	NHMUK PV R 3701	129.07	18.98	32.94	39.67	60.33	11.34	23.02	38.15	41.24	10.62	96.53	12.88	47.32
41	*Neosteneosaurus edwardsi*	NHMUK PV R 2076	157.13	17.28	47.24	45.13	72.74	15.76	29.07	51.62	43.59	14.82	109.92	13.43	67.44
42	*Lemmysuchus obtusidens*	NHMUK PV R 3168	178.00	26.33	60.16	61.29	100.11	–	–	39.40	65.29	–	110.00	17.06	66.67
43	*Machimosaurus hugii*	SMNS 81608	–	–	51.50	21.97	68.00	–	–	45.62	36.43	–	95.28	9.40	56.42

THALATTOSUCHUS SUPERCILIOSUS (BLAINVILLE *IN* EUDES-DESLONGCHAMPS & BLAINVILLE, 1852)

For measurements, see Tables 7-9.

Ilium

The ilium of *Thalattosuchus superciliosus* (Figs 13; 14) resembles those of other metriorhynchids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, *Cricosaurus suevicus*, etc.) due to the absence of a postacetabular process. In this way, it differs from that of teleosauroids (e.g. *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Mycterosuchus nasutus* (Andrews 1909) Andrews, 1913, *Neosteneosaurus edwardsi*, etc.).

The ilium of *Thalattosuchus superciliosus* (Figs 13; 14) displays an overall triangular appearance. There appears to be at least two morphotypes of *Thalattosuchus superciliosus*: one notably portrayed by the specimens NHMUK PV R 2054, GLAHM V1146 and presumably GLAHM V1005 (the 'de Blainville' morphotype), and the other exemplified by SMNS 10116, NMI F21731, and NHMUK PV R 1530 (the 'Leeds' morphotype). This list is not exhaustive. Overall, the ilium of the 'de Blainville' morphotype has relatively smoother posterior and dorsal margins with a proportionally longer preacetabular process, whose apex is thicker and blunt. On the contrary, the ilium of the 'Leeds' morphotype has a more broader-stocky appearance with irregular dorsal and posterior margins due to enlarged sacral rib attachment sites, and its preacetabular process is thin and sharp. In addition, the lateral facet of the pubic peduncle of the 'Leeds' morphotype is relatively more extended dorsally than in 'de Blainville' morphotype.

The preacetabular process of *Thalattosuchus superciliosus* NHMUK PV R 2054 is well-developed with its anteroposterior length almost reaching that of the pubic peduncle, unlike those of *Thalattosuchus superciliosus* SMNS 10116, *Thalattosuchus superciliosus* NMI F21731, *Suchodus durobrivensis*, and also *Geosaurus giganteus*. However, the preacetabular process of all specimens of *Thalattosuchus superciliosus* are proportionally shorter anteroposteriorly than that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. Still, the preacetabular process of *Thalattosuchus superciliosus* NHMUK PV R 2054 is relatively thicker dorsoventrally than those of *Thalattosuchus superciliosus* SMNS 10116, *Thalattosuchus superciliosus* NMI F21731, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Suchodus durobrivensis* (Fig. 28). The preacetabular process of *Thalattosuchus superciliosus* NHMUK PV R 2054 displays almost entirely parallel dorsal and ventral margins, further differing from *Thalattosuchus superciliosus* SMNS 10116, *Thalattosuchus superciliosus* NMI F21731, and also *Suchodus durobrivensis* which display convergent margins at the apex. Consequently, the apex of the preacetabular process of *Thalattosuchus superciliosus* NHMUK PV R 2054 appears blunt and slightly rounded. At the junction between the preacetabular process and the anterior margin of the bone, the ventral border of the preacetabular hook begins to curve, participating in the posterior widening of the process in all specimens of *Thalattosuchus superciliosus*. The base of the preacetabular process represents one of the mediolaterally thickest points of the bone for all *Thalattosuchus superciliosus* specimens (Fig. 14).

The anterior margin of the ilium of NHMUK PV R 2054 and SMNS 10116 underneath the preacetabular process is slightly convex throughout its length, whereas that of NMI F21731 displays a hollow directly above the junction between the anterior margin and the pubic peduncle which appear slightly prominent (Figs 13; 14). Indeed, the pubic peduncle of NMI F21731 appears to form a more protruding bulge than those of NHMUK PV R 2054 and SMNS 10116 which are so weakly bulging that it is almost unnoticeable. In this way, NMI F21731 resembles the dyrosaurid ilia (i.e. *Congosaurus bequaerti* or *Hyposaurus natator*). The pubic peduncle of *Thalattosuchus superciliosus* (Figs 13; 14) is anteroposteriorly shorter than the ischial peduncle, unlike *Suchodus durobrivensis* and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 (for which both are relatively equal). The ventral surface of NHMUK PV R 2054 appears to be slightly concave as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, whereas SMNS 10116 and NMI F21731 display a relatively flat to subtlety convex surface as in *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, and *Tyrannoneustes lythrodectikos*. The ventral margin of the pubic peduncle of *Thalattosuchus superciliosus* is separated from that of the ischial peduncle by a small indentation – the acetabular perforation – whereas the articular facets of both peduncles form a continuum laterally. In NMI F21731, the dorsal border of the pubic peduncle is also proportionally more stretched out dorsally compared to the other *Thalattosuchus superciliosus* specimens (i.e. NHMUK PV R 2054 and SMNS 10116) and other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Geosaurus giganteus*, *Tyrannoneustes lythrodectikos*, *Cricosaurus araucanensis*, etc.). The outline of the lateral facet is not consistent across the different *Thalattosuchus superciliosus* specimens, with NHMUK PV R 2054 displaying a single triangular peak (shifted towards the acetabular perforation) whereas SMNS 10116 and NMI F21731 possess two distinct peaks of differing size and shape (Figs 13; 14).

The ischial peduncle of *Thalattosuchus superciliosus* (Figs 13; 14) is overall similar to that of other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Dakosaurus maximus*, etc.): its outline is triangular (dorsally oriented apex) and its posterior half protrudes laterally to form the posterior border of the bony acetabulum. The ventral surface of the ischial peduncle is slightly concave. It is also marked with deep scars indicating the iliac suture with the ischium.

The bony acetabulum is bordered by two protruding processes: the ischial peduncle posteriorly and the supraacetabular crest dorsally. The latter forms an arched ridge ventral to the preacetabular process. The surface of the supraacetabular crest is deeply scarred in NHMUK PV R 2054 and NMI F21731 (Figs 13; 14). In NMI F21731, the supraacetabular crest strongly impacts the shape of the anterior margin of the ilium, whereas in NHMUK PV R 2054 and SMNS 10116

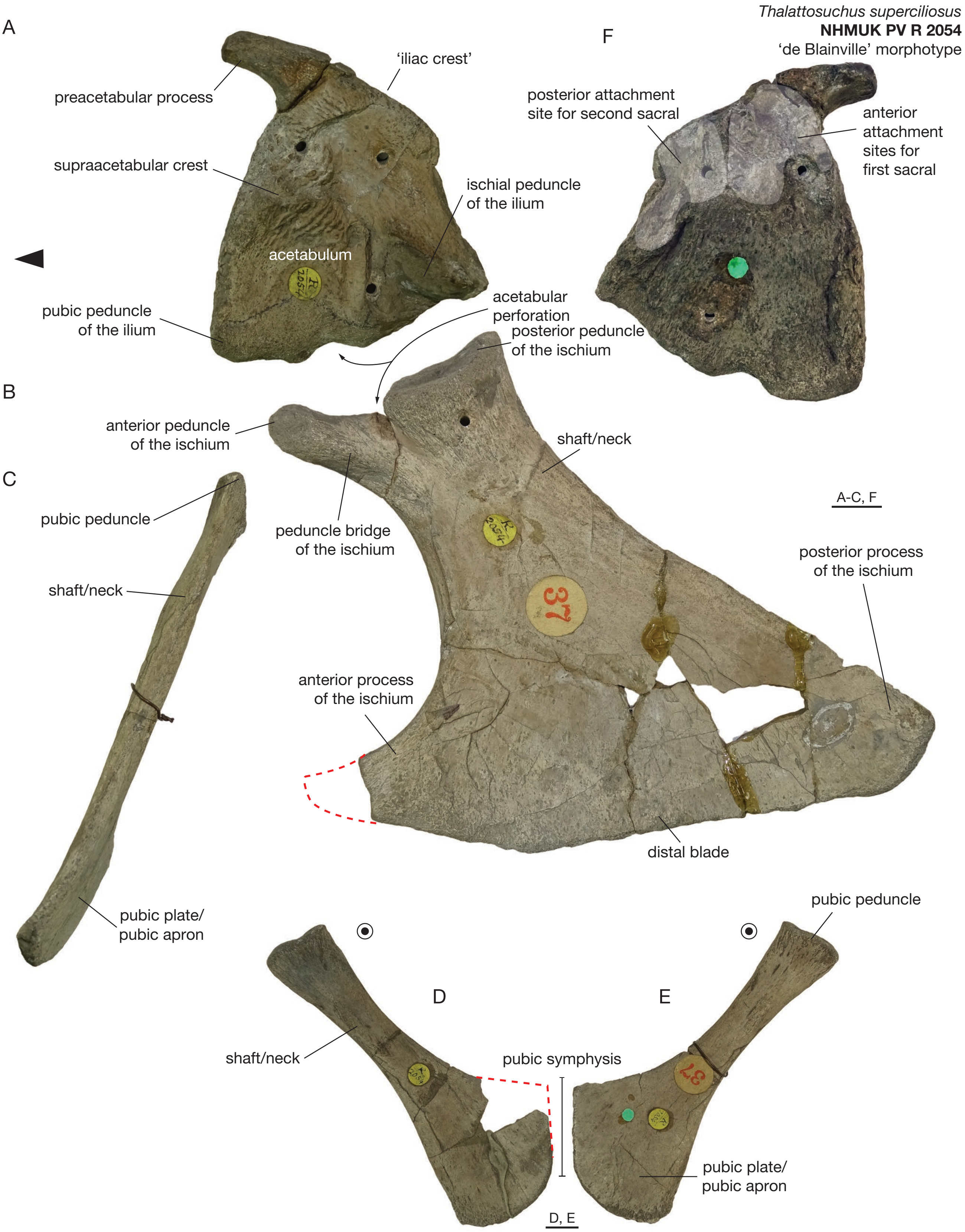


Fig. 13. — Pelvic girdle elements of *Thalattosuchus superciliosus* (Blainville, 1853), NHMUK PV R 2054: **A**, left ilium in lateral view; **B**, left ischium in lateral view; **C**, left pubis in lateral view; **D**, right pubis in anterior view; **E**, left pubis in anterior view; **F**, left ilium in medial view. Target indicates anterior. Arrow points anteriorly. Scale bars: 1 cm.

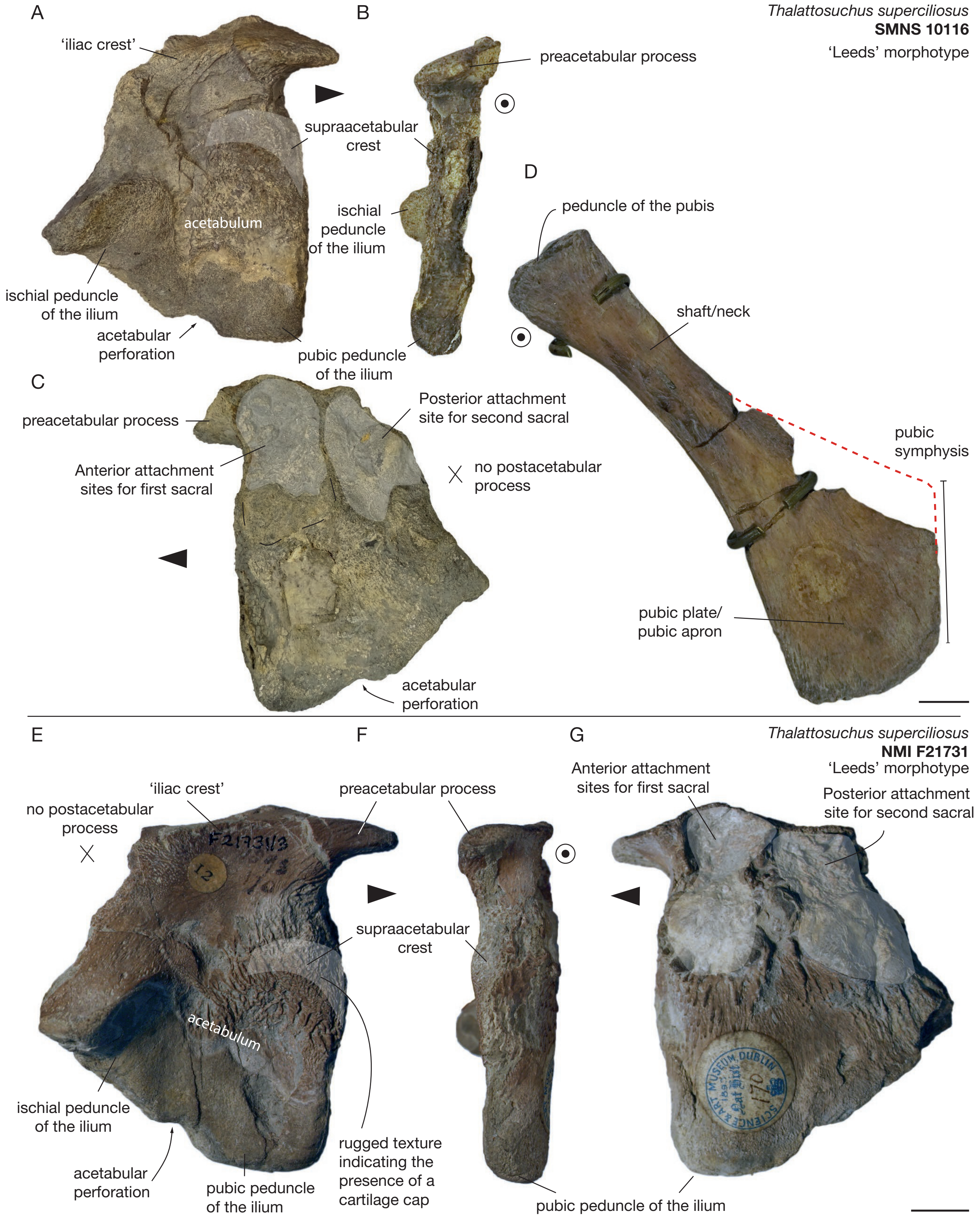


FIG. 14. — Right ilia and pubis of *Thalattosuchus superciliosus* (Blainville, 1853), SMNS 10116 (**A**-**D**) and NMI F21731 (**E**-**G**): **A**, **E**, right ilium in lateral view; **B**, **F**, right ilium in anterior view; **C**, **G**, right ilium in medial view; **D**, right pubis in anterior view. Target indicates anterior. Arrow points anteriorly. Scale bars: 1 cm.

it only forms a subtle bulge. In all specimens, the supraacetabular crest extends posteriorly as far as the dorsal peak of the ischial peduncle.

The posterior margin of the ilium is markedly concave in all *Thalattosuchus superciliosus* specimens (Figs 13; 14). This feature is found in some other metriorhynchoids, such as *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos* and *Geosaurus giganteus*. In comparison, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 possesses a relatively straight posterior margin. The junction between the posterior margin and the dorsal margin is achieved through a posteriorly emerging corner in *Thalattosuchus superciliosus*, similar to *Suchodus durobrivensis*. In NHMUK PV R 2054 and SMNS 10116 (Figs 13; 14), the dorsal margin of the ilium up until the base of the preacetabular process is relatively straight, whereas that of NMI F21731 is markedly concave. Still, the shape of the dorsal margin of SMNS 10116 is disturbed at about its mid-length by a portion of the posterior sacral rib attachment site (on the medial side of the bone) which sticks out dorsally (and hence can be seen in lateral view). In NHMUK PV R 2054 and NMI F21731, the sacral rib attachment sites for the sacrals do not exceed dorsally over the margins of the bone and thus can only be seen medially. There is a small bump marking the intersection between the dorsal margin of the ilium and the base of the preacetabular process in the NHMUK PV R 2054, whereas this junction is more angular in NMI F21731 and SMNS 10116 (Figs 13; 14). The intersection between the dorsal margin of the ilium and the base of the preacetabular process actually corresponds to the dorsal-most portion of the anterior attachment site on the medial side of the bone. The latter more or less influences the shape of the junction, depending on the lateromedial inclination of the dorsal surface of the preacetabular process (see differences between SMNS 10116 and NMI F21731 on Fig. 14).

The attachment sites of the sacral ribs are visible on the medial side of the ilium. They are easily identifiable as shallow impressions and are individually surrounded by a ridge. In this way, they differ from the sacral rib attachment sites of *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. NMI F21731 has more pronounced indentations, and it is the only one possessing tall ridges directly ventral to the sacral rib attachment sites. The position of both imprints are identical in all *Thalattosuchus superciliosus* specimens (Figs 13; 14), and are located near the dorsal border of the ilium similar to other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, *Cricosaurus araucanensis*, etc.). However the outline of each imprint is variable: in NMI F21731 both imprints are bilobate, whereas in SMNS 10116 and NHMUK PV R 2054 the sacral rib attachment sites are more bowed. Both attachment sites are relatively the same size, with some subtle variations across the specimens: in NHMUK PV R 2054 the anterior one is bigger, in SMNS 10116 both seem equal, and in NMI F21731 the posterior one is greater.

Ischium

The ischium of *Thalattosuchus superciliosus* (Fig. 13) displays the typical thalattosuchian triangular shape (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*) due to a well-developed distal blade. The general outline of the ischium shows a strongly concave anterior margin culminating ventrally into a pointed process, an almost flat ventral margin joined to another almost flat posterior margin through a bevelled corner. In GLAHM V1005, the posterior margin of the ischium is not flat but slightly bulged. The ischium of the 'de Blainville' morphotype displays a relatively slender shaft and proportionally longer peduncle bridge compared to the 'Leeds' morphotype. In the 'Leeds' morphotype, the anterior peduncle also seems dorsoventrally thicker.

As in other thalattosuchians, the anterior peduncle is slightly taller dorsally than the posterior one, and is also located further away from the shaft. Indeed, the junction between the anterior peduncle and the shaft of the ischium is achieved through an elongated bony structure called the peduncle bridge. Proportionally, the peduncle bridge of *Thalattosuchus superciliosus* displays a considerable length (longer than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus suevicus*, or *Lemmysuchus obtusidens*, resulting in a more anteriorly projected anterior peduncle. The dorsal surface of the peduncle bridge is slightly concave throughout as it forms the ventral border of the acetabular perforation. Mediolaterally, the peduncle bridge is thinning down towards its base whereas it flares out dorsoventrally in the same direction. In *Thalattosuchus superciliosus*, the acetabular perforation does not appear to form a deep indentation on the medial surface of the ischium which results in both the lateral and medial surfaces of the peduncle bridge appearing similar. This feature contrasts with the more pronounced acetabular perforation of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 *Cricosaurus araucanensis*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, and *Neosteneosaurus edwardsi*.

Similar to other metriorhynchoids, the anterior peduncle is reduced in size and extension and is ovoid in shape (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus suevicus*, *Torvoneustes carpenteri*, etc.) *contra* teleosauroids (e.g. *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, etc.). The anterior peduncle is pitted over almost its entire surface conveying the presence of an extensive cartilage cap *in vivo* (presumably connecting with the ilium and pubis as in extant crocodylians; Claessens & Vickaryous [2012]; Tsai & Holliday [2015]). The anterior peduncle of *Thalattosuchus superciliosus* does not appear to have contacted the ilium (Fig. 15), but was situated directly ventrally to the posterior bump of the pubic peduncle of the ilium, thereby circling the acetabular perforation.

The posterior peduncle of *Thalattosuchus superciliosus* NHMUK PV R 2054 (Fig. 13) is anteroposteriorly longer and mediolaterally wider than the anterior peduncle, as in other thalattosuchians. Dorsally its articular surface is sepa-

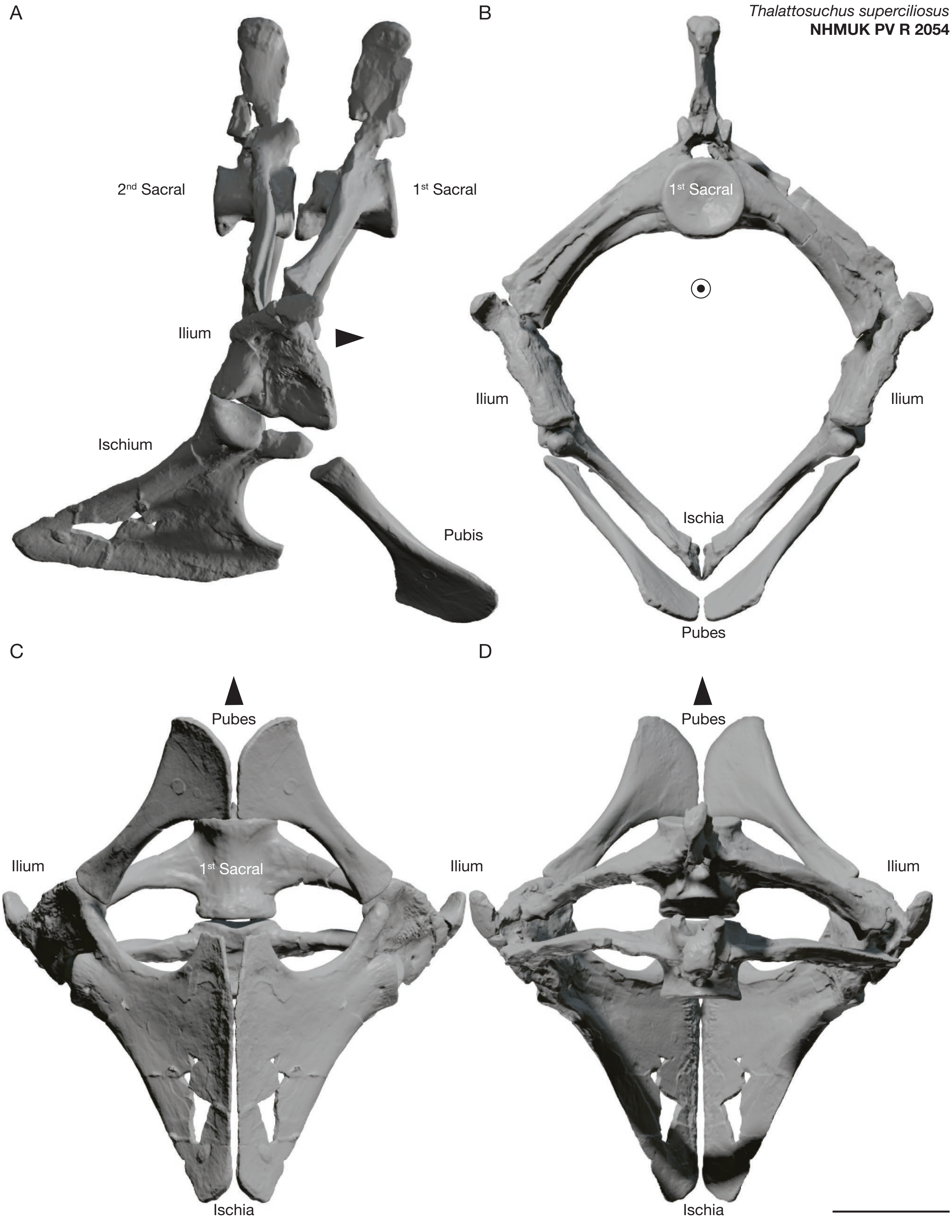


Fig. 15. — Pelvic girdle of *Thalattosuchus superciliosus* (Blainville, 1853), NHMUK PV R 2054: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Target indicates anterior. Arrow points anteriorly. The right ilium, ischium and pubis are mirrored. Scale bar: 5 cm.

rated in two distinct areas: the facet medially oriented which is highly scarred as it was fused with the ilium, and the facet laterally oriented which is smooth and concave. The latter is also the largest and formed the ventral border of the bony acetabulum. The junction between the two areas forms a thick ridge. In dorsal view, the overall outline of the posterior peduncle resembles an ellipse but with an anteriorly flat portion, which borders the acetabular perforation posteriorly. The posterior peduncle is low-built and does not significantly stick out from the shaft of the ischium (unlike the anterior one).

Directly underneath the peduncle is the shaft (or neck) of the ischium (Fig. 13). This portion forms the junction between the distal blade and the peduncle. The neck of the ischium is markedly larger anteroposteriorly than the posterior peduncle is as in *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, and *Torvoneustes carpenteri*. Comparatively, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Dakosaurus maximus* do not display such a difference between the length of the posterior peduncle and that of the shaft. The shaft gradually flares out ventrally to form the distal blade. The latter is well-developed as it constitutes most of the surface of the ischium. Still, like *Dakosaurus maximus* and *Torvoneustes carpenteri*, the distal blade of *Thalattosuchus superciliosus* is overall shorter than in *Pelagosaurus typus* and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763.

Anteriorly, the distal blade culminates in a sharp process whereas it forms a thicker extremity posteriorly, similar to other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*). The anterior process of the distal blade shows a dorsal component in its orientation due to a bend along the ventral margin of the ischium. This bend is located at about ⅓ of the length of the ventral margin anteriorly, and constitutes an angle of approximately 157°. The presence of a marked angle interrupting the otherwise flat surface of the ventral margin of the distal blade appears to be unique to *Thalattosuchus superciliosus* (Fig. 13). On the medial side of the bone, the ventral margin of the distal blade is scarred with deep ridges and sulci perpendicular to the border of the bone. The area is also bevelled medially, starting from the ventral corner of the distal process up until the peak of the anterior process. The entire bevelled and scarred surface corresponds to the suture where both ilia met *in vivo*. Posteriorly, the distal blade forms a posteroventrally facing bevelled corner, rather than a relatively squared one as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 or rounded one as in *Lemmysuchus obtusidens*. It also differs from the more pointed one of *Neosteneosaurus edwardsi*. From the top corner of the posterior process until the shaft, the posterior surface of the distal blade is relatively straight and constitutes the thinnest portion of the bone mediolaterally.

Pubis

There is no major differences observed between the two morphotypes based solely on the pubis. The pubis of *Thalattosuchus superciliosus* (Figs 13; 14) presents a proportionally long shaft along with a relatively quadrangular pubic plate. The lateral and medial margins of the bone present a similar degree of concavity, with their apex situated almost at the mid-height of the bone. The concavity of the margins results in a mediolaterally wide peduncle and pubic plate. The proximal widening of the peduncle is a common trait among Thalattosuchia (e.g. *Suchodus durobrivensis*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Geosaurus giganteus*, or *Lemmysuchus obtusidens*), even if some taxa lack it (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804). The peduncle of *Thalattosuchus superciliosus* shows a teardrop profile (whose great axis is parallel to that of the shaft), as well as an undulating articular surface whose lateral extremity is more elevated proximally than the medial one. Posteriorly, the margin of the articular surface of the peduncle drops slightly more than its counter part on the anterior surface of the bone.

The overall symmetry of the pubic plate contrasts with those of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Cricosaurus suevicus*, *Lemmysuchus obtusidens*, but resembles those of *Geosaurus giganteus*, *Hyposaurus natator* and *Dyrosaurus maghribensis* Jouve, Iarochène, Bouya & Amaghzaz, 2006. However, the shape is relatively different, as the angle between the ventral border of the pubic blade and the pubic symphysis is greater in *Thalattosuchus superciliosus* (about 120°, Figs 13; 14) than in dyrosaurids (about 90°), giving a quadrangular appearance to *Thalattosuchus superciliosus*. *Lemmysuchus obtusidens* also shows a great angle (of about 140°) between its pubic symphysis and ventral margin, but its pubis does not appear symmetrical due to a less convex ventral margin and its subsequent more distal intersection with the posterior margin.

Unlike '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Suchodus durobrivensis*, the length of the pubic symphysis of *Thalattosuchus superciliosus* is short in relation to the size of the pubic plate and the pubis as a whole. However, in *Thalattosuchus superciliosus*, the ventral margin of the pubic blade is longer than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Suchodus durobrivensis*, resulting in a less straight posterior margin and a proportionally mediolaterally wider pubic plate. Comparatively, rhacheosaurines and geosaurines possess the mediolaterally widest pubic blades and the shortest pubic diaphyses.

CRICOSAURUS ARAUCANENSIS (GASPARINI & DELLAPÉ, 1976)

For measurements, see Tables 7-9.

Ilium

The ilium of *Cricosaurus araucanensis* (Figs 16-18) stands out from that of other metriorhynchoids in displaying an almost isosceles triangular outline but with one side (corresponding to the dorsal border of the bone) disrupted by the shape of the sacral rib attachment sites. The latter form another distinctive trait of *Cricosaurus araucanensis* (and presumably other *Cricosaurus* Wagner, 1858 species: see *Cricosaurus albersdoerferi* and *Cricosaurus bambergensis*) as they strongly protrude from the medial surface of the bone, hence impacting its outline in lateral view.

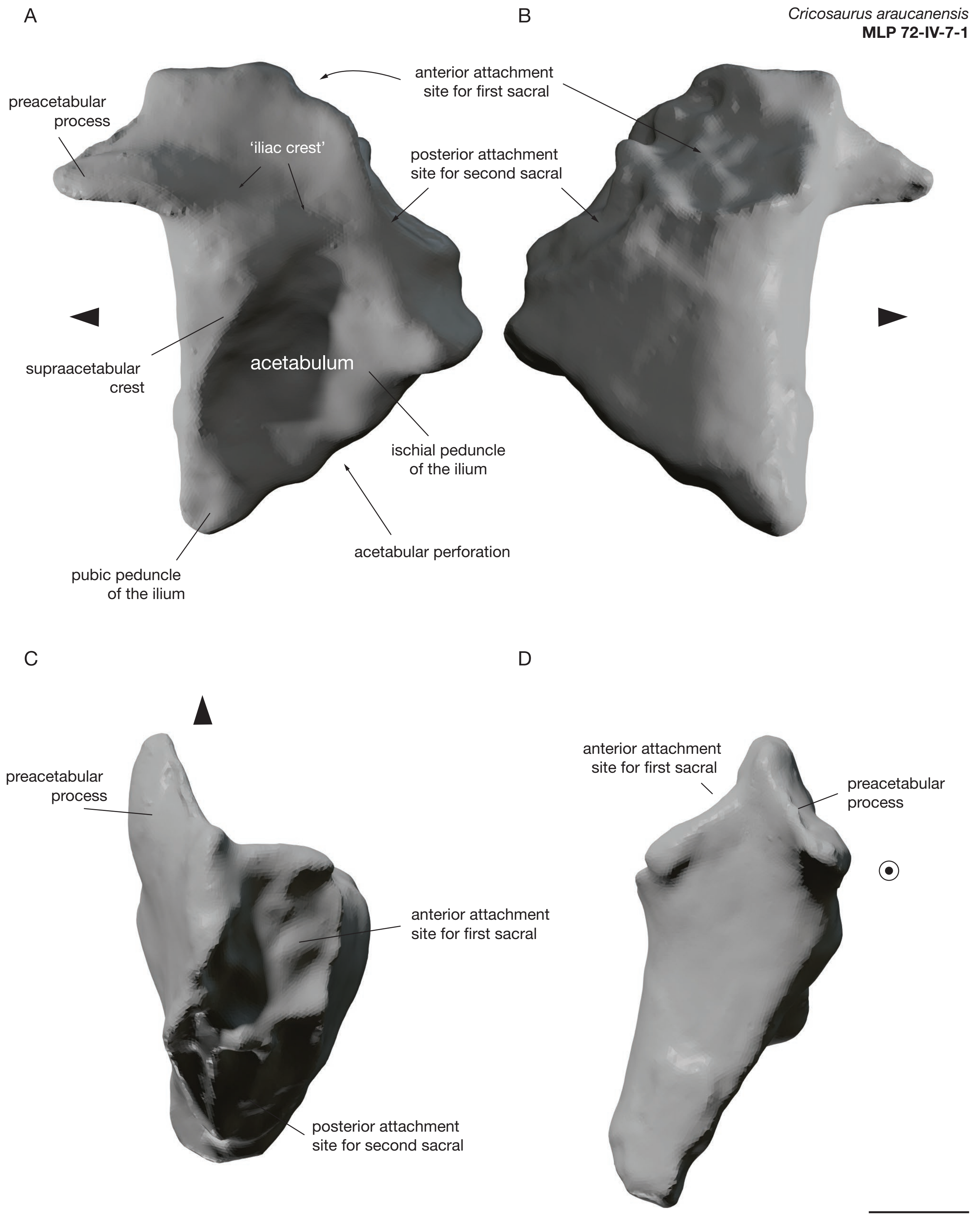


FIG. 16. — Left ilium of *Cricosaurus araucanensis* (Gasparini & Dellapé, 1976), MLP 72-IV-7-1 (holotype): **A**, lateral view; **B**, medial view; **C**, dorsal view; **D**, anterior view. Arrow points anteriorly. Target indicates anterior. 3D models of *Cricosaurus araucanensis* (MLP 72-IV-7-1), courtesy of Dr Yanina Herrera. Scale bar: 1 cm.

The preacetabular process of *Cricosaurus araucanensis* is anteroposteriorly long and dorsoventrally thin and accounts for about ⅓ of the total height of the bone dorsoventrally similar to *Cricosaurus suevicus*. It is possible that the tip of the preacetabular process of *Cricosaurus albersdoerferi* and *Cricosaurus bambergensis* is broken, which could explain their relatively smaller size. The preacetabular process of *Cricosaurus araucanensis* is in line with the iliac crest as in *Cricosaurus suevicus* and *Cricosaurus albersdoerferi*. However, in *Cricosaurus araucanensis* the dorsal margin of the bone and the iliac crest do not coincide as it is the case in most metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*,*Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Geosaurus giganteus*, etc.). Indeed, the iliac crest of *Cricosaurus araucanensis* corresponds to a hollow rather than a ridge due to the protruding attachment sites (Fig. 16). This posterior hollow forms a relatively straight line and culminates ventrally to form the posterior corner of the ischial peduncle.

The ischial peduncle laterally protrudes from the ilium to constitute the posterior border of the bony acetabulum. The lateral facet of the ischial peduncle of *Cricosaurus araucanensis* displays the typical triangular shape found in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Tyrannoneustes lythrodectikos*). The ventral surface of the ischial peduncle is wedge-shaped and slightly concave, similar to other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). Anteriorly, the ventral surface of the ischial peduncle transitions to the ventral surface of the pubic peduncle through a small indentation: the acetabular perforation. On the lateral surface of the ilium, the lateral facet of the ischial peduncle meets with that of the pubic peduncle without interruption. Comparatively, the lateral facet of the pubic peduncle is dorsoventrally shorter than that of the ischial peduncle similar to most thalattosuchians (with the exceptions of *Pelagosaurus typus* [Fig. 10] and *Neosteneosaurus edwardsi*). Ventrally, the articular surface of the pubic peduncle of *Cricosaurus araucanensis* is also wedge-shaped with its concavity laterally facing.

The medial side of the ilium bears the sacral rib attachment sites for the sacral ribs. Those are located along the dorsal margin of the ilium and strongly protrude dorsally, hence markedly impacting the outline of the bone in lateral view (Figs 16-18). Similar to other thalattosuchians, the sacral rib attachment sites of *Cricosaurus araucanensis* are adjacent and share a margin mesially (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). The sacral rib attachment sites of *Cricosaurus araucanensis* are in relief with their surrounding margin forming a bulge. Hence, the sacral rib attachment sites of *Cricosaurus araucanensis* appear to protrude from the surface of the ilium, in the way of a wax seal on an envelope. The outline of the sacral rib attachment sites of *Cricosaurus araucanensis* are bilobate with the biggest lobe positioned ventrally, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, and *Thalattosuchus superciliosus* NMI F21731.

Ischium

The ischium of *Cricosaurus araucanensis* (Fig. 17) displays a relatively thin shaft like other *Cricosaurus* species and is dorsoventrally longer than anteroposteriorly wide (e.g. *Cricosaurus suevicus* and *Cricosaurus bambergensis*). Moreover, the shaft of *Cricosaurus araucanensis* appears relatively small compared to the overall size of the bone due to the position of the maximal constriction of the shaft closer to the proximal peduncle than the mid-height of the bone, similar to *Dakosaurus maximus* and *Torvoneustes carpenteri* among metriorhynchoids. This effect is partly due to the large size of the posterior process of the ischium of *Cricosaurus araucanensis* which increases the overall size of the bone. Indeed, the dorsoventral height of the posterior process accounts for about half of the total proximodistal height of the bone as in *Dakosaurus maximus* and *Torvoneustes carpenteri*. Some other thalattosuchians display an enlarged posterior process but are found mainly among Teleosauroidea (e.g. *Aeolodon priscus*, *Sericodon jugleri*, *Lemmysuchus obtusidens*). Both the anterior and posterior margins of the ischium are concave, but with differing curvatures.

The exact shape of the posterior process of the ischium of *Cricosaurus araucanensis* is unknown due to a partially preserved posterior margin, but appears to have been more similar to *Torvoneustes carpenteri* than to other *Cricosaurus* species due to its large size (e.g. *Cricosaurus suevicus* and *Cricosaurus bambergensis*). Indeed, the posterior process of *Cricosaurus araucanensis* is as long anteroposteriorly as it is high dorsoventrally and thus contrasts with the more slender process of most metriorhynchoids (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus bambergensis*). Due to the relative breadth of the posterior process of the ischium of *Cricosaurus araucanensis*, it is plausible that the apex of the process was more rounded than sharp as in *Torvoneustes carpenteri* and *Lemmysuchus obtusidens*.

The ventral margin of the ischium of *Cricosaurus araucanensis* appears relatively straight, and extends anteriorly to form the anterior process. The anterior margin of the ischium is strongly concave, which contrasts with the posterior margin. The apex of the anterior process is not preserved but the hypothetical extensions of both the anterior and ventral margins result in a sharp and thin junction. Hence, the posterior and anterior process of the ischium of *Cricosaurus araucanensis* are strongly asymmetrical with the anterior process appearing overall reduced, not unlike *Dakosaurus maximus* and *Torvoneustes carpenteri*.

The anterior peduncle of the ischium of *Cricosaurus araucanensis* is located more dorsally (or proximally) than the posterior peduncle, similar to *Pelagosaurus typus*, *Thalat-*

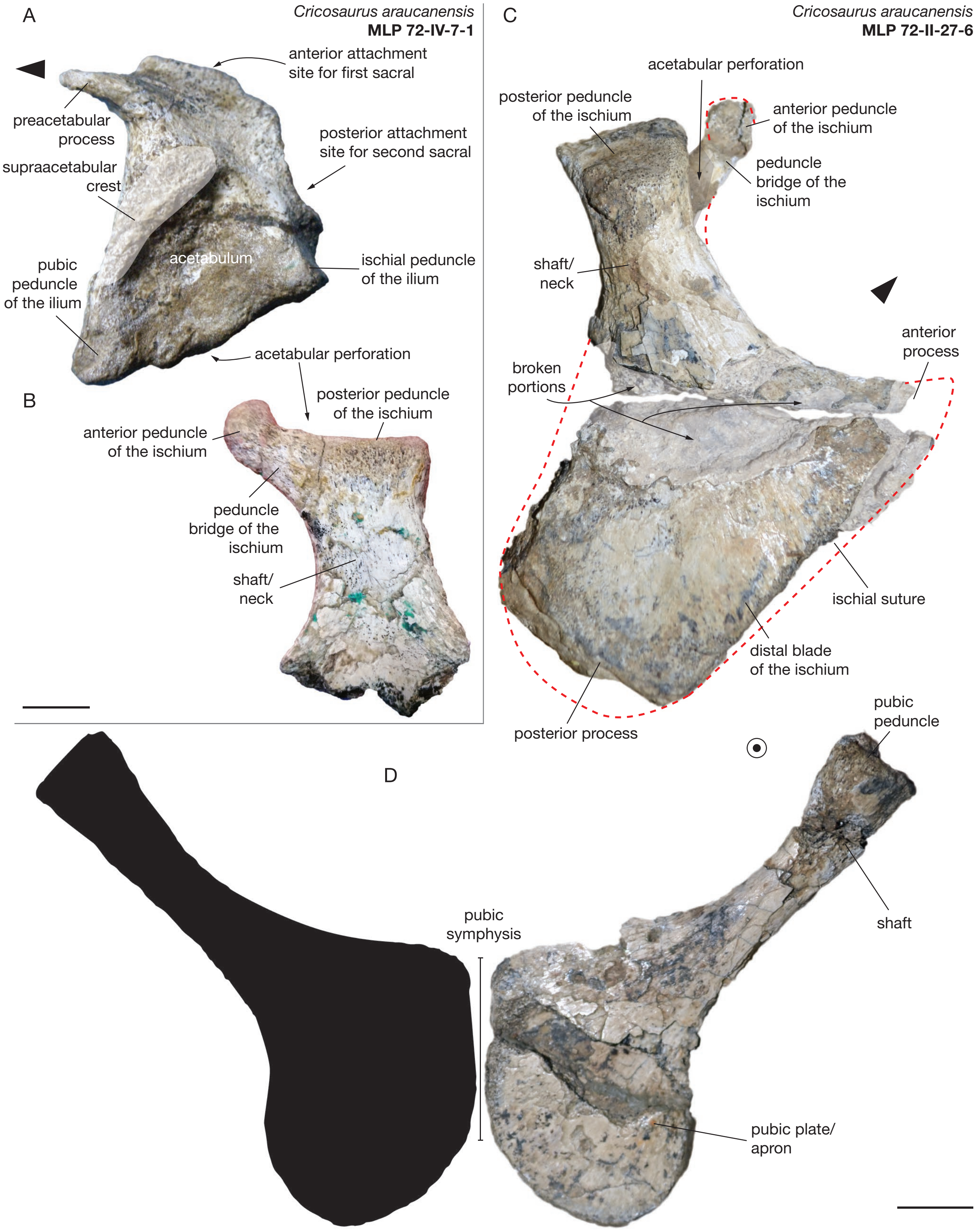


Fig. 17. — Left ilium of *Cricosaurus araucanensis* (Gasparini & Dellapé, 1976), MLP 72-IV-7-1 (holotype) and right ischium and left pubis of MLP 72-II-27-6 (referred): **A**, left ilium of MLP 72-IV-7-1 in lateral view; **B**, left ischium of MLP 72-IV-7-1 in lateral view; **C**, left ischium of MLP 72-II-27-6 in medial view; **D**, left pubis of MLP 72-II-27-6 in anterior view. Arrow points anteriorly. Target indicates anterior. Pictures of *Cricosaurus araucanensis* (MLP 72-IV-7-1 and MLP 72-II-27-6), courtesy of Dr Yanina Herrera. Scale bars: 1 cm.

tosuchus superciliosus NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Torvoneustes carpenteri*, and *Geosaurus giganteus*. Some teleosauroids also possess a laterally reduced acetabular perforation but their anterior peduncle moderately protrudes dorsally: *Aeolodon priscus*, *Proexochokefalos* cf. *bouchardi*, *Teleosaurus* sp. Geoffroy Saint-Hilaire, 1825, *Lemmysuchus obtusidens*, and *Neosteneosaurus edwardsi*. The anterior peduncle of *Cricosaurus araucanensis* displays an overall circular outline as in *Thalattosuchus superciliosus* NHMUK PV R 2054 but to a lesser extent. Indeed, the articular surface of the anterior peduncle of *Cricosaurus araucanensis* is greater than in *Thalattosuchus superciliosus* and other metriorhynchoids, resulting in the anterior peduncle being dorsoventrally thicker than the mid-section of the peduncle bridge. In addition, the anterior peduncle of *Cricosaurus araucanensis* is not entirely in line with the peduncle bridge so it does not point in the exact same direction; the anterior peduncle has a dorsal component in its orientation.

The peduncle bridge of the ischium of *Cricosaurus araucanensis* is relatively short and thick with its dorsal margin concave and its ventral margin convex as in other thalattosuchians. The peduncle bridge is connected to the shaft at the base of the posterior peduncle and thus obstructs the acetabular perforation laterally. For this reason, the posterior peduncle does not appear to protrude from the shaft at all which is similar to *Cricosaurus suevicus* and *Cricosaurus albersdoerferi* among metriorhynchoids. The base of the peduncle bridge is not centred on the bone but is shifted laterally, creating space medially. In addition, the peduncle bridge is curved medially to connect with the pubic peduncle of the ilium, creating additional space for the acetabular perforation.

The posterior peduncle of *Cricosaurus araucanensis* is anteroposteriorly and mediolaterally larger than the anterior peduncle as it connects to the ilium dorsally. The posterior peduncle is composed of two distinct articular facets dorsally: the medial one which connects to the ilium, and the lateral one which borders the acetabulum ventrally. The medial facet is wedge-shaped and is oriented mediodorsally. The surface of the lateral facet is slightly concave, displays a relatively quadrangular shape and is larger than the medial facet (about ⅔ of the total surface).

The acetabular perforation of the ischium of *Cricosaurus araucanensis* is greater than its counterpart on the ilium. As the peduncle bridge stems from the base of the posterior peduncle, the acetabular perforation appears nearly non-existent laterally. The medial curvature of the peduncle bridge leaves room for the acetabular perforation, which also creates a faint burrow on the medial side of the ischium at the base of the peduncle bridge. A similar configuration is found in other thalattosuchians displaying a reduced acetabular perforation laterally (e.g. '*Metriorhynchus*' *brachyrhynchus* 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Torvoneustes carpenteri*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Teleosaurus* sp., *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, etc.). However, the hollow left by the acetabular perforation on the medial side of the bone appears less pronounced in *Cricosaurus araucanensis*, presumably due to the length and dorsal extension of the peduncle bridge which creates a large opening between the bones (Fig. 18).

Pubis

The pubis of *Cricosaurus araucanensis* (Fig. 17) possess a relatively long and thin shaft as in other *Cricosaurus* (i.e. *Cricosaurus suevicus* and *Cricosaurus bambergensis*). Indeed, the maximum mediolateral constriction of the pubis marking the end of the shaft is located at about 36% of the total length of the pubis proximally. Comparatively, this value reaches around 40% in *Cricosaurus suevicus* and *Cricosaurus bambergensis*. Also, the mediolateral width at the constriction of the shaft of *Cricosaurus araucanensis* is lesser than that of the proximal peduncle. However, the latter does not account for about twice the length of the constriction, which differs from *Cricosaurus bambergensis* and *Cricosaurus suevicus* but to a lesser extent.

The pubis of *Cricosaurus araucanensis* (Fig. 17) drastically stands out from that of other *Cricosaurus* species in displaying a well-developed pubic symphysis and distal blade (i.e. *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Cricosaurus bambergensis*). Indeed, the length of the pubic symphysis of *Cricosaurus araucanensis* constitutes about 34% of the total proximodistal height of the pubis, whereas this number reaches about 30% for *Cricosaurus bambergensis* and this number is estimated to be even less for *Cricosaurus suevicus* and *Cricosaurus albersdoerferi* (Fig. 87). However, the pubic symphysis forms an angle of approximately 45° with the median of the shaft in both *Cricosaurus araucanensis* and *Cricosaurus bambergensis*. The junction between the pubic symphysis and the medial margin of the bone forms almost a right angle (about 100°), whereas the transition to the distal margin is achieved through an angle of approximately 144°.

The overall shape of the pubic apron of *Cricosaurus araucanensis* also differs from that of other thalattosuchians due to the shape of the distal blade. Indeed, the distal blade is strongly convex with a relatively long focal length resulting in an almost hemispherical outline. As a result, the apex of the distal blade is set further distally than the lateral corner assuring the junction between the distal blade and the lateral margin, similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Geosaurus giganteus*, and *Rhacheosaurus gracilis* among metriorhynchoids (Fig. 87). Comparatively, other *Cricosaurus* species show a more parabolic distal blade with the lateral corner being the more distal element (Fig. 87).

The medial margin of the pubis of *Cricosaurus araucanensis* is concave throughout whereas the lateral margin appears relatively straight for most of its length. The monotony of the lateral margin is ruptured around the mid-length of the pubis which marks the beginning of the mediolateral flaring of the pubic apron. From this point the lateral margin forms a sinusoidal wave and is first concave then convex distally. The sudden curvature of the lateral margin almost appears like a bent, and this feature is only found in *Cricosaurus suevicus* and *Cricosaurus albersdoerferi* among metriorhynchoids.

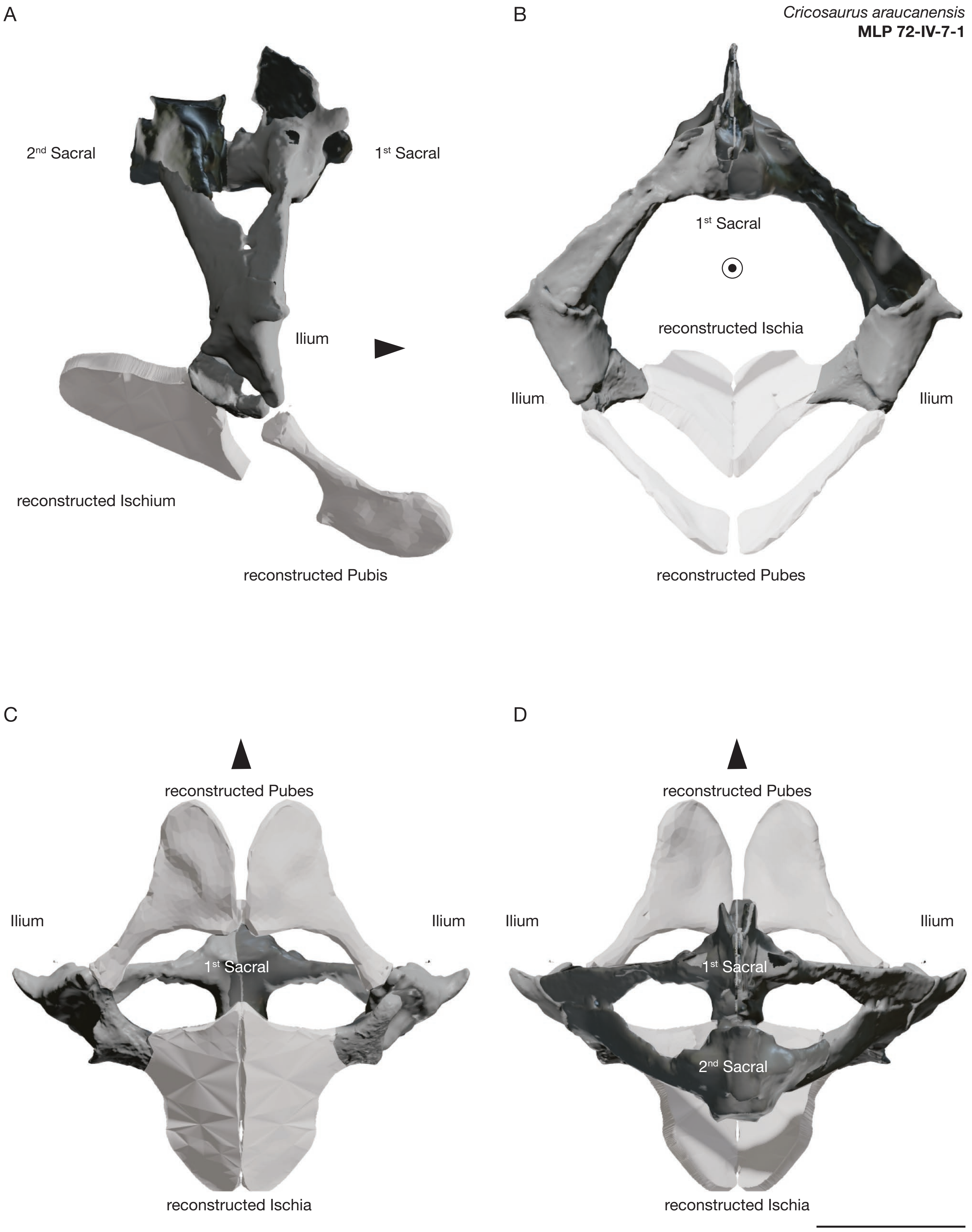


Fig. 18. — Pelvic reconstruction of *Cricosaurus araucanensis* (Gasparini & Dellapé, 1976), MLP 72-IV-7-1 (holotype): **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right ilium and right half of first sacral are mirrored. Distal blade of ischia are reconstructed from MLP 73-II-27-6 (Herrera *et al.* 2017). Pubes modified from *Palaeosuchus palpebrosus (*RVC-JRH-PP1), CT scan courtesy of Professor John Hutchinson. 3D models of *Cricosaurus araucanensis* (MLP 72-IV-7-1) courtesy of Dr Yanina Herrera. Reconstructed ischia and pubes only serve as a qualitative representation to better highlight the remains of *Cricosaurus araucanensis (*MLP 72-IV-7-1). Scale bar: 5 cm.

CRICOSAURUS SUEVICUS (FRAAS, 1901)

For measurements, see Tables 7-9.

Ilium

The ilium of *Cricosaurus suevicus* (Fig. 19) displays an overall triangular outline, similar to other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus albersdoerferi*, *Dakosaurus maximus*, *Geosaurus giganteus*). The orientation of the preacetabular process of *Cricosaurus suevicus* is almost in line with the dorsal margin of the ilium as in *Cricosaurus albersdoerferi*, but also '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* (NHMUK PV R 2054 and NMI F21731), or *Geosaurus giganteus*. The preacetabular process is welldeveloped as it reaches about the anteroposterior length of the pubic peduncle. Comparatively, among metriorhynchoids, the preacetabular process of *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Cricosaurus albersdoerferi* and *Geosaurus giganteus* are proportionally shorter than that of *Cricosaurus suevicus*, and only '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 exceeds its length. The preacetabular process of *Cricosaurus suevicus* is also stout with its consequent dorsoventral thickness. This trait is also recovered in *Cricosaurus albersdoerferi*, and to a lesser extent in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos* and *Thalattosuchus superciliosus* NHMUK PV R 2054. The mediolateral thickness of the preacetabular process appears to reach its climax towards its base; there the lateral surface of the ilium gradually sinks towards the centre of mass of the bone (where the acetabulum lies). This elevated area on the lateral side of the ilium underneath the preacetabular process corresponds to the supraacetabular crest. Like in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, etc.), the supraacetabular crest of *Cricosaurus suevicus* forms a thick prominent dome bordering the acetabulum dorsally.

The anterior margin of the ilium underneath the preacetabular process is relatively straight (notably due to a smooth transition between the anterior margin and the pubic peduncle), as in *Cricosaurus albersdoerferi*, *Suchodus durobrivensis*, *Dakosaurus maximus*, and *Geosaurus giganteus*. The junction between the anterior margin of the ilium and the pubic peduncle is smooth (like in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos* or *Geosaurus giganteus*) and does not form a bump nor a depression unlike in *Thalattosuchus superciliosus*.

The ventral margin of the ilium of *Cricosaurus suevicus* is undulating and hence marks the position of each peduncle. Similar to other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*), the dorsal border of the acetabular perforation is found underneath the second posterior half of the pubic peduncle, where the ventral margin of the ilium is concave. The articular surfaces of the peduncles form a continuum, which fills almost half of the height acetabulum dorsoventrally. The posterior-most portion of the ischial peduncle protrudes laterally in order to form the posterior border of the bony acetabulum and act as a physical obstacle. The ventral margin of the ischial peduncle is located more dorsally than that of the pubic peduncle, similar to other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Tyrannoneustes lythrodectikos*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, etc.). In *Cricosaurus suevicus* and *Cricosaurus albersdoerferi*, there is a smooth transition between the dorsal and posterior margins of the ilium, so that the entire surface extending from the tip of the preacetabular process up until the ischial peduncle appears convex.

Ischium

The ischium of *Cricosaurus suevicus* (Fig. 19) is similar to other thalattosuchians in possessing well-developed anterior and posterior processes (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus bambergensis*, *Dakosaurus maximus*, *Macrospondylus bollensis*, *Lemmysuchus obtusidens*, *Aeolodon priscus*, *Neosteneosaurus edwardsi*, *Teleosaurus* sp., *Proexochokefalos* cf. *bouchardi*, etc.).

In *Cricosaurus suevicus*, the anterior peduncle is smaller than the posterior peduncle but not as drastically as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Torvoneustes carpenteri*. Indeed, the dorsoventral height of the anterior peduncle reaches about half of the anteroposterior length of the posterior peduncle. Like in other metriorhynchoids, the anterior peduncle of *Cricosaurus suevicus* is ovoid in shape, and is located at the extremity of a relatively long peduncle bridge (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Geosaurus giganteus*, *Torvoneustes carpenteri*). Contrary to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Torvoneustes carpenteri*, and *Cricosaurus araucanensis*, the peduncle bridge of *Cricosaurus suevicus* is dorsoventrally as thick as the anterior peduncle, and its thickness remains constant throughout its length as in *Geosaurus giganteus*. This effect is imputable to the dorsal margin of the peduncle bridge which is concave and medially facing so that its lateral rim is situated more dorsally than the medial one, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus araucanensis*, and *Dakosaurus maximus*. Also, the peduncle bridge of *Cricosaurus suevicus* is not centred as its base is closer to the lateral side of the ischium. In addition, the peduncle bridge as a whole is curved towards the medial side of the ischium to contact the ilium medially.

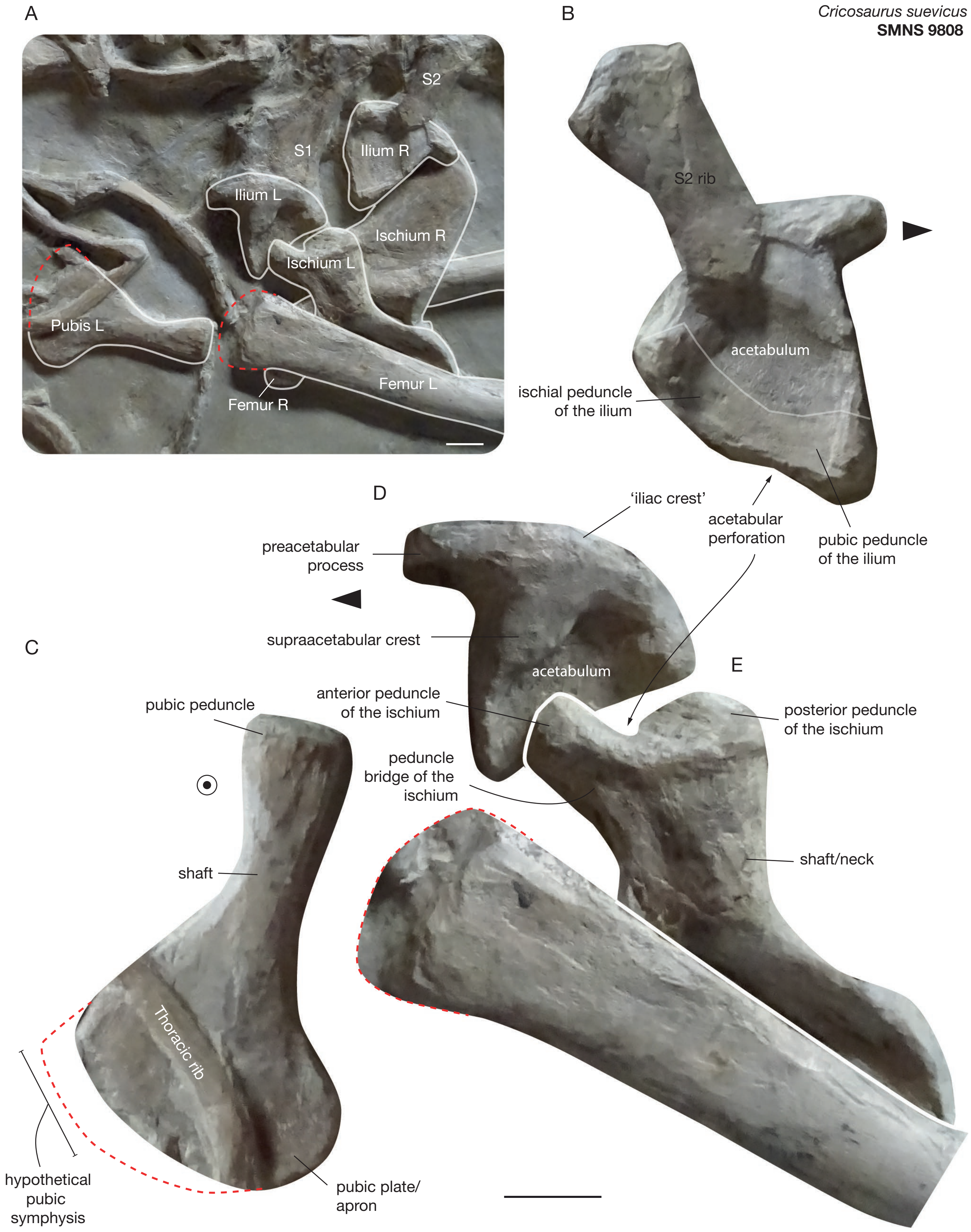


FIG. 19. — Pelvic girdle elements of *Cricosaurus suevicus* (Fraas, 1901), SMNS 9808 (lectotype); the left pelvic girdle elements are relatively complete, with only the femur missing the top of its proximal head (reconstructed in **red**): **A**, overview of the pelvic girdle; **B**, right ilium in lateral view; **C**, left pubis in anterior view; **D**, left ilium in lateral view; **E**, left ischium in lateral view. Target indicates anterior. Arrow points anteriorly. Scale bars: 1 cm.

The tilted dorsal surface of the peduncle bridge, coupled with its laterally position and medial curvature forms an opening for the acetabular perforation.

Similar to *Dakosaurus maximus*, *Cricosaurus araucanensis*, *Torvoneustes carpenteri* and *Cricosaurus albersdoerferi*, the posterior peduncle of *Cricosaurus suevicus* does not excessively protrude from the shaft of the ischium since its articular facet is located almost on the same level as the acetabular perforation, and as its dorsoventral length does not extend further posteriorly than that of the shaft (i.e. the dorsal margin of the ischium is relatively straight and perpendicular to the articular facet of the posterior peduncle). The articular facet of the posterior peduncle forming the ventral border of the bony acetabulum is slightly concave, however the other side connecting to the ilium is not recovered. The indentation for the acetabular perforation is shallow on the lateral side of the ischium.

The shaft of the ischium is located directly ventrally to the peduncles and is identifiable as the portion of the bone extending from the base of the peduncles up until the anteroposterior constriction of the bone (see Material and methods). The anterior and posterior margins of the ischium underneath the peduncles, which form the shaft, are both markedly concave as in *Cricosaurus bambergensis* and *Dakosaurus maximus*. Still, the shaft of *Cricosaurus suevicus* is proportionally thick since the anteroposterior length of this section exceeds that of the posterior peduncle (here by about ½), which is a trait found in other thalattosuchians regardless of the degree of concavity of the anterior and posterior margins (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Torvoneustes carpenteri*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, etc.).

In *Cricosaurus suevicus* the anterior process of the ischium is not recovered. In parallel, the shape of the posterior process of the left ischium of *Cricosaurus suevicus* is very characteristic: its dorsal margin is highly sinusoidal starting from its junction with the neck of the ischium, and its extremity is therefore thick and rounded. From what is preserved of the right ischium, it appears that the posterior process apex was elliptic as in *Lemmysuchus obtusidens* and *Torvoneustes carpenteri* (and presumably *Dakosaurus maximus*), with a relatively flat distal blade ventrally.

Pubis

The pubis of *Cricosaurus suevicus* (Fig. 19) is closer to that of extant crocodylians (e.g. *Caiman crocodilus* [Fig. 9] or *Mecistops cataphractus* [Fig. 8]) than to that of most thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.) in possessing a relatively reduced pubic symphysis and subsequent extended distal blade. This feature is found in other highly pelagic forms among Thalattosuchia, namely rhacheosaurines (e.g. *Cricosaurus albersdoerferi*, *Cricosaurus bambergensis*) and some geosaurines (e.g. *Geosaurus giganteus*). However, the species *Cricosaurus araucanensis* shows a larger pubic symphysis and thus differs from other *Cricosaurus* species. Overall, the pubis of *Cricosaurus suevicus* is large, especially in relation to the ilium as in *Cricosaurus albersdoerferi* and *Geosaurus giganteus* where the mediolateral breadth of the pubic plate exceed the anteroposterior length of the ilium.

The lateral and medial margin of the pubis of *Cricosaurus suevicus* are both strongly concave, but with differing intensity and position of their vertex. As a consequence, the shaft displays a rather undulating appearance with asymmetrical margins. Indeed, the medial portion of the shaft appears almost straight as it is subtlety concave, whereas the lateral margin is intensely titled towards the thinnest portion of the bone and the vertex of the lateral concavity. The asymmetrical appearance of the shaft is also recovered in the pubic peduncle whose centre is shifted laterally. In addition, the pubic peduncle is twice as large mediolaterally as the thinnest portion of the shaft is, as in *Geosaurus giganteus*, *Pelagosaurus typus* or *Macrospondylus bollensis*. *Suchodus durobrivensis* also displays a pubic peduncle larger than its shaft, but the difference is more subtle.

The substantial degree of concavity of the lateral and medial margins of the pubis encompass the important mediolateral enlargement of the pubic apron. The distal margin of the pubis of *Cricosaurus suevicus* – i.e. the distal blade – is convex with its vertex shifted medially, giving it a highly asymmetrical look. Thalattosuchian pubes are usually convex between the lateral margin and the pubic symphysis e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, etc.), but the relative shortness of the distal blade in some taxa presumably reduces the possibility of asymmetry. The junction between the distal blade and the medial margin of the pubis is achieved through a smooth round corner corresponding to the pubic symphysis.

CRICOSAURUS ALBERSDOERFERI (SACHS, YOUNG, ABEL & MALLISON, 2021)

For measurements, see Tables 7-9.

Ilium

The ilium of *Cricosaurus albersdoerferi* (Fig. 20) is overall triangular in shape due to a lack of postacetabular process, as that of other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Geosaurus giganteus*, etc.). In *Cricosaurus albersdoerferi*, the preacetabular process seems almost as dorsoventrally thick as it is anteroposteriorly long, giving it a short and stout aspect. Yet, it is possible that the preacetabular process has been flattened and thus shows both dorsal and lateral sides at once. Similar to *Cricosaurus suevicus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* (NHMUK PV R 2054 and NMI F21731), or *Geosaurus gigan-*

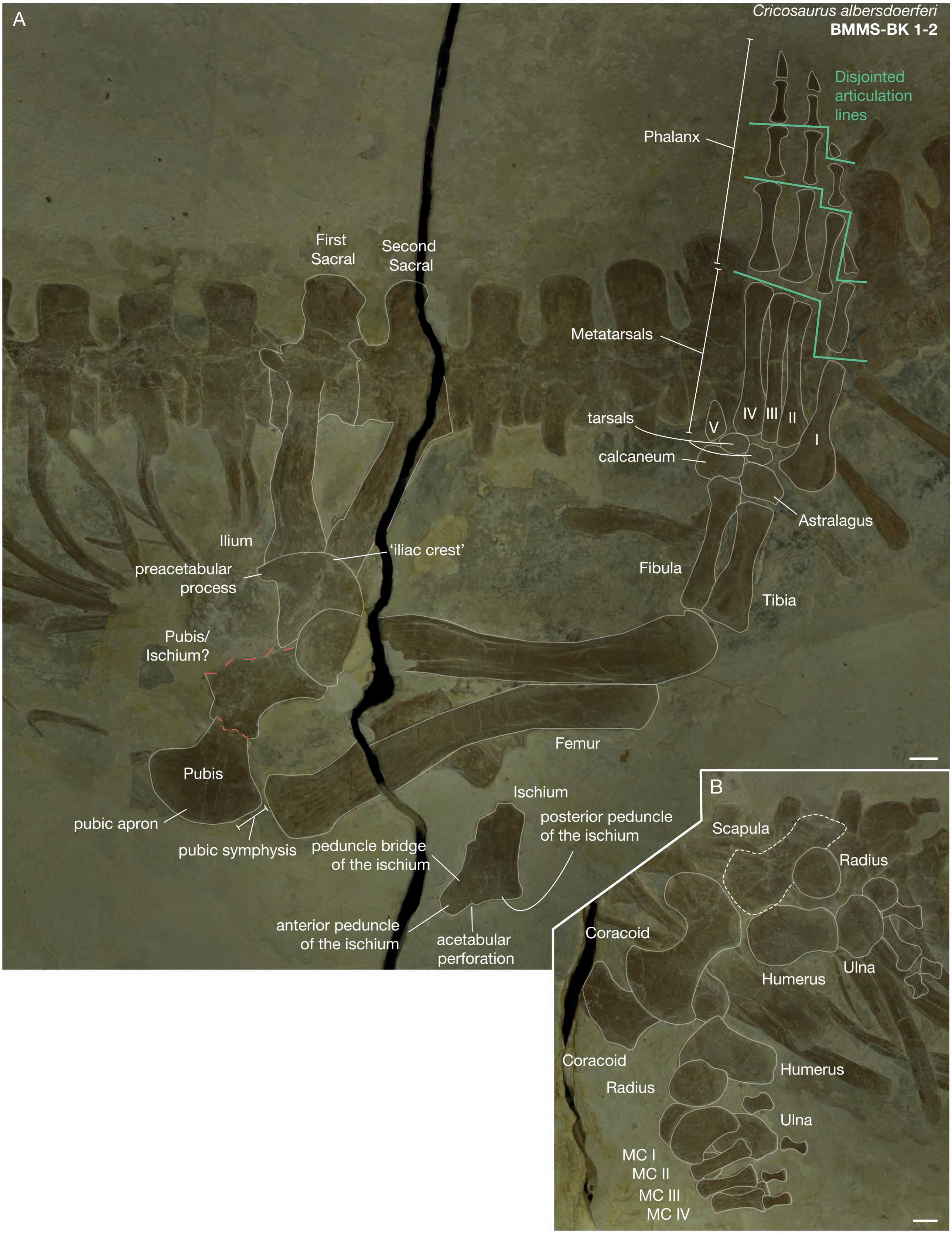


FIG. 20. — Pelvic and thoracic girdle elements of *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021) (Sachs *et al.* 2021), BMMS-BK 1-2 (holotype): **A**, pelvic girdle and hindlimb; **B**, thoracic girdle and forelimb. Modified from Sachs *et al.* (2021). Scale bars: 1 cm.

teus, *Tyrannoneustes lythrodectikos*, the preacetabular process of *Cricosaurus albersdoerferi* appears in line with the dorsal margin of the bone. Moreover, the preacetabular process of *Cricosaurus albersdoerferi* seems almost parallel to the ventral margin of the pubic peduncle, as in *Suchodus durobrivensis* or *Geosaurus giganteus*.

The anterior margin of the ilium of *Cricosaurus albersdoerferi* is slightly undulating underneath the preacetabular process: at about its mid height, the concavity of the anterior margin switches from concave dorsally to convex ventrally. Presumably, the sinusoidal shape of the bone along the anterior margin is caused by a faint supraacetabular crest as in *Dakosaurus maximus* and *Geosaurus giganteus*. The dorsal and posterior margins of the ilium of *Cricosaurus albersdoerferi* appear to for a smooth convex continuum almost hemispherical. *Cricosaurus suevicus* also shows a convex posterodorsal border but the shape is less harmonious.

Ischium

The ischium of *Cricosaurus albersdoerferi* (Fig. 20) shows the presence of a short and thick peduncle bridge, leading to a rounded anterior peduncle. The anteroposterior length of the peduncle bridge and anterior peduncle of *Cricosaurus albersdoerferi* is lesser than that of the posterior peduncle, unlike *Cricosaurus suevicus*. The anterior and posterior margins of the ischium of *Cricosaurus albersdoerferi* appear concave as in *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Torvoneustes carpenteri* and *Dakosaurus maximus*, but are not entirely preserved. Still, it seems that the shaft of *Cricosaurus albersdoerferi* is larger than the posterior peduncle, similar to many other thalattosuchians (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Torvoneustes carpenteri*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, etc.).

Pubis

The pubis of *Cricosaurus albersdoerferi* (Fig. 20) shows a relatively reduced pubic symphysis and a mediolaterally expanded pubic plate similar to other rhacheosaurines (e.g. *Cricosaurus suevicus*, *Cricosaurus bambergensis*). Hence, due to the reduction of the pubic symphysis, the distal margin of the pubic plate of *Cricosaurus albersdoerferi* is convex throughout. Like in *Cricosaurus suevicus*, the pubic apron of *Cricosaurus albersdoerferi* is not symmetrical compared to the shaft of the pubis, and is more expanded on the medial side of the bone. Compared to other *Cricosaurus* species, *Cricosaurus albersdoerferi* shows an abrupt and angular widening of the pubis rather than a smooth concave curve.

Cricosaurus bambergensis (Sachs, Young, Abel & Mallison, 2019)
For measurements, see Tables 7-9.

Ischium

Like other thalattosuchians, the ischium of *Cricosaurus bambergensis* (Fig. 21) possesses well-developed anterior and posterior processes (e.g. *Pelagosaurus typus*, ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, *Macrospondylus bollensis*, *Lemmysuchus obtusidens*). The anterior process is thinner than the posterior one but only slightly. Moreover, it does not appear sharp unlike for example in ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Dakosaurus maximus*, *Pelagosaurus typus*, *Torvoneustes carpenteri*, *Lemmysuchus obtusidens*, or *Macrospondylus bollensis*. The distal margin of the ischium of *Cricosaurus bambergensis* uniting both processes is straight as for many other thalattosuchians (e.g. *Pelagosaurus typus*, ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, etc.).

The anterior and posterior margins of the ischium of *Cricosaurus bambergensis* are markedly concave as in *Cricosaurus suevicus* and *Dakosaurus maximus*, *Torvoneustes carpenteri*, with the anterior margin displaying the greatest intensity. Dorsally, the anterior margin of the ischium leads to the anterior peduncle, which appears to be short and rounded as in other metriorhynchoids (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Torvoneustes carpenteri*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, etc.).

Pubis

The pubis of *Cricosaurus bambergensis* (Fig. 21) resembles those of other geosaurines and rhacheosaurines (i.e. *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, and *Geosaurus giganteus*) in possessing a relatively reduced pubic symphysis. However, it differs from *Geosaurus giganteus* in displaying a mediolaterally larger pubic apron (i.e. greater than twice the size of the pubic peduncle, as in other *Cricosaurus* species). The pubic blade of *Cricosaurus bambergensis* looks like an axe head as its distal margin is entirely convex, and as the margins leading to it are strongly concave (i.e. the anterior and posterior margins of the pubis). Still, the pubic apron of *Cricosaurus bambergensis* is slightly asymmetrical with its medial half being larger than the lateral one, not unlike other *Cricosaurus* species for which the effect was more pronounced (*Cricosaurus suevicus*, *Cricosaurus albersdoerferi*). In *Cricosaurus bambergensis*, the junction between the distal margin and the lateral margin is sharper than the opposite corner. Like *Cricosaurus suevicus*, *Dakosaurus maximus* , and *Geosaurus giganteus*, the thinnest portion of the shaft of *Cricosaurus bambergensis* is smaller mediolaterally than the pubic peduncle. The articular surface of the pubic peduncle of *Cricosaurus bambergensis* presents a slightly convex outline. Its extremities form rounded corners laterally and medially where they meets with the margins of the shaft.

‘*Metriorhynchus*’ *brachyrhynchus* (Eudes-Deslongchamps, 1867) NHMUK PV R 4763
For measurements, see Tables 7-9.

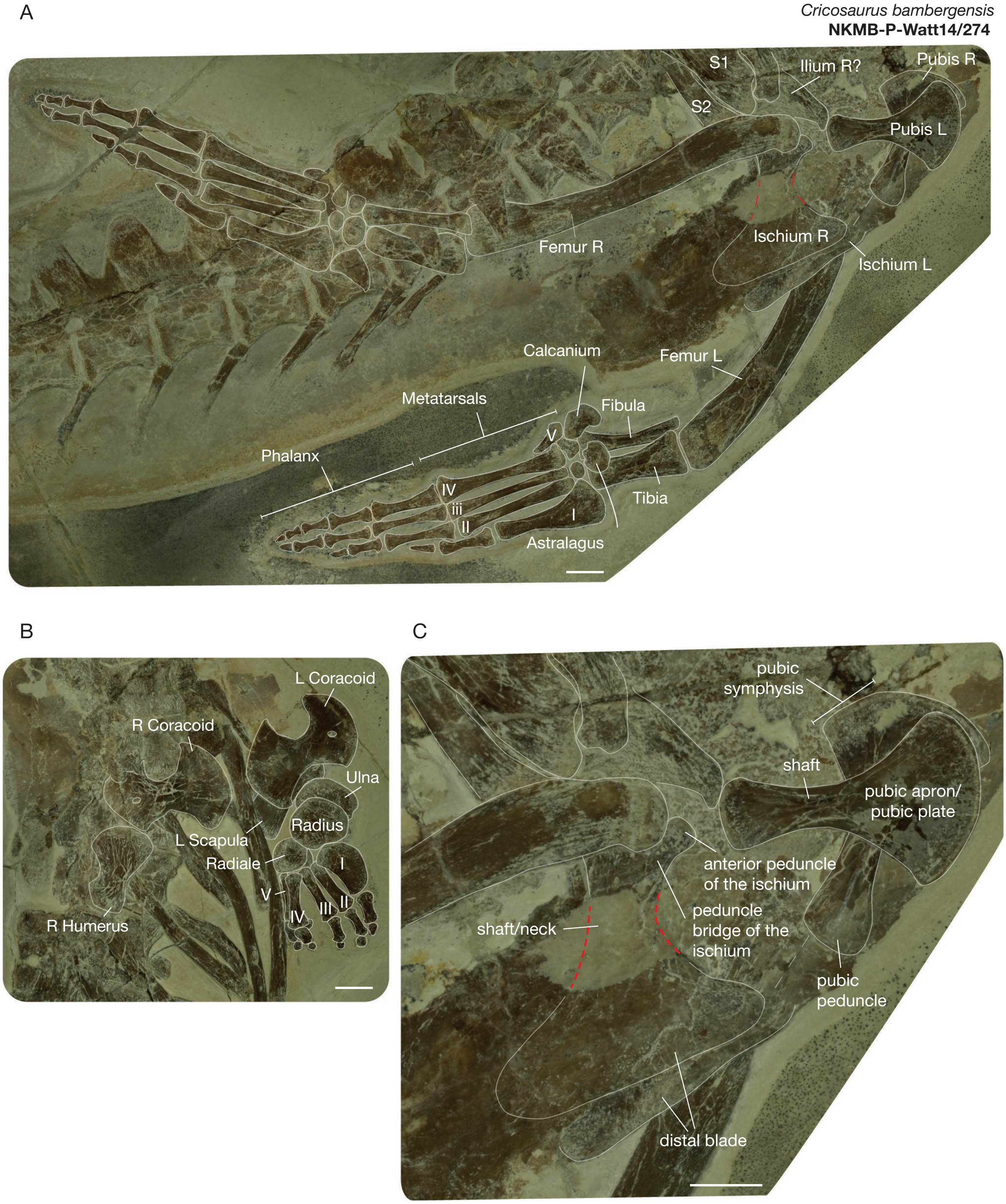


Fig. 21. — Pelvic and thoracic girdle elements of *Cricosaurus bambergensis* (Sachs, Young, Abel & Mallison, 2019) (Sachs *et al.* 2019), NKMB-P-Watt14/274 (holotype): **A**, overview of pelvic girdle and hindlimb; **B**, overview of thoracic girdle and forelimb; **C**, detail of pelvic girdle. Modified from Sachs *et al.* (2019). Scale bars: 1 cm.

Ilium

The ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 (Fig. 22) stands out from that of other metriorhynchoids in displaying an overall isosceles triangular shape, with its anterior and posterior margins almost equal in length with the ventral margin. Like for other derived metriorhynchoids, the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is strongly reduced and lacks a postacetabular process. However, the preacetabular process of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is well developed as it reaches about 59 % of the dorsoventral height and about 48 % of the anteroposterior length of the ilium at the peduncles (Fig. 22). Furthermore, the overall thin and elongated shape of the preacetabular process of NHMUK PV R 4763 is not found in other metriorhynchoids. The preactebular process of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is directly in line with the dorsal margin of the ilium similar to most metriorhynchoids except some *Thalattosuchus superciliosus* specimens (i.e. SMNS 10116 and NMI F21731). In '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, the dorsal margin of the ilium is extremely short (as opposed to that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804) and almost appears non-existent between the size of the posterior margin of the ilium and that of the preacetabular process. *Geosaurus giganteus* also possesses a short dorsal margin but the later is more pronounced due to the smaller inclination with the posterior margin. Indeed, in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 the junction between the dorsal and posterior margins of the ilium is obtained through an obtuse angle (about 140°), as in most metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus* NHMUK PV R 2054 but not SMNS 10116 and NMI F21731, *Cricosaurus araucanensis*, etc.). The posterior margin of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is only subtlety concave, as opposed to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, and *Suchodus durobrivensis*.

The ventral margin of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is strongly undulating and shows three successive recess areas: two marking the centre of each peduncle, and one for the acetabular perforation. The latter marks the transition between the peduncles ventrally but does not separate them on the lateral side of the ilium as in other derived metriorhynchoids. The acetabular perforation of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is more pronounced than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, and *Cricosaurus* species. However, it is less marked than in *Thalattosuchus superciliosus* or *Dakosaurus maximus*. The ischial peduncle of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is tall as it almost doubles the height of the pubic peduncle. Furthemore, the ischial peduncle strongly protrudes laterally and its articular facet is strongly concave with an important anterior orientation, which differs from other metriorhynchoids. The pubic peduncle of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is less concave than the posterior peduncle and its anterior edge follows the curve of the anterior margin, as in *Thalattosuchus superciliosus* NHMUK PV R 2054 and *Suchodus durobrivensis*. The outline of the pubic peduncle on the lateral surface of the ilium is wavy, similar to other metriorhynchoids. However, in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 the pubic peduncle forms a pointed summit where the supraacetabular crest starts, unlike in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, *Cricosaurus araucanensis*, *Thalattosuchus superciliosus* where they meet in a recess. The anterior margin of ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is gently convex throughout, as in *Thalattosuchus superciliosus* NHMUK PV R 2054, *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, or *Tyrannoneustes lythrodectikos*. The supraacetabular crest of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is slightly arched and rigidly follows the shape of the anterior margin, unlike in most metriorhynchoids where the supraacetabular crest differs from the anterior margin dorsally to curl up and/or form a wide rugged area (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Cricosaurus araucanensis*, etc.). The supraacetabular crest of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is also scarred along its surface indicating the existence of a cartilage cap *in vivo*. The bony acetabulum of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is bordered by the ischial peduncle posteriorly and the supraacetabular crest anteriorly and dorsally. It forms a relatively narrow (anteroposterioly) and mediolaterally deep recess compared to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804. The bony acetabulum of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 displays a rugged surface as in *Thalattosuchus superciliosus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, and *Suchodus durobrivensis* (where it is at least preserved). The whole acetabulum hollow of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 stretches up to 69% (22.6 mm) of the dorsal height and 45% (16.53 mm) of the anteroposterior length of the ilium

On the medial side of the ilium, the sacral rib attachment sites for both sacrals are borne towards the dorsal portion of the bone as in other derived metriorhynchoids. Each scar is composed of a round base and a slender but more deeply rugged dorsal portion extending from the round base to the dorsal margin of the ilium. The circular base is raised rather than imprinted, similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis* but unlike in *Thalattosuchus superciliosus*, *Cricosaurus araucanensis*, or *Dakosaurus maximus*. The overall shape of the sacral rib attachment sites of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 strongly differ from those of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, and *Suchodus durobrivensis* which are bilobate and less medially protruding.

Ischium

The ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 stands out from most metriorhynchoids in displaying a slender and tubular posterior process, culminating in a reactively thick and rounded apex. In comparison, *Pelagosaurus typus* (SMNS 17758) also shows a tubular poste-

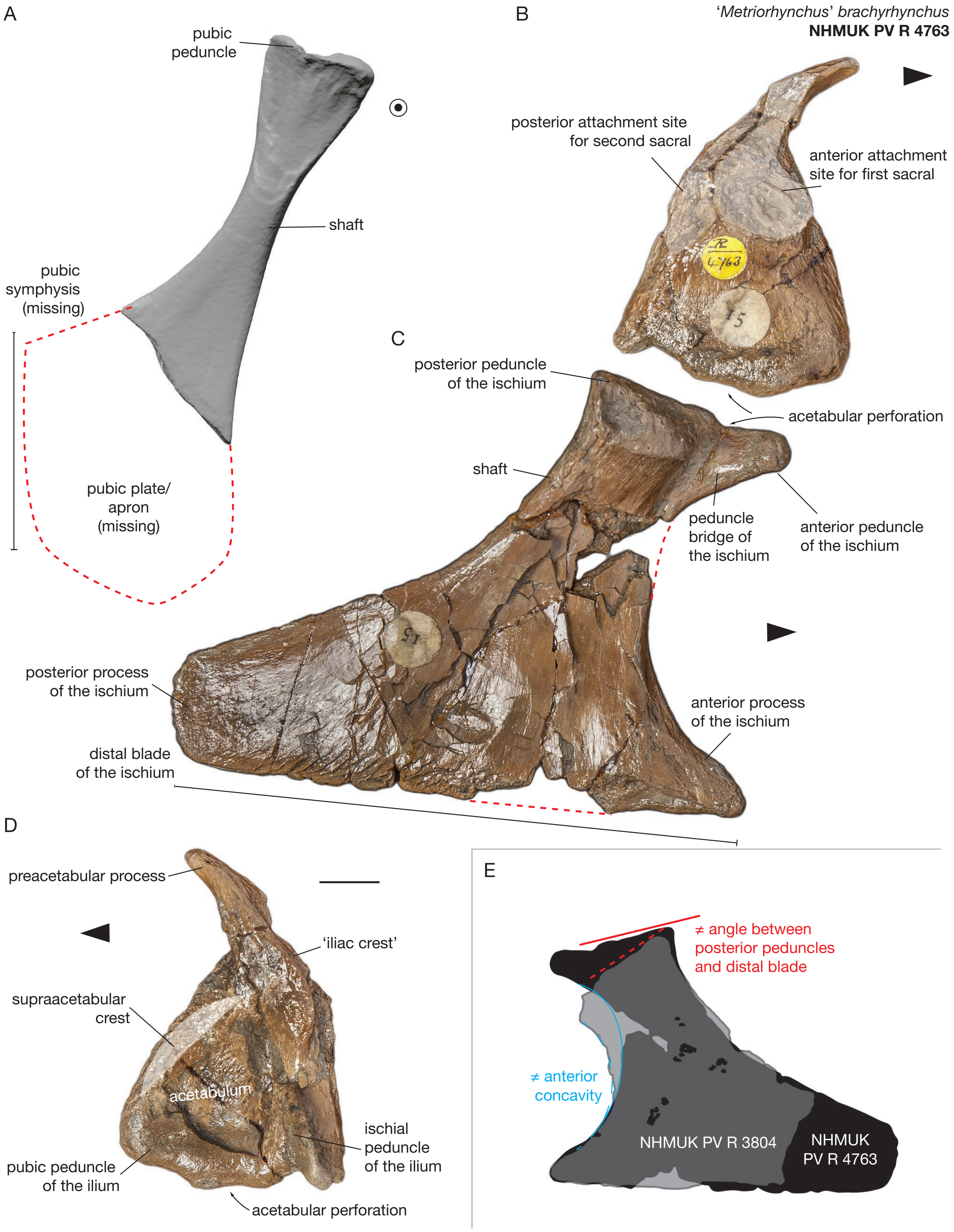


FIG. 22. — Pelvic girdle elements of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867), NHMUK PV R 4763: **A**, left pubis in anterior view (obtained from 3D model); **B**, left ilium in medial view; **C**, left ischium in medial view; **D**, left ilium in lateral view; **E**, superimposed outlines of the ischia of NHMUK PV R 4763 and NHMUK PV R 3804. Target indicates anterior. Arrow points anteriorly. Pictures of '*Metriorhynchus*' *brachyrhynchus,* NHMUK PV R 4763, copyright from The Trustees of the Natural History Museum. Scale bar: 1 cm.

rior process but the latter displays a thinner apex. The apex of the posterior process of the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 forms a squared end with rounded angles (Figs 22; 23), which is also seen in some teleosauroids (e.g. *Proexochokefalos* cf. *bouchardi* and *Charitomenosuchus leedsi*, and *Aeolodon priscus* MNHN.F.CNJ78 to a lesser extent). The posterior process corresponds to the thinnest portion of the ischium mediolaterally. The distal blade of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 appears relatively straight like most metriorhynchoids, which contrasts with *Thalattosuchus superciliosus* NHMUK PV R 2054. Anteriorly, the distal blade forms a sharp apex – the anterior process – whose dorsal margin is slightly curved (concave) like other metriorhynchoids. The anterior process of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is directly in line with the distal blade, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Dakosaurus maximus*, and *Torvoneustes carpenteri*. On the medial side, the distal blade bears a pitted or rugged texture over most of its length indicating the presence of a cartilage cap in *vivo* but also the area where both ischia were connected. Anteriorly, the pitted texture stops around the base of the anterior process and becomes smoother as in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, etc.). Posteriorly, the ischial suture stops at the base of the posterior process. Also, the surface of the ischial suture is not perpendicular to the lateral surface of the distal blade but rather protrudes to form an angle of approximately 45° with the latter, indicating that both ischia were presumably set at about 90° (Fig. 25D).

Proximally, the ischium bears two protuberances: the anterior and posterior peduncles (Figs 22; 25). The posterior peduncle of the ischium is the biggest of the two and its medial surface connects directly to the ilium. Comparatively, the lateral margin of the posterior peduncle is slightly longer anteroposteriorly than the medial one, and was part an attachment site for the hip cartilage (*cartilago acetabularis* [Cong *et al.* 1998]) which covered all portions involved the in acetabulum in *vivo* (Tsai & Holliday 2015). The proximal surface of the posterior peduncle is concave to form the ventral portion of the acetabulum, and is relatively close to the shaft of the ischium which differs from the protruding posterior peduncle of Dyrosauridae (e.g. *Acherontisuchus guajiraensis*). Oppositely, the anterior peduncle of the ischium is greatly protruding from the shaft of the ischium and from the posterior peduncle, thus creating an open space between the two peduncles called the acetabular perforation (Romer 1956). The anterior peduncle of the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 (about 26-28% of the length of the posterior peduncle) is greatly reduced in size compared to Dyrosauridae (*e.g Hyposaurus natator* NJSM 23368, *Dyrosaurus maghribensis* OCP DEK-GE 252 and 255) or Crocodylia (e.g. *Palaeosuchus palpebrosus* RVC-JRH-PP1 [Fig. 7]; *Mecistops cataphractus* [Fig. 8]; *Caiman crocodilus* [Fig. 9]). The anterior peduncle of metriorhynchoids is also reduced compared to that of teleosauroids as its mediolateral width is about the same size as its anteroposterior length (*contra Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, etc.).

The peduncle bridge of the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, which bears the anterior peduncle, stems from the lateral surface of the ischium and is thus decentred compared to the posterior peduncle. The base of the peduncle bridge is also directly connected to the base of the posterior peduncle, which is the reason why the acetabular perforation appears shallow when looking at the bone laterally (like in *Cricosaurus araucanensis*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, or several teleosauroids like *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, *Proexochokefalos* cf. *bouchardi*, *Teleosaurus* sp.). However, this imprint is scattered when looking at the medial side of the ischium as is other thalattosuchians. In addition, the peduncle bridge of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is strongly arched towards the medial side of the bone as to bring the anterior peduncle directly underneath the pubic peduncle of the ilium, similar to *Cricosaurus araucanensis*, and *Cricosaurus suevicus* among metriorhynchoids. The dorsal surface of the peduncle bridge, forming the ventral margin of the acetabular perforation, is strongly concave and medially tilted. Hence, the acetabular perforation of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 actually forms a relatively deep hollow which is tilted towards the sagittal plane (medially-bound). The combination of the curvature of the peduncle bridge along with its dorsal concavity creates a relatively large opening for the acetabular perforation, which counterbalances the fact that the position of the peduncle bridge laterally obstruct the canal. In '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and other thalattosuchians (e.g. *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, etc.), most of the acetabular perforation is actually constituted by the ischium (as it is greatly reduced on the ilium). Comparatively, the acetabular perforation of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is downsized in relation to extant crocodylians (e.g. *Mecistops cataphractus*) and dyrosaurids (e.g. *Acherontisuchus guajiraensis*), and was likely covered by a membrane. Hence, the dorsal or medial portion of the peduncle bridge of the ischium was presumably the attachment site for one of the intrinsic ligaments, the anterior portion of the *Ligamentum capitis femoris*.

The anterior and posterior peduncles of the ischium emerge from the shaft of the ischium, which constitutes the shortest portion of the bone anteroposteriorly. This constriction flares out distally to form the distal blade: its posterior and anterior surfaces are both concave, with the posterior surface displaying a greater radius of curvature. In NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*), NHMUK PV R 4763, LEICT G.418.1956.13.5 and LEICT G.418.1956.13.6 all display differing radius of curvature for the anterior concavity, leading to differences in the angle between the posterior peduncle to the distal blade, and in the width of the neck constriction.

There is a difference between the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and '*Metriorhynchus*'

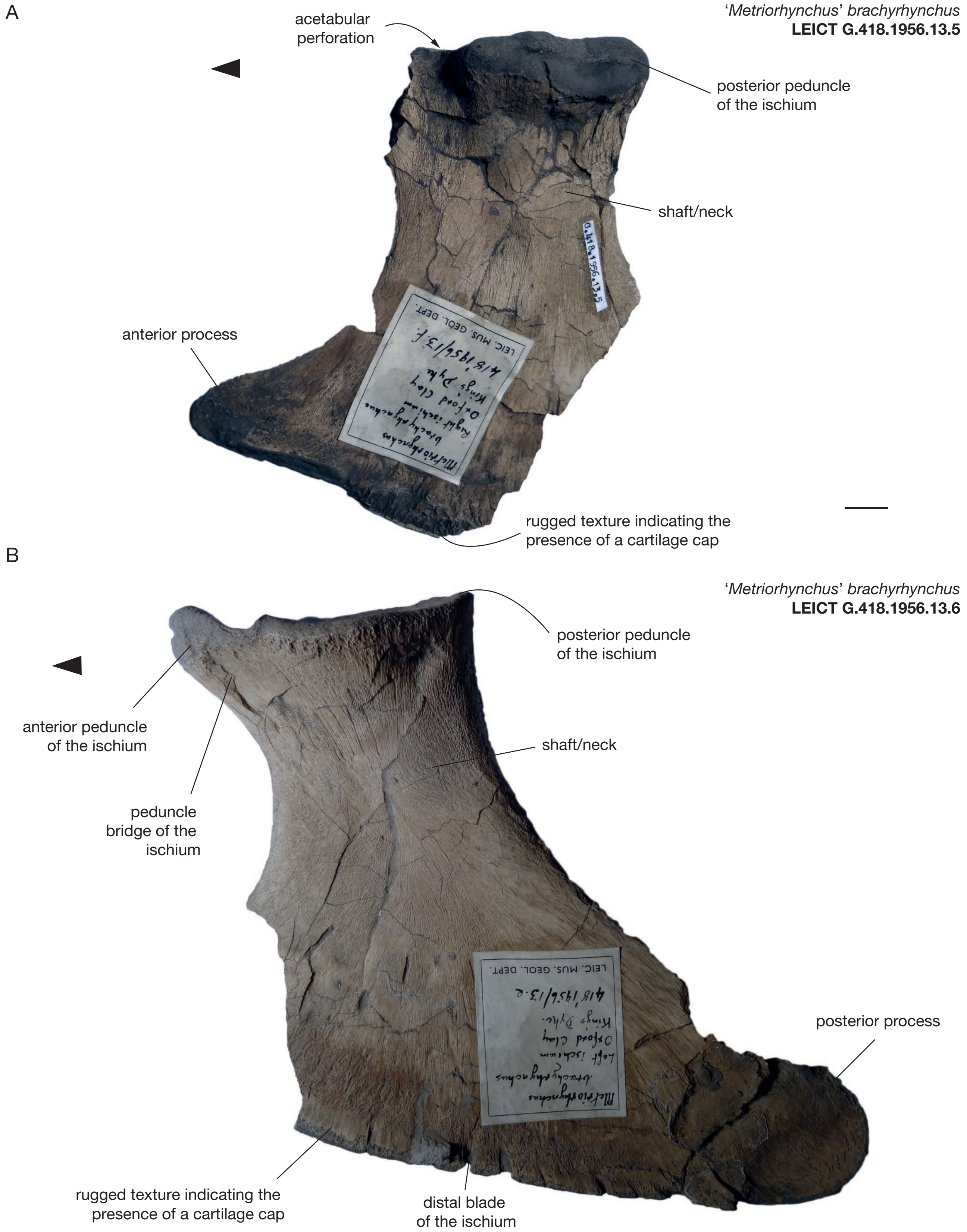


FIG. 23. — Ischium of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867) (skull identified by Dr Mark Young on 19th September 2012, as stipulated in the records): **A**, LEICT G.418.1956.13.5, right ischium in medial view; **B**, LEICT G.418.1956.13.6, left ischium in lateral view. Arrow points anteriorly. Scale bar: 1 cm.

brachyrhynchus NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*; see Figs 22, 24 and Young *et al.* [2010, 2013] for taxonomic affiliation), where the former displays a slender ischial neck compared to the latter. Indeed, when both are resized (Fig. 5) the NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*) appears shorter and thicker: its neck is longer anteroposteriorly and its anterior concavity is characterized by a shorter radius of curvature. Moreover, the two specimens are also distinguishable based on the inclination of the proximal surface of the posterior peduncle with the distal margin of the distal blade: NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*) displays a greater angle with the distal blade than NHMUK PV R 4763 does, while both exhibit the same height between the distal blade and the posterior-most portion of the posterior peduncle. The ischium of LEICT G.418.1956.13.6 (Fig. 23) appears more similar to NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*), but unfortunately comparisons cannot be taken further as the only shared bone of the pelvic girdle between the three specimens is the ischium. The distinct differences of '*Metriorhynchus*' *brachyrhynchus* (NHMUK PV R 4763 and NHMUK PV R 3804 holotype of '*Metriorhynchus*' *cultridens*, Fig. 24), and LEICT G.418.1956.13.6 (Fig. 23), could presumably be attributed to intraspecific variation as both have been attributed to the same species (Young *et al.* 2010; 2011b; 2012; 2020a, b). Sexual dimorphism could hypothetically explain such differences, as a change in size and shape of the ischium (specifically the length between its posterior peduncle and its distal blade) would directly affect the dimensions of the abdominal cavity. This view supports the conclusions of Herrera *et al.* (2017) with metriorhynchids being viviparous.

Pubis

The pubis of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 (Fig. 22) strongly differs from that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 in displaying a stronger shaft constriction along with more pronounced proximal and distal flaring. Indeed, the medial and lateral margins of the pubis of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 are both symmetrically markedly concave as opposed to the less incurvated margins of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804. In addition, the mediolateral constriction of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 reaches less than ⅓ of the total shaft length whereas the constriction of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 corresponds almost to half of the shaft length.

The proximal peduncle of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is mediolaterally large as it accounts for twice the mediolateral thickness of the shaft constriction. Compared to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, the peduncle of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 is not dorsoventrally twisted in relation to the shaft so that its greatest axis lies parallel to that of the shaft. Distally, the pubic apron of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 apperas to markedly flare out but it is missing its extremity. The overall shape of the shaft and peduncle of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 superficially resembles that of *Suchodus durobrivensis* among Thalattosuchia.

'*METRIORHYNCHUS*' *BRACHYRHYNCHUS* (EUDES-DESLONGCHAMPS, 1867) NHMUK PV R 3804

For measurements, see Tables 7-9.

Ilium

The ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 (Fig. 24) bear the typical metriorhynchoid characteristics, which are an overall small size in relation to the other pelvic bones, and the absence of a postacetabular process. The preacetabular process of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 is short but lateromedially thick and points anterodorsally (forms an angle of approximately 36° with the ventral margin of the ischial peduncle) rather than strictly anteriorly like extant crocodylians (e.g. *Crocodylus niloticus* NMW 31137) and dyrosaurids (e.g. *Congosaurus bequaerti* MRAC 1806). This difference in inclination of the preacetabular process can be attributed to the different way the ilium is borne by the sacrals: the ilium of thalattosuchians is rather tilted in relation to the coronal plane (e.g. Herrera *et al.* 2017) compared to extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) or dyrosaurids (*Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*). The preacetabular process of NMH PV R 3804 strongly differs from that of NHMUK PV R 4763, and resembles those of *Suchodus durobrivensis*, *Thalattosuchus superciliosus* and more specifically *Tyrannoneustes lythrodectikos*.

The anterior margin of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 underneath the preacetabular process is convex, and meets distally with the pubic peduncle of the ilium. The dorsal margin is globally reduced as the anterior and posterior margins almost directly connect with the large base of the preacetabular process (Fig. 24). The junction between the dorsal and posterior margins is achieved through an obtuse and rounded corner, similar to those of *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos* and *Thalattosuchus superciliosus* NHMUK PV R 2054. The posterior margin of the ilium is concave and ends distally to form the posterior corner of the ischial peduncle of the ischium. The ventral margin of the ilium is slightly undulated: it bears the pubic peduncle of the ilium anteriorly, and the ischial peduncle of the ischium posteriorly. The undulation of the ventral margin of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 is more subtle than that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 or *Thalattosuchus superciliosus*, and closely resembles that of *Tyrannoneustes lythrodectikos* and *Suchodus durobrivensis*. The ischial peduncle represents the region where the ilium is the thickest mediolaterally. Comparatively, the ischial peduncle is subtlety longer dorsoventrally than the pubic peduncle, so that both peduncles appear to have the same height. Like in other metriorhynchoids, the ischial peduncle takes the shape of an isosceles triangle whose orientation is both lateral and anterior. The outline of the

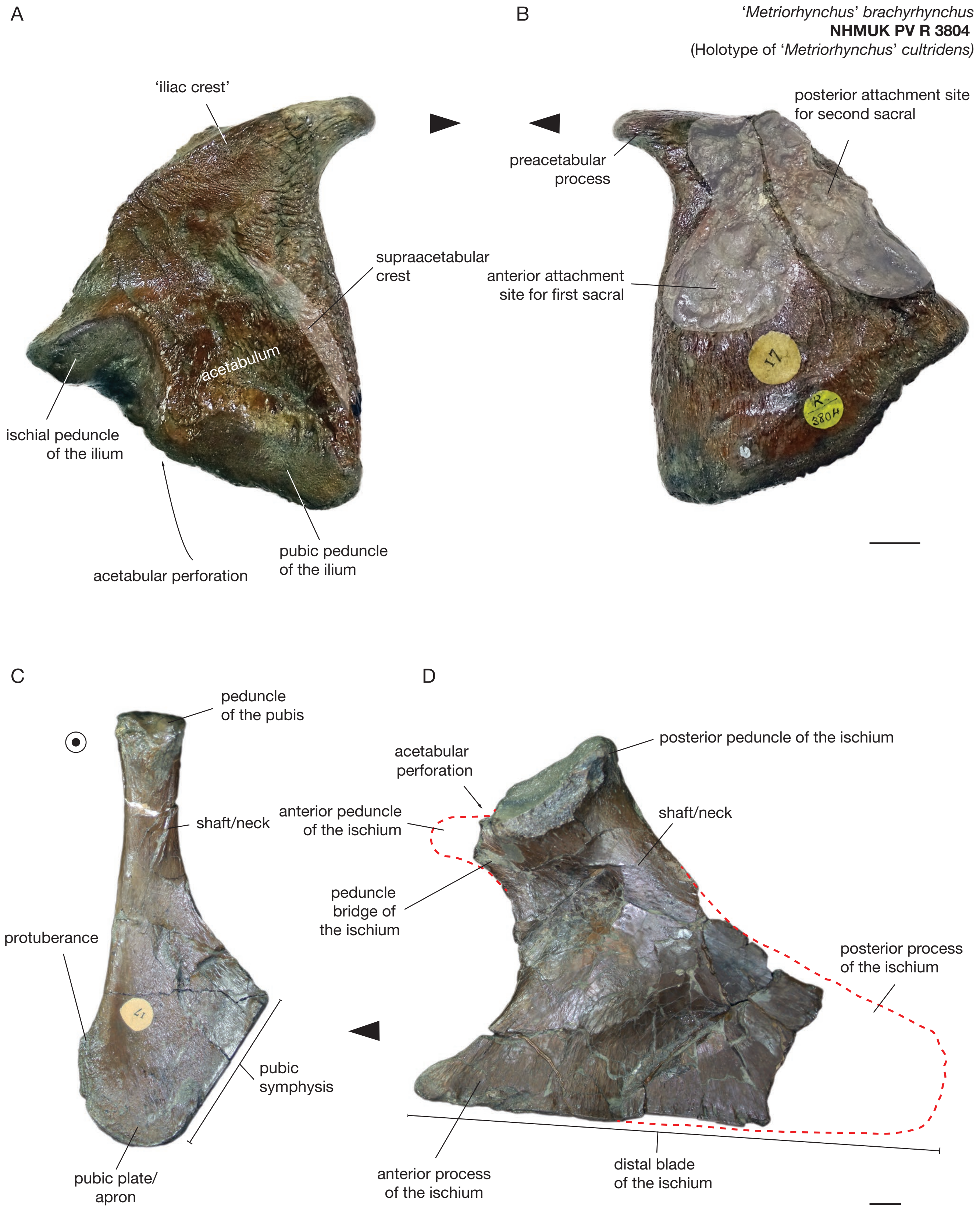


FIG. 24. — Pelvic girdle elements of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867), NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens* Andrews, 1913): **A**, right ilium in lateral view; **B**, right ilium in medial view; **C**, right pubis in anteroposterior; **D**, left ischium in lateral view. Target indicates anterior. Arrow points anteriorly. Scale bars: 1 cm.

pubic peduncle diplays three successive triangular mounds, with the supraacetabular crest originating from the hollow between the two first summits. On the lateral side of the ilium, the pubic peduncle gradually transitions to the ischial peduncle through a recess but without rupturing the articular surface (as in other metriorhynchoids). There is a subtle opening along the ventral margin of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 corresponding to the acetabular perforation. The acetabular perforation almost indiscernible in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, as in *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, and *Cricosaurus* species. The acetabular perforation of the ilium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 does not separate the peduncles of the ilium but is rather indicating the transition between both. Indeed, the acetabular perforation on the ilium is slightly shifted anteriorly, thus ending up within the posterior-most portion of the pubic peduncle. Furthermore, the peduncles of the ilium meet each other on the lateral surface of the ilium, well above the ventral margin of the bone, meaning that both peduncles where brought together presumably at the expense of the acetabular perforation. This highly contrasts with dyrosaurids (*Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*) and extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) where both peduncles are entirely separated by a large acetabular perforation. In '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and other metriorhynchoids (e.g. *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, etc.), the ilium is greatly reduced while still conserving the bony acetabulum and the connections to the other hip bones (i.e. the peduncles), and this reduction presumably happened at the expense of the acetabular perforation and the postacetabular process. The bony acetabulum is limited dorsally by the supraacetabular crest, and runs all the way down to the peduncles ventrally. The supraacetabular crest is a parabolic-shaped ridge that is prominent anteriorly and fades posteriorly. The supraacetabular crest is not centered on the ilium, and its posterior border is slightly closer to the posterior margin of the bone than its anterior border is to the anterior margin of the ilium unlike in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. The area comprising the anterodorsal surface of the acetabulum up to the anterior margin of the ilium, across the supraacetabular crest, is rugged thus reflecting the anchoring of cartilage. Like in other metriorhynchoids, this coarse area extends over the anterior portion of the acetabulum as the rest of the surface is smoother (e.g. *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, etc.). The anterior margin of the ilium and supraacetabular crests are, however, strongly pitted and presumably hosted a structure similar to the acetabular labrum of extant crocodylians. *In vivo*, the bony acetabulum was probably covered in cartilage which likely extended over the ischium and pubis, forming a puboischial synchondrosis like that of extant crocodylians (Claessens & Vickaryous 2012; Tsai & Holliday 2015).

The attachment sites for the two sacral ribs are visible on the medial side of the ilium. They are recognizable by their overall bilobate shape, with the biggest lobe positioned ventrally as in *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. The anterior attachment site is slightly larger than the posterior one, and both show a relatively smooth ventral lobe along with a rougher dorsal lobe indicating the existence of cartilage joining the ribs and the ilium *in vivo*. The attachments sites do not form depressions on the ilium, but are rather in relief or raised, unlike in *Thalattosuchus superciliosus*, *Cricosaurus araucanensis* or *Dakosaurus maximus*. Furthermore, the sacral rib attachment sites are adjacent, and both situated relatively high on the ilium near the preacetabular process, which is similar to other derived metriorhynchoids (e.g. *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus araucanensis*, *Thalattosuchus superciliosus*, *Tyrannoneustes lythrodectikos*, etc.). Yet, all these traits differ from dyrosaurids (e.g. *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*) which show distinct elliptic attachments sites for each sacral process. In addition, in dyrosaurids the attachments sites for each sacral are separated by the acetabular perforation of the ilium, and are borne near the ventral margin of the bone. The ventral deflection of the pelvic girdle of metriorhynchoids, which presumably happened concurrently with its reduction, can be held responsible for the dorsal position of the sacral rib attachment sites near the preacetabular process. In comparison, dyrosaurids possess short and upright sacral processes which are anchored along the anterior and posterior margins of the ilium, leading to pelvic girdles positioned higher dorsally than in metriorhynchoids.

The shape of the ilium – both overall and in detail – of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 is strongly similar to that of *Tyrannoneustes lythrodectikos* so that both putatively belong to the same taxon. At the present stage '*Metriorhynchus*' *brachyrhynchus* is a polyphyletic wastebasket taxon (Waskow *et al.* 2018) as it is filled with markedly differing specimens on both cranium and postcranium levels (see '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 for a striking example). In parallel, the cranium (skull and mandible) of *Tyrannoneustes lythrodectikos* has been introduced with some characters that appear sometimes approximate and dubious (see Foffa & Young 2014), especially pertaining to '*Metriorhynchus*' *brachyrhynchus* (Waskow *et al.* 2018).

Ischium

The ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 (Fig. 24) possesses a short and thick shaft similar to *Tyrannoneustes lythrodectikos* and *Dakosaurus maximus* among metriorhynchoids. Indeed, the shaft of the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 is ⅓ longer anteroposteriorly as it is tall proximodistally. Still, the minimum thickness of the shaft (defining the extension of the shaft) is not drastically greater than the largest anteroposterior length of the posterior peduncle like *Tyrannoneustes*

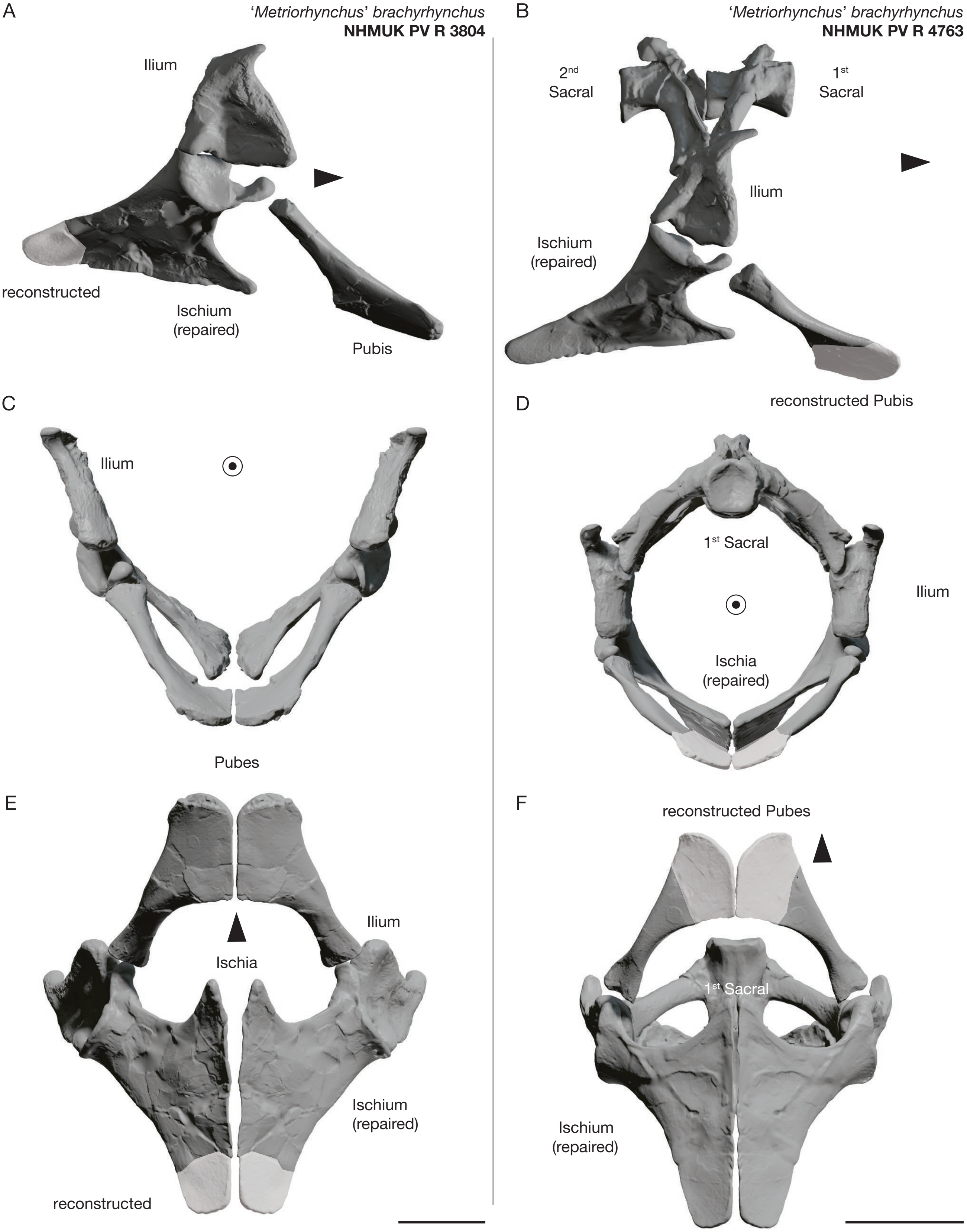


Fig. 25. — Reconstruction of the pelvic girdle of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867), NHMUK PV R 4763 and NHMUK PV R 3804 (holotype of '*Metriorhynchus*' *cultridens*): **A**, NHMUK PV R 3804, right lateral view; **B**, NHMUK PV R 4763, right lateral view; **C**, NHMUK PV R 3804, anterior view; **D**, NHMUK PV R 4763, anterior view; **E**, NHMUK PV R 3804, ventral view; **F**, NHMUK PV R 4763, ventral view. Target indicates anterior. Arrow points anteriorly. The right ischium and left ilium and pubis of NHMUK PV R 3804 are mirrored. The sacral ribs of NHMUK PV R 4763 have been modified to contact the ilium. Scale bars: 5 cm.

lythrodectikos, and *Dakosaurus maximus* to a lesser extent. As in other metriorhynchoids, the acetabular perforation is strongly reduced on the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, and corresponds to a shallow notch between both peduncle which then transitions to a shallow groove on the medial margin of the bone (e.g. *Thalattosuchus superciliosus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*, etc.). The anterior margin of the ischium underneath the peduncles is strongly concave even semicircular (greater than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763). The anterior margin culminates ventrally to form the anterior process of the distal blade, which is sharp as in several metriorhynchoids (i.e. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and LEICT G .418.1956.13.5, *Geosaurus giganteus*, *Dakosaurus maximus*, and *Torvoneustes carpenteri*). The posterior margin of the ischium of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 appears slightly concave as opposed to its anterior margin.

Pubis

The pubis of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 (Fig. 24) displays a well-developed pubic symphysis like other thalattosuchians. The proximal peduncle of the bone is oval in proximal view, but its anterior margin shows a deep extension towards the shaft (vs *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). Also, the greatest axis of the pubic peduncle is not in line with that of the section of the shaft but is tilted at about 30° (Fig. 25). Overall, the pubis of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 takes the shape of a palette knife with a rod-like shaft and a distal blade bearing a straight surface medially (i.e. the large pubic symphysis; Fig. 28) and a rounded one laterally. Thereby, it differs from that of extant crocodylians which show an almost isosceles triangular distal blade. Indeed, in *Caiman crocodilus* (Fig. 9) or *Mecistops cataphractus* (Fig. 8), the lateral and medial margins are almost symmetrical thus displaying a reduced pubic symphysis. The dyrosaurids *Hyposaurus natator* and *Dyrosaurus maghribensis* (OCP DEK-GE 252 and OCP DEK-GE 255) further differ from '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 as they also possess a rather symmetrical isosceles triangular distal blade, but this is not the case for *Cerrejonisuchus improcerus* which displays a strongly asymmetrical pubis.

Comparatively, the pubes of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Cerrejonisuchus improcerus* may appear similar with a short and concave medial margin of the shaft leading to a straight portion of the distal blade, and a more elongated lateral margin of the shaft ending with a rounded portion of the distal blade (the posterior protuberance). In both cases, the medial margin of the shaft and the distal blade meet at an angle slightly greater than 90°. Yet, the main difference resides in the junction between the lateral margins of the shaft and the distal blade: while those are aligned in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, in *Cerrejonisuchus improcerus* they form an angle lesser than 180°. The overall flat lateral margin of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 along with its larger distal blade, creates a smooth and gradual transition between the shaft and the distal blade. On the contrary, in extant crocodylians (e.g. *Mecistops cataphractus* [Fig. 8]) and in other thalattosuchians the shaft of the pubis flares out both laterally and medially to form the distal blade (e.g. *Pelagosaurus typus*, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Mycterosuchus nasutus*).

In '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, the pubic blade displays a posterior protuberance similar to what is observed in dyrosaurids (i.e. *Hyposaurus natator*, and *Dyrosaurus maghribensis* OCP DEK-GE 252 & OCP DEK-GE 255), but unlike most thalattosuchians (e.g. *Pelagosaurus typus*, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). Comparatively, *Mycterosuchus nasutus* also possesses a posterior protuberance but of greater intensity than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804.

TYRANNONEUSTES LYTHRODECTIKOS YOUNG, DE ANDRADE, BRUSATTE, SAKAMOTO & LISTON, 2012

For measurements, see Tables 7-9.

Ilium

The ilium of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 (Figs 26; 27) is similar to that of other derived metriorhynchoids in lacking the presence of postacetabular process (e.g. *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus araucanensis*, *Geosaurus giganteus*, etc.). The ilium of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 is strongly similar to that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 both in overall shape and in details (see below).

The ilium of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 possesses a short and stout preacetabular process similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 or *Thalattosuchus superciliosus* NHMUK PV R 2054. Indeed, the anteroposterior length of the preacetabular process of the ilium of *Tyrannoneustes lythrodectikos* almost reaches the total dorsoventral height of its base. In addition, the preacetabular process does not drastically slim down from its base thickness, and is topped with a rounded apex (as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 or *Thalattosuchus superciliosus* NHMUK PV R 2054). The preacetabular process of *Tyrannoneustes lythrodectikos* is directly in line with the dorsal margin of the ilium. The latter is only slightly longer than the preacetabular process and also subtly convex (similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Thalattosuchus superciliosus* NHMUK PV R 2054). The junction between the slightly convex dorsal margin and strongly concave posterior margin of the ilium of *Tyrannoneustes lythrodectikos* is achieved through a rounded obtuse

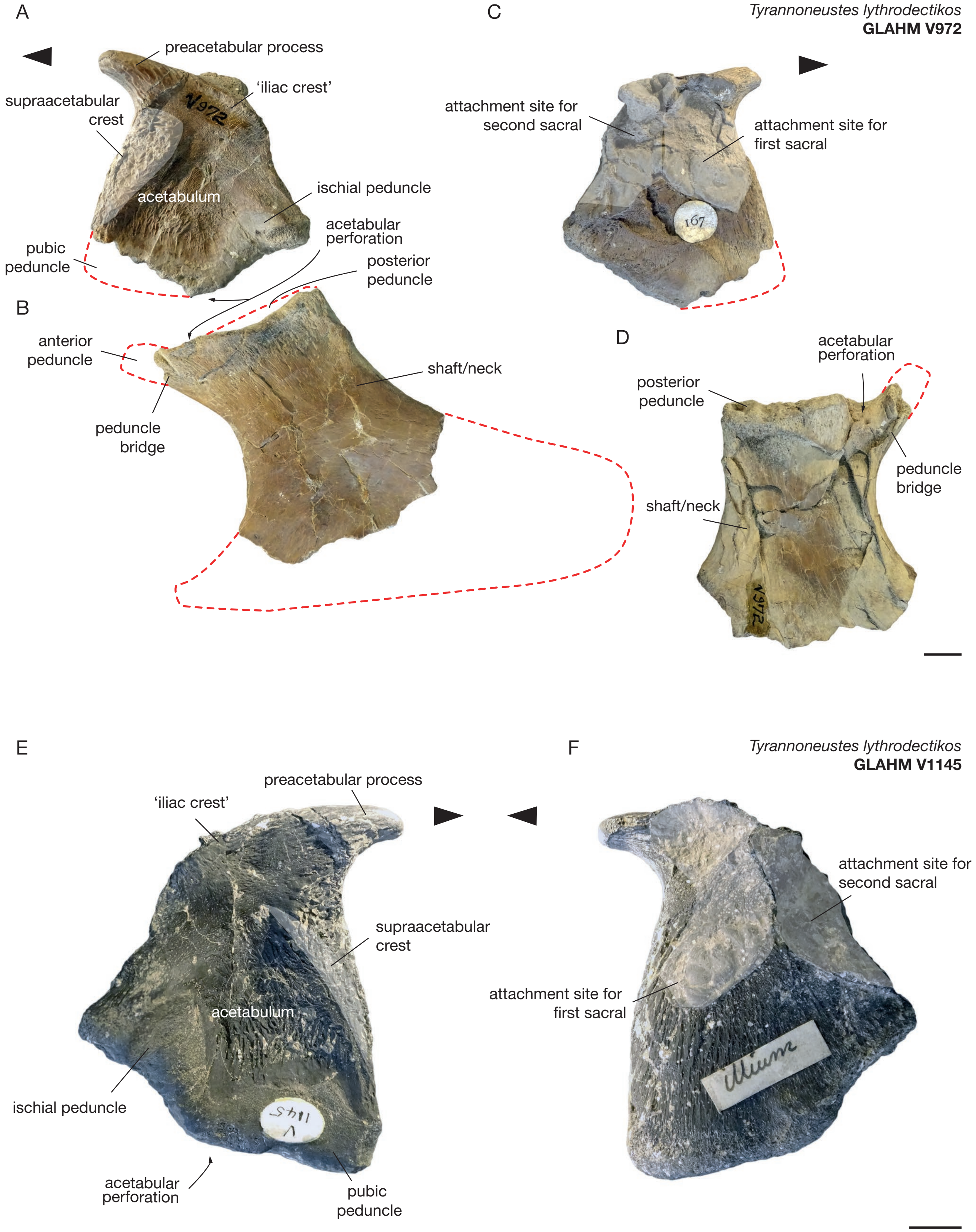


FIG. 26. — Ilium and ischium of *Tyrannoneustes lythrodectikos* Young, de Andrade, Brusatte, Sakamoto & Liston, 2012, GLAHM V972 (holotype) and ilium of GLAHM V1145 (referred): **A**, left ilium of GLAHM V972 in lateral view; **B**, left ischium of GLAHM V972 in lateral view; **C**, left ilium of GLAHM V972 in lateral view; **D**, left ischium of GLAHM V972 in medial view; **E**, right ilium of GLAHM V1145 in lateral view; **F**, right ilium of GLAHM V1145 in medial view. Arrow points anteriorly. Target indicates anterior. The right ischium and left pubis are mirrored. Scale bars: 1 cm.

angle as in *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Thalattosuchus superciliosus* NHMUK PV R 2054. As in other metriorhycnhoids, the dorsal margin of the ilium of *Tyrannoneustes lythrodectikos* is shorter than the anterior margin, and ends ventrally to form the posterior corner of the ischial peduncle. The ischial peduncle of the ilium of *Tyrannoneustes lythrodectikos* displays an overall triangular outline as in other thalattosuchians, crocodylians and dyrosaurids (e.g. *Suchodus durobrivensis*, *Macrospondylus bollensis*, *Mecistops cataphractus*, *Congosaurus bequaerti*, etc.). The anterior and posterior margins of the facet of the ischial peduncle of *Tyrannoneustes lythrodectikos* are overall similar in length, which gives the ischial peduncle the aspect of an isosceles triangle like for many other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, etc.). The ischial peduncle is oriented both anteriorly and laterally, with its posterior corner laterally protruding compared to its anterior corner. In this way, the ischial peduncle forms a bony barrier posteriorly to the bony acetabulum as in other crocodyliformes. The articular facet of the ischial peduncle where it connects to the ischium is not located on the same level as the ventral facet of the pubic peduncle, resulting in an undulating ventral margin for the ilium of *Tyrannoneustes lythrodectikos*. On the lateral side of the ilium, the outline of the ischial peduncle gradually changes to the pubic peduncle without any ruptures unlike in other crocodyliformes bearing a postacetabular process (i.e. teleosauroids, dyrosaurids, crocodylians, etc.). The pubic peduncle of the ilium of *Tyrannoneustes lythrodectikos* GLAHM V1145 reaches threequarters of the ischial peduncle's total dorsoventral height but is slightly longer anteroposteriorly. The outline of the pubic peduncle is undulating: its overall shape is that of a dome with a peak present on each side and a corresponding hollow in between. There is another peak formed by the pubic peduncle situated on the anterior margin of the ilium which is separated from the rest by the 'root' of the supraacetabular crest as in *Mecistops cataphractus*, *Thalattosuchus superciliosus*, and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804. The ventral surface of the pubic and ischial peduncles are lunate as in other thalattosuchians due to their lateral surface displaying a component oriented towards the bony acetabulum. The ventral surfaces of the pubic and ischial peduncles are separated by a subtle recess or notch corresponding to the acetabular perforation. The latter is strongly reduced and almost imperceptible, like for '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804. For *Tyrannoneustes lythrodectikos* (and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804), most of the acetabular perforation is formed by the curved peduncle bridge of the ischium (Fig. 27). The pubic peduncle of the ilium of *Tyrannoneustes lythrodectikos* forms a rounded corner anteriorly which does not protrude, unlike in some metriorhynchoids (e.g. *Pelagosaurus typus*, *Thalattosuchus superciliosus* NMI F21731, *Cricosaurus araucanensis*). The anterior margin of the ilium of *Tyrannoneustes lythrodectikos* is gently convex and forms a smooth rounded re-entrant at its junction with the preacetabular process.

The supraacetabular crest originates on the anterior edge of the ilium, near the lateral facet of the pubic peduncle. It takes the shape of an arch which protrudes laterally to border the bony acetabulum dorsally and anteriorly. The supraacetabular crest of *Tyrannoneustes lythrodectikos* is deeply scarred as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, and *Suchodus durobrivensis*. The rugged area is not limited to the supraacetabular crest (like in aforementioned taxa): it extends anterodorsally up until the base of the preacetabular process, and it also covers the entire bony acetabulum. Unlike '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, the supraacetabular crest of *Tyrannoneustes lythrodectikos* does not follow the anterior margin of the ilium but rather differs from it dorsally.

The attachment sites for the sacral ribs form bilobate areas on the medial side of the ilium, as in *Suchodus durobrivensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. The sacral rib attachment sites share a margin mesially and are located towards the dorsal margin of the ilium. The dorsal lobe of the sacral rib attachment sites are imprinted on the ilium and display a dorsal bony wall as a result. On the contrary, the ventral lobe appears to be slightly raised. Underneath the sacral rib attachment sites, the medial surface of the ilium shows concentric ridges as seen in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, etc.).

The ilium of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 resembles that of *Thalattosuchus superciliosus* (all morphotypes) but with key differences. First, the acetabular perforation of the ilium of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 is strongly reduced (and appears almost absent as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Suchodus durobrivensis*) whereas all *Thalattosuchus superciliosus* bear a small but characteristic notch at the junction of their peduncle. Then, the preacetabular process of *Tyrannoneustes lythrodectikos* GLAHM V972 and GLAHM V1145 is proportionally shorter than in *Thalattosuchus superciliosus* NHMUK PV R 2054, GLAHM V1146 (which we would call the 'de Blainville' morphotype) but still presents the same rounded tip aspect. Compared to *Thalattosuchus superciliosus* SMNS 10116, NHMUK PV R 1530, NMI F21731 or GLAHM V960 (which we would call the 'Leeds' morphotype), the tip of the preacetabular process of of *Tyrannoneustes lythrodectikos* is shorter and more rounded like that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804.

Ischium

The ischium of *Tyrannoneustes lythrodectikos* GLAHM V972 (Figs 26; 27) stands out with its short and thick shaft whose proximodistal length accounts for about ¾ of its anteroposterior constriction. Other metriorhynchoids with short and thick ischial shaft include '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Dakosaurus maximus*. Underneath the shaft, the ischium of *Tyrannoneustes lythrodectikos*

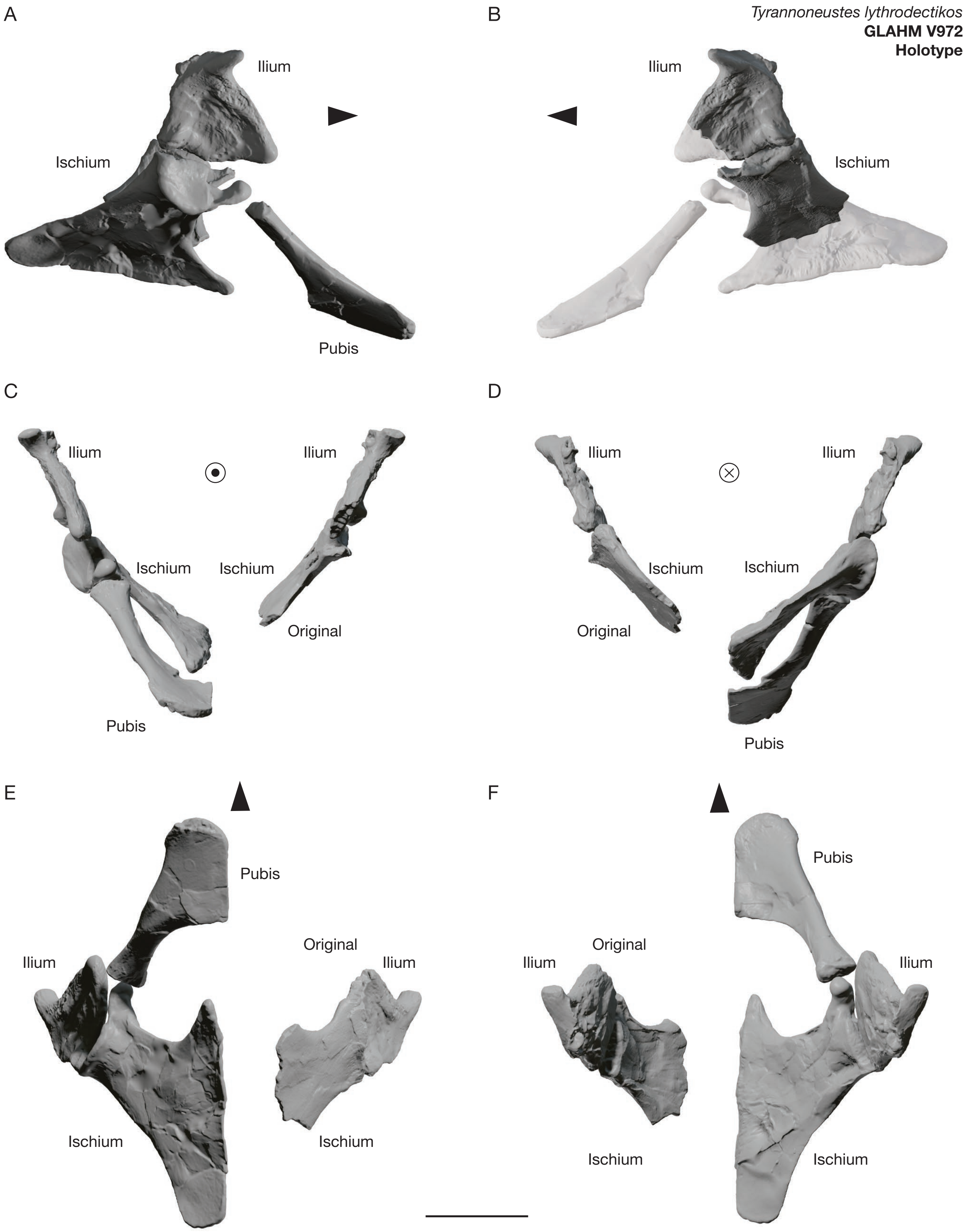


Fig. 27. — Pelvic reconstruction of *Tyrannoneustes lythrodectikos* Young, Andrade, Brusatte, Sakamoto & Liston, 2013*,* GLAHM V972 (holotype), based on the ilium of *Tyrannoneustes lythrodectikos,* GLAHM V1145 (referred), and the ischium and pubis of '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1868), NHMUK PV R 3804: **A**, lateral view of reconstructed portion; **B**, lateral view of original ilium and ischium; **C**, anterior view; **D**, posterior view; **E**, ventral view; **F**, dorsal view. Arrow points anteriorly. Target indicates anterior. Scale bar: 5 cm.

appears to rapidly flare out distally. This effect is accentuated by the strongly concave and almost hemispherical anterior margin of the ischium as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Dakosaurus maximus*. Comparatively, the posterior margin of the ischium of *Tyrannoneustes lythrodectikos* is concave but with a lesser degree of curvature. The posterior peduncle of the ischium of *Tyrannoneustes lythrodectikos* is large: its anteroposterior length almost reaches that of the shaft constriction. However, the posterior peduncle is mediolaterally slender with a thickness reaching half of its total anteroposterior length. Laterally, the peduncle bridge of the ischium stems from the corner of the posterior peduncle resulting in the complete obstruction of the acetabular perforation on this side of the bone, similar to several derived metriorhynchoids (e.g. *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Geosaurus giganteus*). Starting from its base, the peduncle bridge of *Tyrannoneustes lythrodectikos* bends towards the medial side of the bone to bring the anterior peduncle (not preserved) near the ilium. In this way, the peduncle bridge creates a gap for the acetabular perforation. The latter is visible on the medial side of the ischium, where it forms an oblique notch or burrow tilted towards the medial side of the bone as in most metriorhynchoisd (e.g. *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Geosaurus giganteus*).

SUCHODUS DUROBRIVENSIS LYDEKKER, 1890

For measurements, see Tables 7-9.

Ilium

The ilium of *Suchodus durobrivensis* can easily be identified as metriorhynchoid as it is reduced in size compared to the pubis (Figs 28; 29), and as it does not display a postacetabular process. Similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, the preacetabular process is not parallel to the ventral margin of the ilium and points anterodorsally. The dorsal margin of the ilium forming a short iliac crest, directly posterior to the preacetabular process, is more developed in *Suchodus durobrivensis* than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, as it is almost as long as the preacetabular process. The anterior margin of the ilium is convex while the posterior margin is concave. The ventral margin is undulating, with the concave portion corresponding to the ischial peduncle, and the overall convex part belonging to the pubic peduncle. Like in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Geosaurus giganteus*, *Tyrannoneustes lythrodectikos*), the acetabular perforation of *Suchodus durobrivensis* is reduced to a slight indentation along the ventral margin of the ilium. Hence, it does not separate the peduncles as in teleosauroids (e.g. *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, etc.). Similar to *Thalattosuchus superciliosus* and *Dakosaurus maximus*, the acetabular perforation of *Suchodus durobrivensis* is positioned underneath the anterior portion of the ischial peduncle, whereas it was placed within the extension of the pubic peduncle in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. In '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Tyrannoneustes lythrodectikos*, the acetabular perforation appears to be in between the peduncles. As opposed to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, and *Dakosaurus maximus*, the acetabular perforation of *Suchodus durobrivensis* is strongly reduced. Only *Tyrannoneustes lythrodectikos* GLAHM V1145 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 display an acetabular perforation so shallow it appears almost indistinguishable. The acetabulum, and the pubic and ischial peduncles take up almost all of the available space on the ilium of *Suchodus durobrivensis* similar to other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Tyrannoneustes lythrodectikos*, etc.). Thereby, the reduction of the ilium happened at the expense of the acetabular perforation and postacetabular process in order to preserve the parts involved in the hip articulation as in other derived metriorhynchoids.

The ischial peduncle is dorsoventrally higher than the pubic peduncle (about 1.8 times taller), and also protrudes laterally, leaving a sharp edge posteriorly (like in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763). The ischial peduncle takes the shape of triangle pointing dorsally as in other crocodyliformes, whereas the pubic peduncle is more rectangular as in *Geosaurus giganteus*. The pubic peduncle of *Suchodus durobrivensis* seems slightly domed dorsally but does not display distinct peaks as in other metriorhynchoids (e.g. *Thalattosuchus superciliosus*, *Tyrannoneustes lythrodectikos*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763).

The majority of the lateral surface of the ilium is covered by an elliptic concave area, the bony acetabulum, which appears slightly offset posteriorly. Most of the acetabulum is scarred, and this rugged area extends over the whole anterior portion of the ilium, overpassing the supraacetabular crest as well as in *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763. This region was presumably the anchoring site of a structure similar to the acetabular labrum of extant crocodylians. The acetabulum comprises two distinct concave subareas: the anterior strongly rugged and shallow portion, and the posterior deeper part. *In vivo* the whole acetabulum was presumably covered in cartilage, with the actual articular capsule probably centered over the posterior concavity as the anterior portion would potentially form, or at least partake in, the anterior wall of the capsule (i.e. the acetabular labrum). The supraacetabular crest demarcates the dorsal border of the acetabulum. In *Suchodus durobrivensis*, it appears like a sheared parabolic ridge leaning posteriorly, with the anterior rim prominent and the posterior one smoothed. The ventral portion of the supraacetabular crest stems from the anterior-most portion of the ilium, unike in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Tyrannoneustes lythrodectikos*. The dorsal portion of the supraacetabular crest is offset in relation to the

Fig. 28. — Pelvic girdle elements of *Suchodus durobrivensis* Lydekker, 1890, NHMUK PV R 2618: **A**, right ilium in lateral view; **B**, right ilium in medial view; **C**, right pubis in anterodorsal view; **D**, right pubis in lateral view; **E**, left pubis in posteroventral view. Target indicates anterior. Cross indicates posterior. Arrow points anteriorly. Scale bar: 1 cm.

anterior margin of the ilium, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Tyrannoneustes lythrodectikos*.

On the medial side, the ilium is convex at the site where the sacral processes attach to the bone as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*. Similar to other derived metriorhynchoids, the attachments sites are located dorsally near the preacetabular process. This further differs from dyrosaurids (e.g. *Congosaurus bequaerti*, *Hyposaurus natator*, *Dyrosaurus maghribensis*, or *Acherontisuchus guajiraensis*) and extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus*, or *Caiman crocodilus* [Fig. 9]) where the sacral rib attachment sites are fully separated and positioned along the ventral margin of the ilium. The two attachment sites of *Suchodus durobrivensis* are bilobed and adjacent, and their global outline is slightly in relief or raised (like in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Tyrannoneustes lythrodectikos*). They are not clearly discernible from one another, except for the bilobate ventral margin which hints at the exact position of the split. Compared with '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, or *Tyrannoneustes lythrodectikos*, the sacral rib attachment sites of *Suchodus durobrivensis* are less pitted, but occupy a larger area of the ilium as they account for 65.8% of the anteroposterior length of the bone.

Pubis

The pubis of *Suchodus durobrivensis* (Figs 28; 29) displays a rod-like shaft culminating in a truncated distal blade. The lateral and medial margins of the shaft are concave, with the medial margin possessing the greatest degree of curvature and the shortest length. The distal extremity of the pubic plate shows a straight margin medially (i.e. the pubic symphysis) and a convex one ventrolaterally, with a gradual transition between the two. Medially, the concave margin of the shaft and the straight one of the pubic symphysis meet at an angle of approximately 90°, and form a pointed peak. Laterally, the shaft gradually transforms into the pubic plate with an undulation of small intensity. The rugged area marking the existence of cartilage *in vivo* is present on the whole distal extremity of the pubic plate, and extends over a small portion of the lateral margin. The pubic peduncle is oval in proximal view, with its posterior margin extending slightly towards the shaft in posterior view. The shaft represents the thickest portion of the bone anteroposteriorly.

There are several differences on the shaft and distal blade which make the distinction between *Suchodus durobrivensis* and other metriorhynchoids. Overall, the pubis of *Suchodus durobrivensis* is asymmetrical mediolaterally with an extended pubic symphysis but narrow pubic plate mediolaterally. In this way, the pubis of *Suchodus durobrivensis* differs from that of most thalattosuchians, extant crocodylians (e.g. *Caiman crocodilus* [Fig. 9], *Mecistops cataphractus* [Fig. 8]) and dyrosaurids (e.g. *Hyposaurus natator*, *Dyrosaurus maghribensis*). Like other thalattosuchians, the pubis of *Suchodus durobrivensis* displays an oval peduncle proximally. In *Suchodus durobrivensis*, the shape of the medial and lateral margins are strongly dissimilar: the medial margin of the pubis is strongly concave whereas the degree of concavity is lesser for the lateral margin. Among metriorhynchoids, a similar difference is observed in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Geosaurus giganteus*. The pubis of *Suchodus durobrivensis* presents a strong constriction of the shaft relatively far from the peduncle of the pubis (at about 35% of the total length of the pubis), as in *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Geosaurus giganteus*. Among metriorhynchoids, *Pelagosaurus typus*, *Cricosaurus araucanensis*, and *Dakosaurus maximus* also present a strong constriction but it is located proportionally more closely to the peduncle.

In *Suchodus durobrivensis* (Fig. 29) the transition between the lateral margin of the shaft and the distal blade is both smooth and gradual, as it does not show a posterior protuberance as in'*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804. Consequently, the arched distal margin of the pubic plate is shorter and has a smaller degree of curvature in *Suchodus durobrivensis*, and also appears more elliptic (as opposed to other mertriohynchoids). The shortness of the distal blade namely accounts for the narrow appearance of the pubic plate of *Suchodus durobrivensis*. In addition, the relative size of the pubic symphysis (about 32% of the total pubic length) and its angular relation with the distal blade (about 140°) accentuate the narrow appearance of the bone. Similar to other metriorhynchoids with a developed pubic symphysis, the junction between the medial margin and the pubic symphysis of *Suchodus durobrivensis* forms a pointed right-angled corner (e.g. *Thalattosuchus superciliosus*, *Cricosaurus araucanensis*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804).

GEOSAURUS LAPPARENTI
(DEBELMAS & STRANNOLOUBSKY, 1957)

The bones referred to the pelvic girdle of *Geosaurus lapparenti* in Debelmas (1958) are not included in our work. Indeed, those remains do not correspond to the shape of any element of a metriorhynchoid pelvic girdle. We hypothesize that those elements correspond to either girdle of a plesiosaur.

GEOSAURUS GIGANTEUS VON SÖMMERRING, 1816

For measurements, see Tables 7-9.

Ilium

The ilium of *Geosaurus giganteus* (Figs 30; 31) almost takes the shape of an isosceles trapezoid. Indeed, the anterior and posterior margins of the bone appear to display a similar angular relation with the ventral margin of the bone, and the latter seems parallel to the dorsal margin of the ilium. Proportionally, the ilium of *Geosaurus giganteus* (Fig. 30) is almost as large as the pubis, which is a trait also seen in *Suchodus durobrivensis*. The preacetabular process of *Geosaurus giganteus* is sharp but extremely reduced, unlike other metriorhynchoids (e.g.'*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV

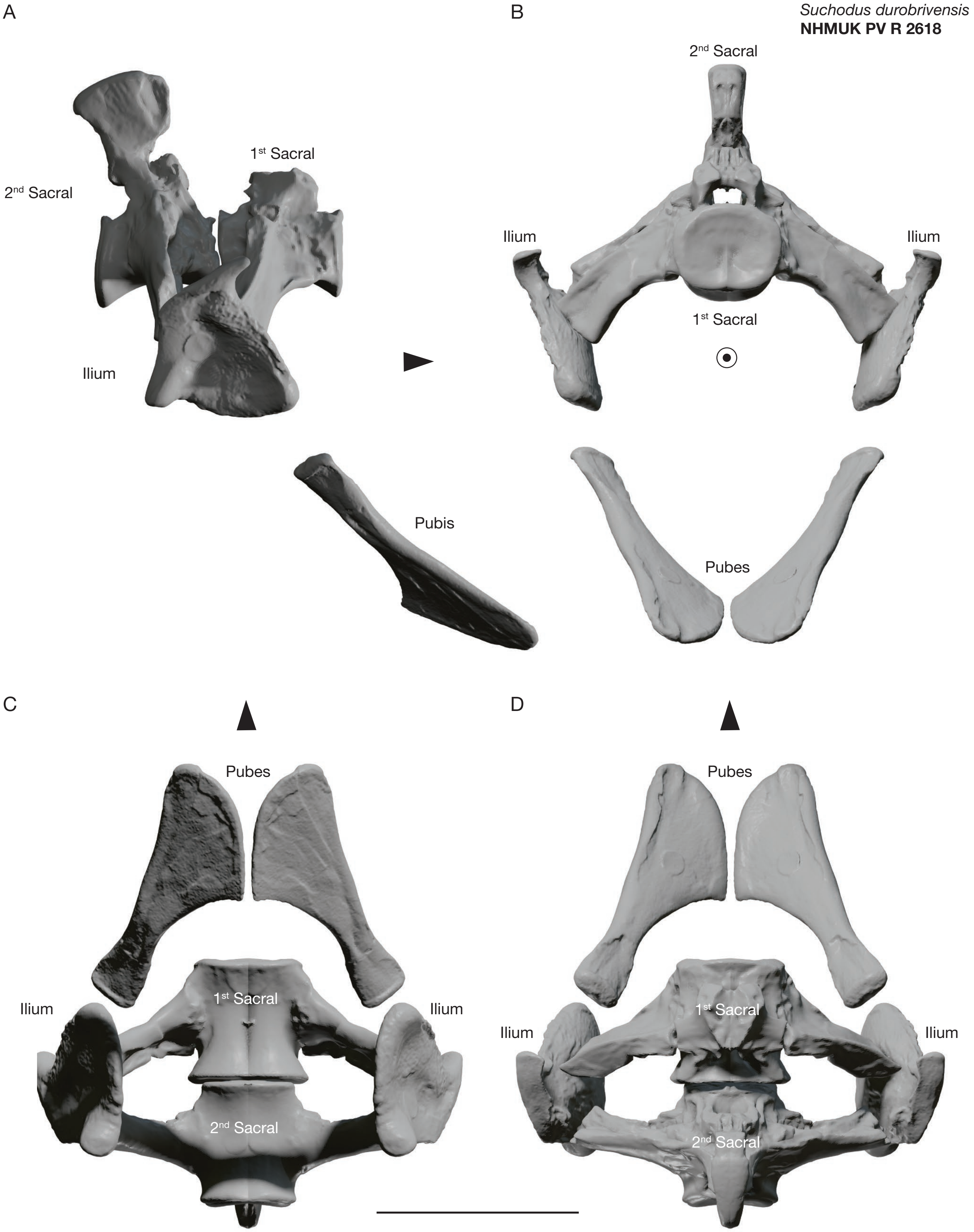


FIG. 29. — Pelvic reconstruction of *Suchodus durobrivensis* Lydekker, 1890, NHMUK PV R 2618: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The left ilium and pubis are mirrored. Scale bar: 5 cm.

R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Tyrannoneustes lythrodectikos*, etc.). Geometrically, the preacetabular process of *Geosaurus giganteus* is in line with the dorsal margin of the ilium, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*. Underneath the preacetabular process, on the lateral surface of the ilium, runs a subtlety protruding arch which constitutes the supraacetabular crest. The supraacetabular crest borders the bony acetabulum dorsally. The latter forms a shallow depression, extending over most of the ilium. Posteriorly, the bony acetabulum is bordered my the ischial peduncle, which is similarly faintly protruding.

The anterior margin of the ilium underneath the preacetabular process shows a subtle concavity over most of its length, which becomes straight or slightly convex where the pubic peduncle starts. The pubic peduncle of does not appear to protrude anteriorly, as in *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, and *Dakosaurus maximus*. On the lateral side of the ilium, the pubic peduncle shows a dorsal extension of about one fourth of the total dorsoventral height of the bone. Also, both the dorsal and ventral margins of the pubic peduncle are undulated. The ischial peduncle is fragmentary but forms the posteroventral corner of the ilium. The posterior margin of the ilium of *Geosaurus giganteus* appears slightly concave similar to the anterior margin. The junction between the dorsal and posterior margin is achieved through a smooth rounded corner.

Ischium

The ischium of *Geosaurus giganteus* (Figs 30; 31) is fragmentary. The anterior peduncle is rounded and appears reduced like that of other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, etc.). The peduncle bridge is borne at the extremity of the peduncle bridge, which is formed by two slightly concave margins dorsally and ventrally. Dorsally, at the junction between the peduncle bridge and the posterior peduncle is a notch corresponding to the acetabular perforation. The posterior peduncle of the ischium of *Geosaurus giganteus* does not extends further dorsally than the anterior peduncle.

The anterior margin of the ischium is strongly concave and takes the shape of a Lancet arch rather than a hemispherical parabola as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Torvoneustes carpenteri*, *Thalattosuchus superciliosus* NHMUK PV R 2054, and *Cricosaurus albersdoerferi*. Among teleosauroids,

Aeolodon priscus NHMUK PV R 1086 and *Charitomenosuchus leedsi* also show relatively narrow anterior concavity as in *Geosaurus giganteus*. The anterior margin of the ischium ends ventrally into a sharp peak constituting the anterior process of the ischium. The latter is formed by a curved (concave) margin dorsally and a more straight one ventrally, and points in the same direction as the anterior peduncle (i.e. anterodorsally). The shape and orientation of the distal blade of the ischium is however unknown. Anteriorly, the anterior process of the ischium extends slightly further than the anterior peduncle, unlike in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 or *Thalattosuchus superciliosus* NHMUK PV R 2054.

Pubis

The pubis of *Geosaurus giganteus* (Figs 30; 31) is highly symmetrical lateromedially, unlike that of other thalattosuchians (i.e.'*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi* , *Macrospondylus bollensis*, etc.). Hence, the pubis of *Geosaurus giganteus* appears more similar to that of extant crocodylians (e.g. *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) due to almost identical lateral and medial margins. This effect is notably imputable to the reduction of the pubic symphysis, but is here emphasized by the decrease in size of the pubic apron mediolaterally. Indeed, in *Cricosaurus suevicus* and *Cricosaurus albersdoerferi*, the pubic plate shows a larger pubic apron mediolaterally for a similarly reduced pubic symphysis leading to a mediolaterally unbalanced pubic apron.

The shape of the distal blade, uniting the lateral and medial margin of the pubis is markedly convex and almost hemispherical due to the symmetry of the bone. Its junction with the medial margin is achieved through a short straight surface constituting the pubic symphysis. The latter is practically parallel to the median of the pubic shaft. The latter constitutes almost half of the total height of the pubis. Proximally, the shaft of the pubis flares out to form the pubic peduncle, which is almost twice as large lateromedially as the thinnest portion of the shaft, similar to *Cricosaurus suevicus*.

DAKOSAURUS MAXIMUS (PLIENINGER, 1846)

For measurements, see Tables 7-9. The specimen SMNS 8203 is fragmentary and hence includes potential reconstructions.

Ilium

The ilium of *Dakosaurus maximus* (Figs 32; 33) seems to display the typical triangular silhouette of metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, etc.), conveying the absence of a postacetabular process.

The anterior margin of the ilium underneath the preacetabular process is straight as in *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Suchodus durobrivensis*, and *Geosaurus giganteus*. The bony acetabulum of *Dakosaurus maximus* forms a relatively marked hollow, extending up until about half the height of the ilium dorsoventrally as in other metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, etc.). Moreover, the acetabulum of *Dakosaurus maximus* appears to be bordered anteriorly by a laterally prominent pubic peduncle-supraacetabular complex acting here as a physical barrier. Such a structure is

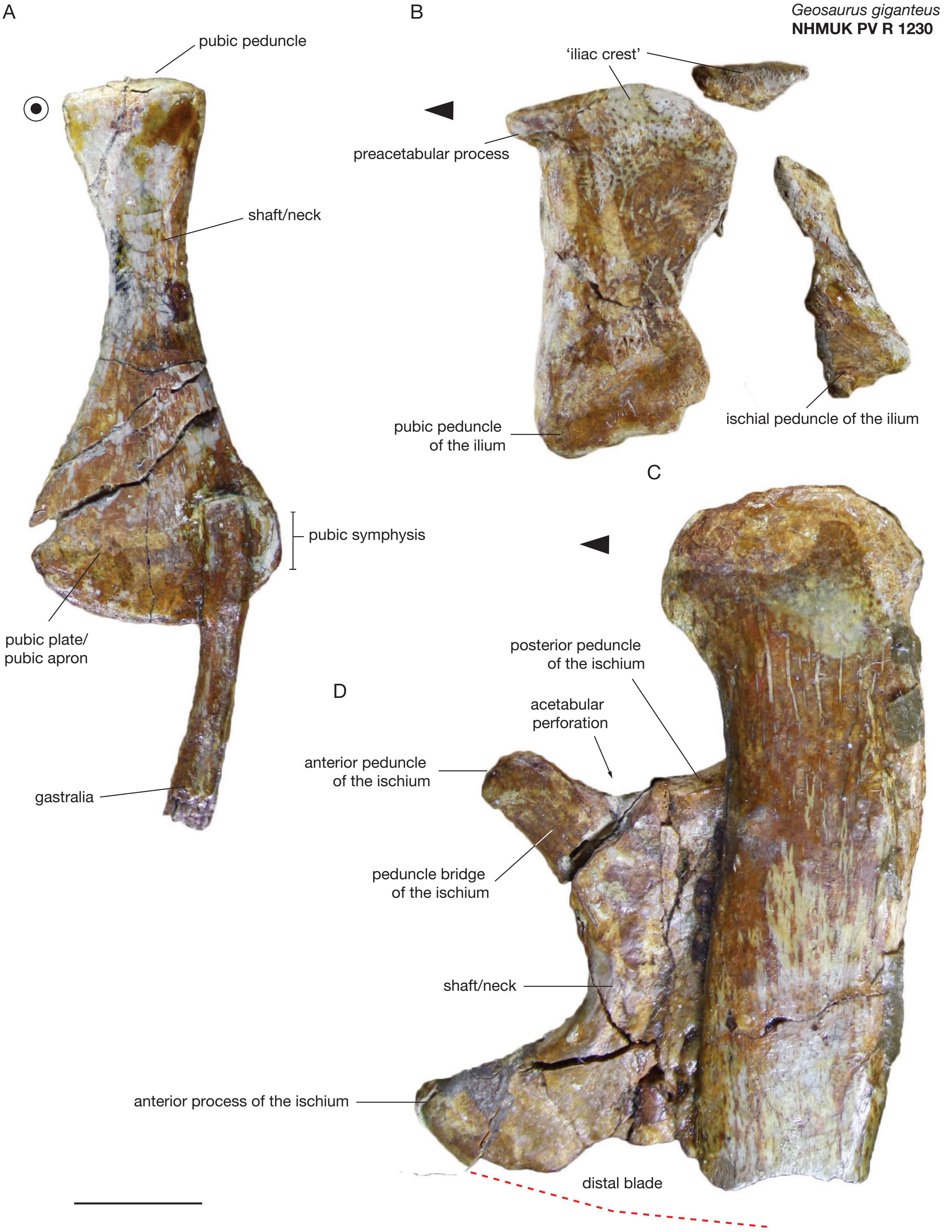


FIG. 30. — Pelvic girdle elements of *Geosaurus giganteus* (Von Sömmerring, 1816), NHMUK PV R 1230: **A**, right pubis anterior; **B**, left ilium in lateral view; **C**, right femur in ventral view; **D**, right ischium in lateral view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

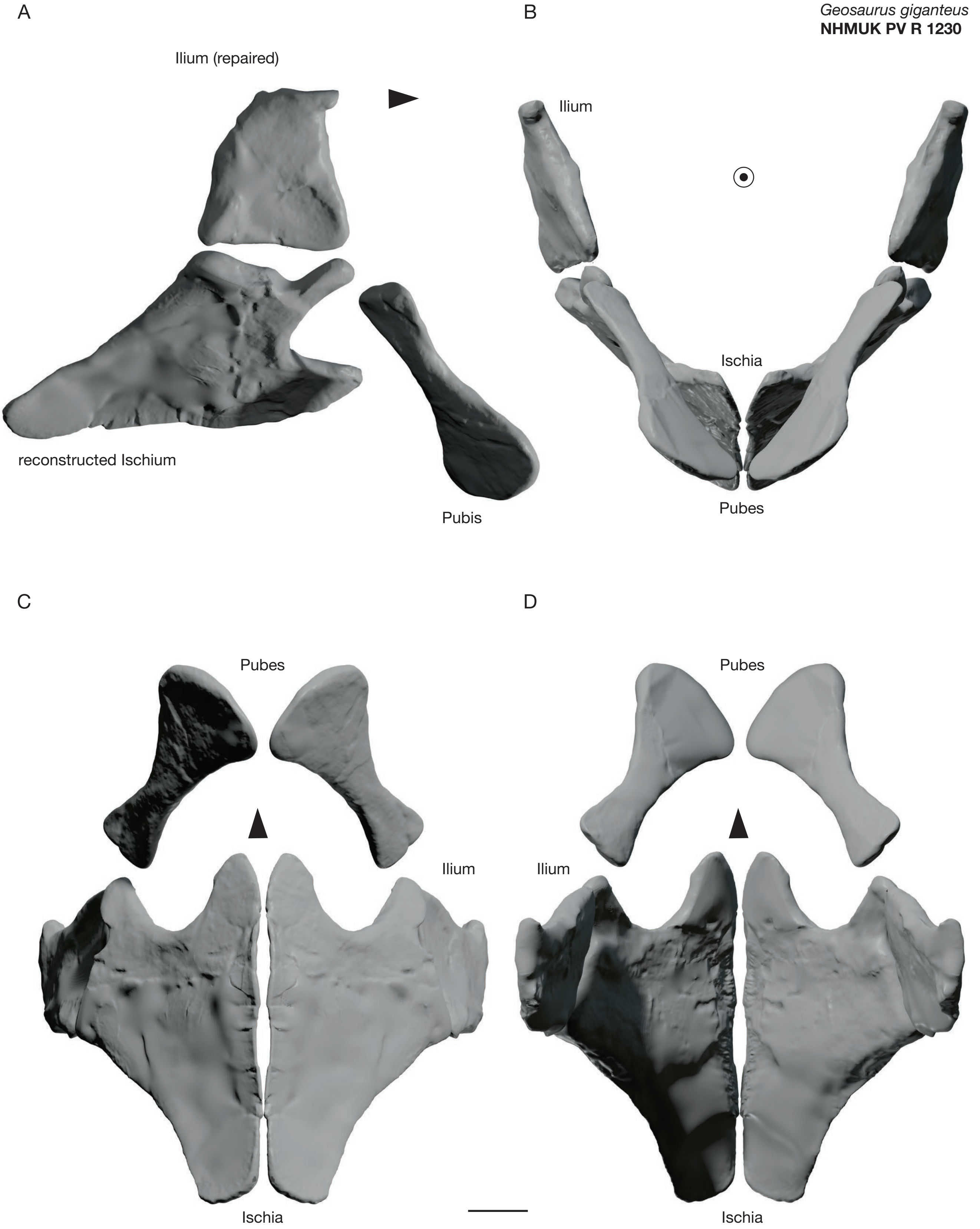


FIG. 31. — Pelvic reconstruction of *Geosaurus giganteus* (Von Sömmerring, 1816), NHMUK PV R 1230; illium and pubis have been repaired; ischium has been reconstructed based on NHMUK PV R 4763: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right ilium, ischium and pubis are mirrored. Scale bar: 1 cm.

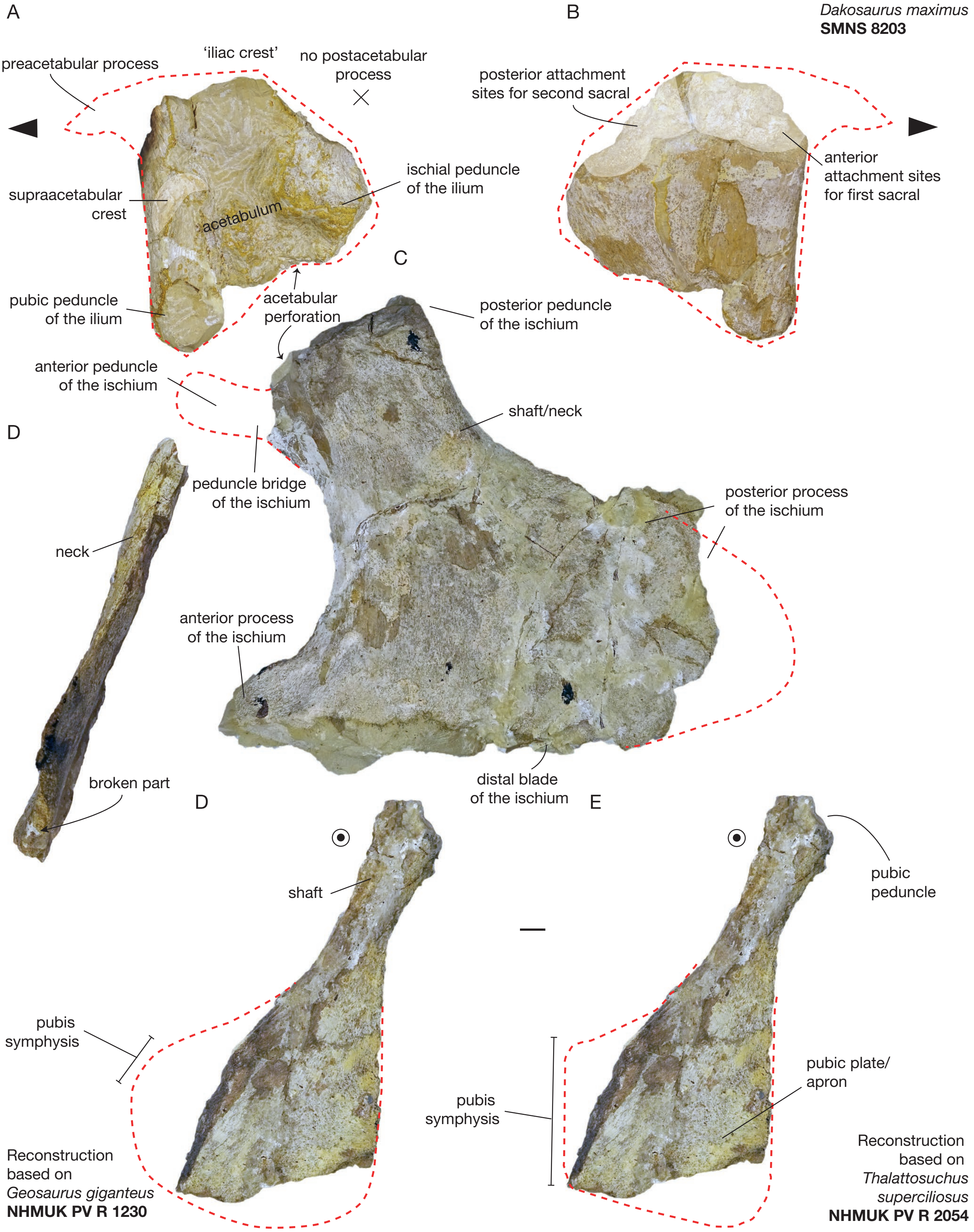


FIG. 32. — Left and right ilia of *Dakosaurus maximus* (Plieninger, 1846) Von Quenstedt, 1856, SMNS 8203: **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, left ischium in lateral view; **D**, left pubis in lateral view; **E**, left pubis in anterior view. Target indicates anterior. Arrow points anteriorly. Scale bar: 1 cm.

also observed '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, and maybe *Cricosaurus suevicus*, but does not seem present in *Thalattosuchus superciliosus*. Comparatively, this pubic peduncle– supraacetabular complex is still less protruding laterally than the ischial peduncle is, which is a common relation found in all other crocodyliforms. The acetabular perforation of *Dakosaurus maximus* forms a shallow notch on the ventral margin of the ilium, and also marks the position of the ischial peduncle.

The sacral rib attachment sites on the medial side of the ilium are set in a way indicating that the position of the ilium *in vivo* was anteriorly tilted (i.e. the ventral margin of the ilium was not placed horizontally) similar to several thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, etc.), but unlike extant crocodylians (e.g. *Caiman crocodilus* [Fig. 9] or *Mecistops cataphractus* [Fig. 8]) and dyrosaurids (e.g. *Congosaurus bequaerti*, *Hyposaurus natator*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*). The exact shape of the sacral rib attachment sites is uncertain, but they seem to have been distinct bilobate structures (at least along their ventral margins). The sacral rib attachment sites form deep imprints on the ilium of *Dakosaurus maximus*, similar to *Thalattosuchus superciliosus* but unlike the raised ones of *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763.

Ischium

The ischium of *Dakosaurus maximus* (Figs 32; 33) stands out from that of most thalattosuchians in displaying the combination of a short and thick shaft and a short anterior process along with a dorsoventrally thick posterior process. *Torvoneustes carpenteri* also displays a short anterior process and thick posterior process, but its shaft is slightly more elongated.

The posterior peduncle of *Dakosaurus maximus* is large as its anteroposterior width almost reaches that of the shaft at its thinnest portion or constriction. Unfortunately, the posterior peduncle is partially trapped with sediments so the exact shape of its articular surfaces is unclear. In parallel, the posterior peduncle of *Dakosaurus maximus* does not significantly protrude dorsally from the shaft as in most thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Torvoneustes carpenteri*, *Tyrannoneustes lythrodectikos*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, *Proexochokefalos* cf. *bouchardi*). This effect is due to the relative position of the base of the peduncle bridge, which is located near the base of the posterior peduncle in *Dakosaurus maximus*. Indeed, the peduncle bridge stems from the proximal edge of the ischium. Another consequence of this situation is the impression of an almost non-existent or reduced acetabular perforation on the lateral side of the bone, unlike in *Macrospondylus bollensis* and *Charitomenosuchus leedsi* which display a deeper acetabular perforation laterally. Presumably, the acetabular perforation of *Dakosaurus maximus* formed a titled burrow on the medial side of the bone like all other thalattosuchians displaying the same configuration (especially methriorhynchoids). The acetabular perforation is borne by the dorsal surface of the peduncle bridge, which is unfortunately ruptured shortly after the start of its anterior slimming.

The shaft as a whole is thick (anteroposteriorly longer than dorsoventrally high) similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and *Tyrannoneustes lythrodectikos*, but unlike the more slender ones of *Cricosaurus suevicus* or *Cricosaurus albersdoerferi*. *Torvoneustes carpenteri* and *Thalattosuchus superciliosus* NHMUK PV R 2054 possess a slightly slender shaft than that of *Dakosaurus maximus* but not too markedly. The posterior and anterior margins of the ischium, constituting notably the shaft, are both concave with the anterior margin displaying the greatest intensity. However, the posterior margin of the shaft appears to become straight or slightly convex shortly after transitioning from the shaft to the posterior process. Hence, the ischium gradually widens ventrally to form the distal blade, which possesses a sharp anterior process and a relatively large one posteriorly. The distal blade of *Dakosaurus maximus* is incomplete but appears to have been relatively straight throughout. The margin of the distal blade forms an angle of approximately 58° with the median of the shaft like that of '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, but which differs from the more erect ones of *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus bambergensis* and *Torvoneustes carpenteri*.

The anterior process of the ischium of *Dakosaurus maximus* is in line with the rest of the ventral margin of the distal blade which contrasts with *Thalattosuchus superciliosus* NHMUK PV R 2054 and *Pelagosaurus typus* among metriorhynchoids. Compared to the posterior process, the anterior process of *Dakosaurus maximus* appears strongly reduced (Fig. 32) as in *Torvoneustes carpenteri*, *Cricosaurus araucanensis*; both the anteroposterior length and dorsoventral height (at its base) of the anterior process are markedly inferior to those of the posterior process (even partially incomplete). Whereas the anterior process is always anteroposteriorly shorter than the posterior process, the difference in dorsoventral height is usually less marked in most metriorhynchoids (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, etc.). It is possible that this dissimilarity in the shape of the ischium reflects a difference in the muscles arrangement.

Similar to *Thalattosuchus superciliosus* NHMUK PV R 2054 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, the anterior process of *Dakosaurus maximus* is mediolaterally thicker than the rest of the distal blade and the junction of both ischia forms a platform.

The posterior process of *Dakosaurus maximus* is large and greatly exceeds the size of the anterior process, as in *Crico-*

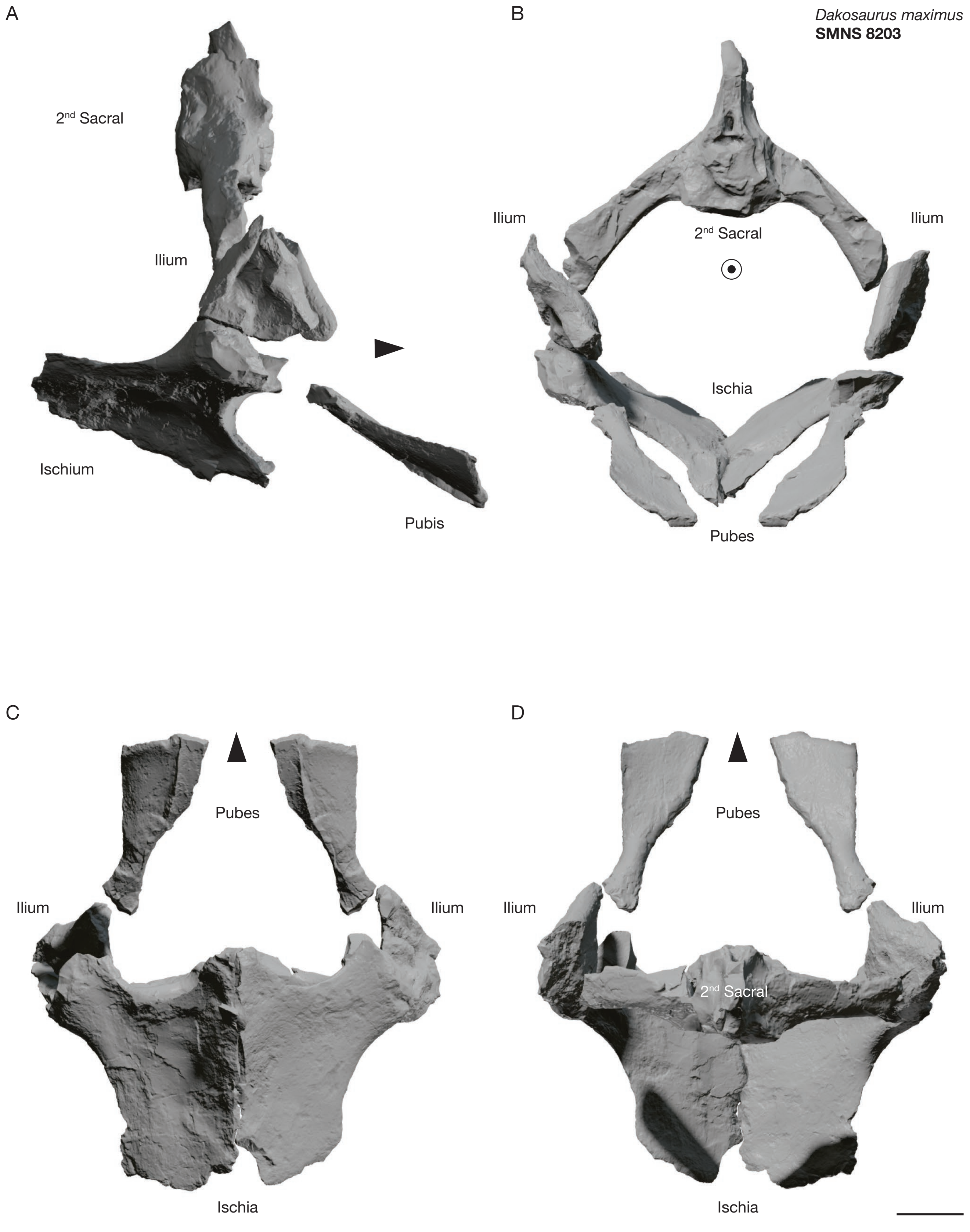


Fig. 33. — Pelvic reconstruction of *Dakosaurus maximus* (Plieninger, 1846), SMNS 8203: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right pubis is mirrored. Scale bar: 5 cm.

saurus araucanensis, *Torvoneustes carpenteri* and *Lemmysuchus obtusidens*. Indeed, the dorsoventral height of the base of the posterior process can fit more than twice that of the anterior process. The exact shape of the apex of the posterior process of *Dakosaurus maximus* is not preserved but presumably formed a blunt and rounded extremity similar to *Cricosaurus araucanensis*, *Torvoneustes carpenteri* and *Lemmysuchus obtusidens*. The shape of the posterior process is hypothetically reconstructed from the overall slope of the posterior margin of the ischium, which is more gentle than in *Thalattosuchus superciliosus* NHMUK PV R 2054 or '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763.

Pubis

The pubis of *Dakosaurus maximus* (Fig. 32) is fragmentary and is missing most of its pubic plate. The extension of the pubic symphysis is therefore unknown and two distinct reconstructions are proposed on Fig. 32. Comparatively, the closest taxa to *Dakosaurus maximus* – *Suchodus durobrivensis* and *Geosaurus giganteus* (Young *et al.* 2020a) – possess extremely distinct pubic shapes. The peduncle of the pubis of *Dakosaurus maximus* is also poorly preserved, but appears to be larger than the thinnest portion of the shaft but not as markedly as in *Cricosaurus suevicus* or *Geosaurus giganteus*. Hence, the lateral and medial margins of the pubis of *Dakosaurus maximus* are both concave, with the lateral margin showing a slightly greater intensity of curvature. The portion extending from the base of the peduncle until the thinnest portion of the bone corresponds to the shaft. The shaft of the pubis of *Dakosaurus maximus* is strongly reduced in length and appears amongst the shortest of Thalattosuchia (e.g. *Suchodus durobrivensis* & *Geosaurus giganteus*).

Torvoneustes carpenteri (Wilkinson, Young & Benton, 2008)
For measurements, see Tables 7-9.

Ischium

The ischium of *Torvoneustes carpenteri* (Figs 34; 35) strongly resembles those of *Cricosaurus araucanensis*, *Dakosaurus maximus* and *Lemmysuchus obtusidens* in displaying a strongly reduced anterior process and a large posterior one. This effect is mainly imputable to the shape of the anterior and posterior margins of the ischium of *Torvoneustes carpenteri*: the anterior margin is concave throughout with a large focal width whereas the posterior margin displays a strong sinusoidal shape. Indeed, the posterior margin is proximally concave and switches to convex around its mid-length and hence forms the rounded extremity of the posterior process. The early change in convexity of the posterior margin results in a dorsoventrally high posterior process, unlike those of most metriorhynchoids (i.e. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Cricosaurus bambergensis*, etc.).

The posterior process of the ischium of *Torvoneustes carpenteri* is overall oval, with its apex decentred and pointing posteroventrally rather than strictly posteriorly as in *Lemmysuchus obtusidens*. The entirety of the apex of the posterior process is scarred along its margin both laterally and medially, and this pitted area forms a continuum with that of the distal blade. These structures mark the presence of a cartilage cap *in vivo*. The extremity of the posterior process transitions to the ventral margin of the ischium – and thus the distal blade – through a rounded corner.

The distal blade of *Torvoneustes carpenteri* displays a relatively straight surface with limited undulations, similar to most thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus araucanensis*, *Cricosaurus bambergensis*, *Dakosaurus maximus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Proexochokefalos* cf. *bouchardi*, *Teleosaurus* sp., *Macrospondylus bollensis*, etc.). On the medial side of the distal blade the pitted area is globally larger than on the lateral side, and shows limited bursts of enlargement drawing a series of wavy outlines. The greatest burst of pitted area on the distal blade is located near the base of the anterior process. In *Thalattosuchus superciliosus* NHMUK PV R 2054, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, and *Dakosaurus maximus*, this area is mediolaterally thicker and forms a dorsal platform when both ischia are joined. It is possible that a similar structure was borne by the ischia of *Torvoneustes carpenteri* due to the outline of the pitted area anteriorly (Fig. 34). The whole pitted area on the medial side of the distal blade corresponds to the ischial suture where both ischia were connected through soft tissues *in vivo*.

The anterior process of *Torvoneustes carpenteri* (Fig. 34) is sharp and drastically smaller than the posterior process: the dorsoventral height of its base accounts for less than half of the dorsoventral height of the base of the posterior process. Also, the anteroposterior length of the anterior process exceeds the dorsoventral height of its base giving the process an elongated aspect. Overall, the anterior process points strictly anteriorly, so that it is directly in line with the ventral margin of the ischial blade as in *Dakosaurus maximus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 (or the teleosauroids *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*,*Proexochokefalos* cf. *bouchardi*). This orientation of the anterior process contrasts with the more anterodorsally recurved one found in other thalattosuchians (e.g. *Pelagosaurus typus*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus bambergensis*, *Geosaurus giganteus*, *Aeolodon priscus*, *Teleosaurus* sp., *Lemmysuchus obtusidens*, etc.). The anterior process of *Torvoneustes carpenteri* is composed of a relatively straight dorsal margin (corresponding to the ventral flank of the anterior margin) and a convex ventral one which merge into a pointed extremity.

The anterior peduncle of *Torvoneustes carpenteri* appears reduced due to both its relative and absolute small size. In this way, it is comparable to *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, and *Geosaurus giganteus* (and for example the teleosauroids *Aeolodon priscus*,*Proexochokefalos*

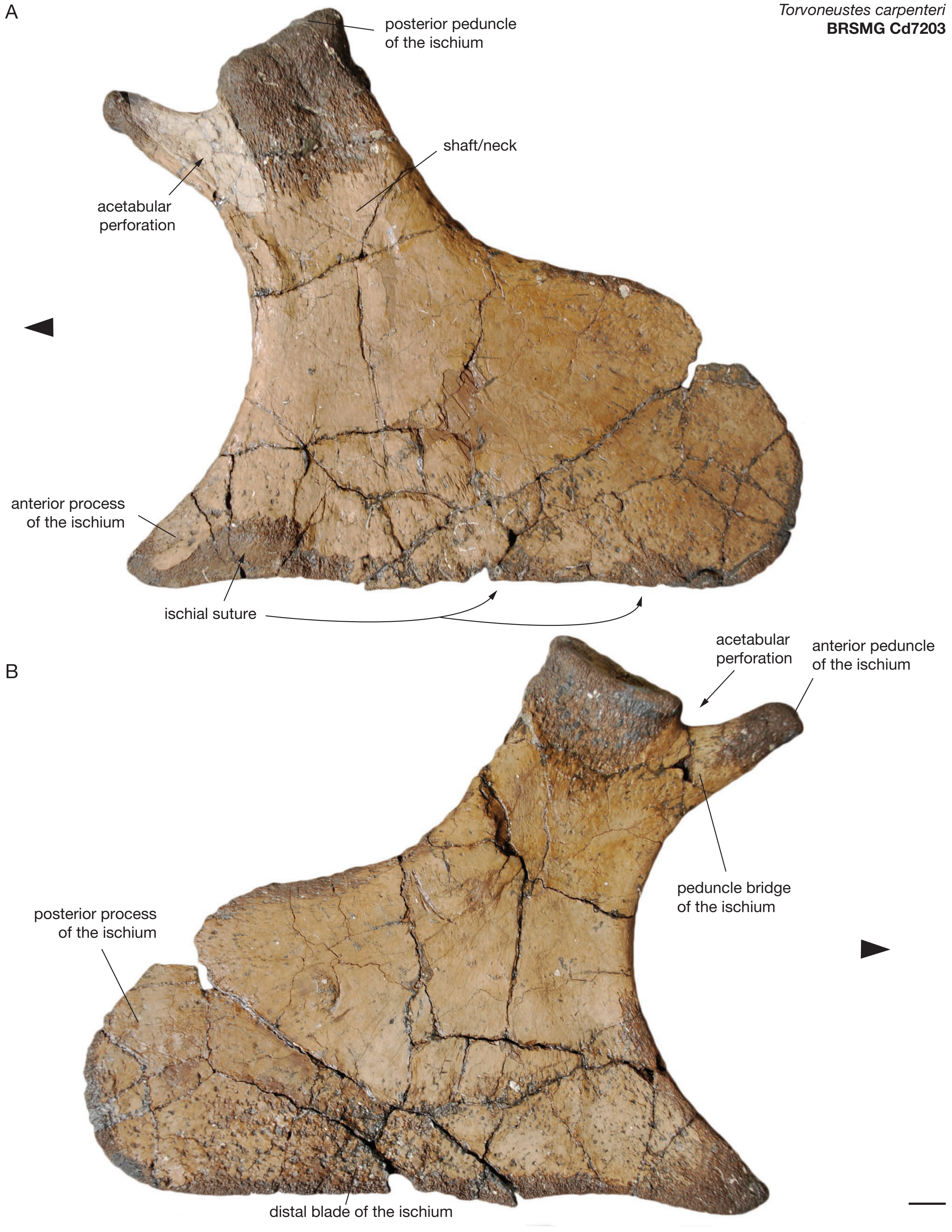


Fig. 34. — Right ischium of *Torvoneustes carpenteri* (Wilkinson, Young & Benton, 2008), BRSMG Cd7203 (paratype): **A**, right ischium in medial view; **B**, right ischium in lateral view. Arrow points anteriorly. Pictures courtesy of Dr. Davide Foffa. Scale bar: 1 cm.

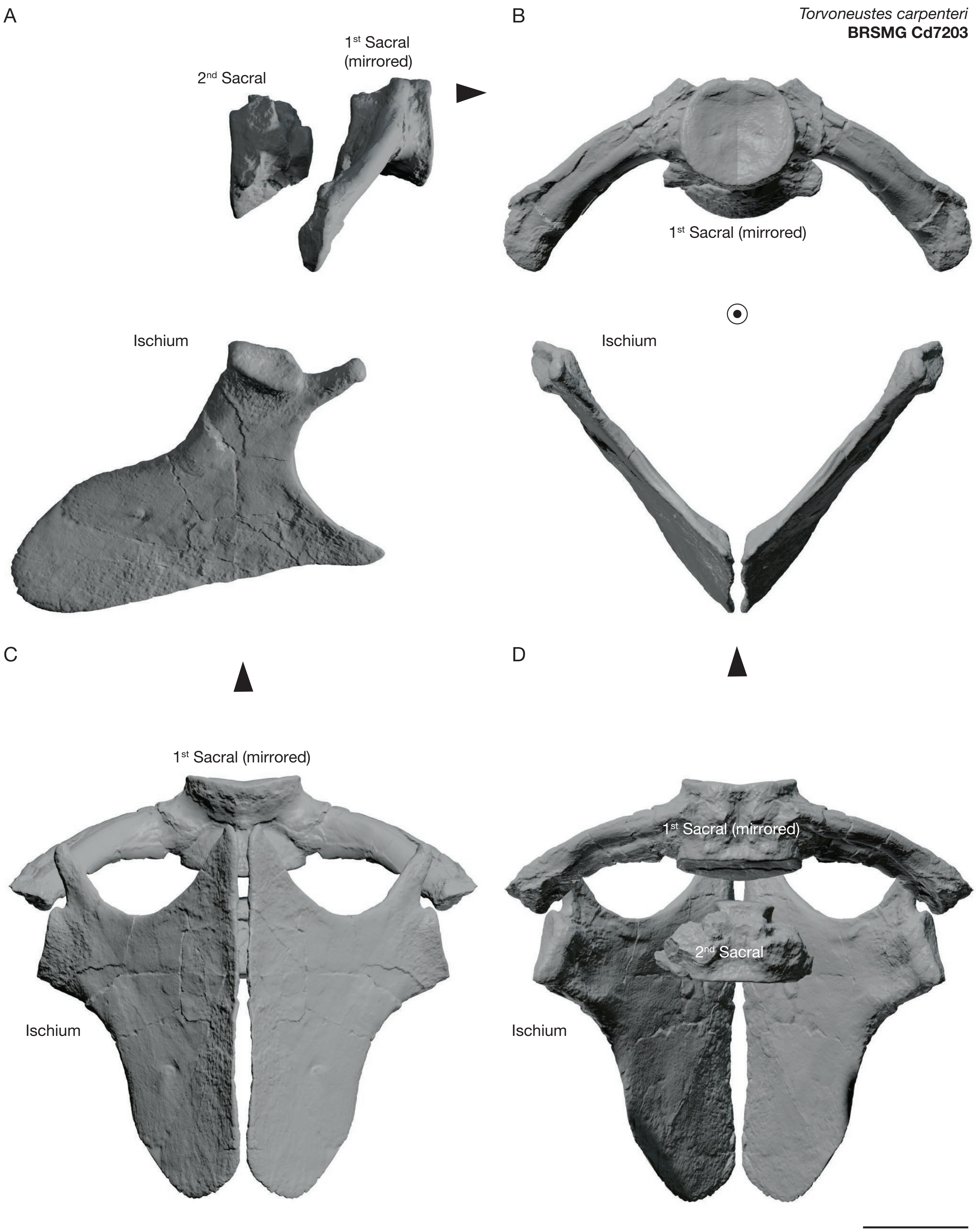


FIG. 35. — Reconstruction of the pelvic girdle of *Torvoneustes carpenteri* (Wilkinson, Young & Benton, 2008), BRSMG Cd7203: **A**, right lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Scale bar: 5 cm.

cf. *bouchardi*, *Sericodon jugleri*, *Teleosaurus* sp.). Indeed, the maximum dorsoventral thickness of the anterior peduncle of *Torvoneustes carpenteri* is inferior to any section of the peduncle bridge, which is similar to the aforementioned taxa but greatly contrasts with *Cricosaurus araucanensis*, *Cricosaurus suevicus*, *Cricosaurus bambergensis* among metriorhynchoids, and other teleosauroids.

The anterior peduncle is borne on the extremity of the peduncle bridge, which is an elongated process in *Torvoneustes carpenteri* (Fig. 34). Similar to *Pelagosaurus typus*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus araucanensis*, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, and *Geosaurus giganteus*, the peduncle bridge of *Torvoneustes carpenteri* extends further dorsally (or proximally) than the posterior peduncle which creates additional space for the acetabular perforation between the peduncles. The dorsal margin of the peduncle bridge of the ischium is concave and forms the ventral border of the acetabular perforation whereas the ventral margin of the peduncle bridge is slightly convex. Both margins are slightly divergent towards the base of the process, so that the peduncle bridge slightly thickens towards its junction with the shaft of the ischium. The base of the peduncle bridge is located slightly more ventrally than in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Cricosaurus araucanensis*, *Cricosaurus albersdoerferi* which renders the acetabular perforation more apparent laterally as in other metriorhynchoids (i.e. *Pelagosaurus typus*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Geosaurus giganteus*, and *Dakosaurus maximus*). Still, the acetabular perforation forms a hollow area on the medial side of the peduncle bridge which extends until the base of the posterior peduncle as in other thalattosuchians (e.g.'*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Torvoneustes carpenteri*, *Cricosaurus araucanensis*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*).

The posterior peduncle of *Torvoneustes carpenteri* is large and accounts for about ¾ of the anteroposterior width of the shaft (Fig. 34). In *Torvoneustes carpenteri*, the posterior peduncle slightly protrudes dorsally, which renders the acetabular perforation clearly visible on the lateral side of the ischium, as in *Thalattosuchus superciliosus* NHMUK PV R 2054, *Geosaurus giganteus*, and *Dakosaurus maximus* among metriorhynchoids.

THE PELVIC GIRDLE SKELETON OF THALATTOSUCHIANS: TELEOSAUROIDS

PLAGIOPHTHALMOSUCHUS GRACILIROSTRIS (WESTPHAL, 1961)

For measurements, see Tables 7-9.

Ilium

The ilium of *Plagiophthalmosuchus gracilirostris* (Westphal, 1961) (Fig. 36) bears the typical postacetabular process of teleosauroids contrasting with the metriorhynchoids iliac morphology (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Geosaurus giganteus*, etc.). The ilium of *Plagiophthalmosuchus gracilirostris* is not complete, but appears to possess a rather slender postacetabular process, in the way of *Platysuchus multiscrobiculatus*. Indeed, the junction between the ventral margin of the postacetabular process and the posterior margin of the ilium seems to form an angle closer to 90° than to an obtuse angle like seen in other teleosauroids (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.). The exact shape of the extremity of the postacetabular process of *Plagiophthalmosuchus gracilirostris* is unclear, but was presumably elliptic as in other teleosauroids.

The dorsal margin of the ilium of *Plagiophthalmosuchus gracilirostris*, which corresponds to the iliac crest, appears to have been relatively straight or slightly convex as in *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, and *Neosteneosaurus edwardsi*. The junction between the iliac crest and the base of the preacetabular process is partially broken but was potentially slightly concave as in other teleosauroids. Likewise, the preacetabular process of *Plagiophthalmosuchus gracilirostris* is not preserved but presumably presented the shape of a hook. The surface underneath the base of the preacetabular process, corresponding to the anterior margin of the ilium, is straight as in *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus* and *Neosteneosaurus edwardsi contra Charitomenosuchus leedsi*.

AEOLODON PRISCUS (VON SÖMMERRING, 1814)

For measurements, see Tables 7-9.

The specimen NHMUK PV R 1086 is a juvenile, whereas the specimen MNHN.F.CNJ78 corresponds to a more mature individual. Differences in shape are presumably related to ontogeny.

Ischium

The ischium of *Aeolodon priscus* NHMUK PV R 1086 (Fig. 37) displays a relatively short and thick shaft, whereas it appears more slender and elongated in MNHN.F.CNJ78 (Fig. 38). In comparison, *Macrospondylus bollensis* also displays a thick shaft. The anterior and posterior margins of the ischium of *Aeolodon priscus* NHMUK PV R 1086, notably constituting the shaft, are both concave. However, the posterior margin of the ischium switches to convex at about its mid-length as it forms the posterior process of the ischium. The posterior process of *Aeolodon priscus* NHMUK PV R 1086 is relatively thick as its dorsoventral height accounts for roughly half of the total height of the bone. The posterior process of NHMUK PV R 1086 is dorsoventrally thicker than that of MNHN.F.CNJ78 due to differences in the concavity of their posterior margin. In comparison, *Sericodon jugleri* displays a relatively thick posterior process, whose extremity is slightly dorsoventrally thicker than *Aeolodon priscus* MNHN.F.CNJ78, but not as broad as in NHMUK PV R 1086. Another factor adding to the relative thickness (i.e. almost ½) of the posterior process of *Aeolodon priscus* NHMUK PV R 1086 is the angular relation between the ventral margin of the ischium and the shaft. The ventral margin is almost perpendicular to the median of the shaft, whereas this angular relation is slightly greater for

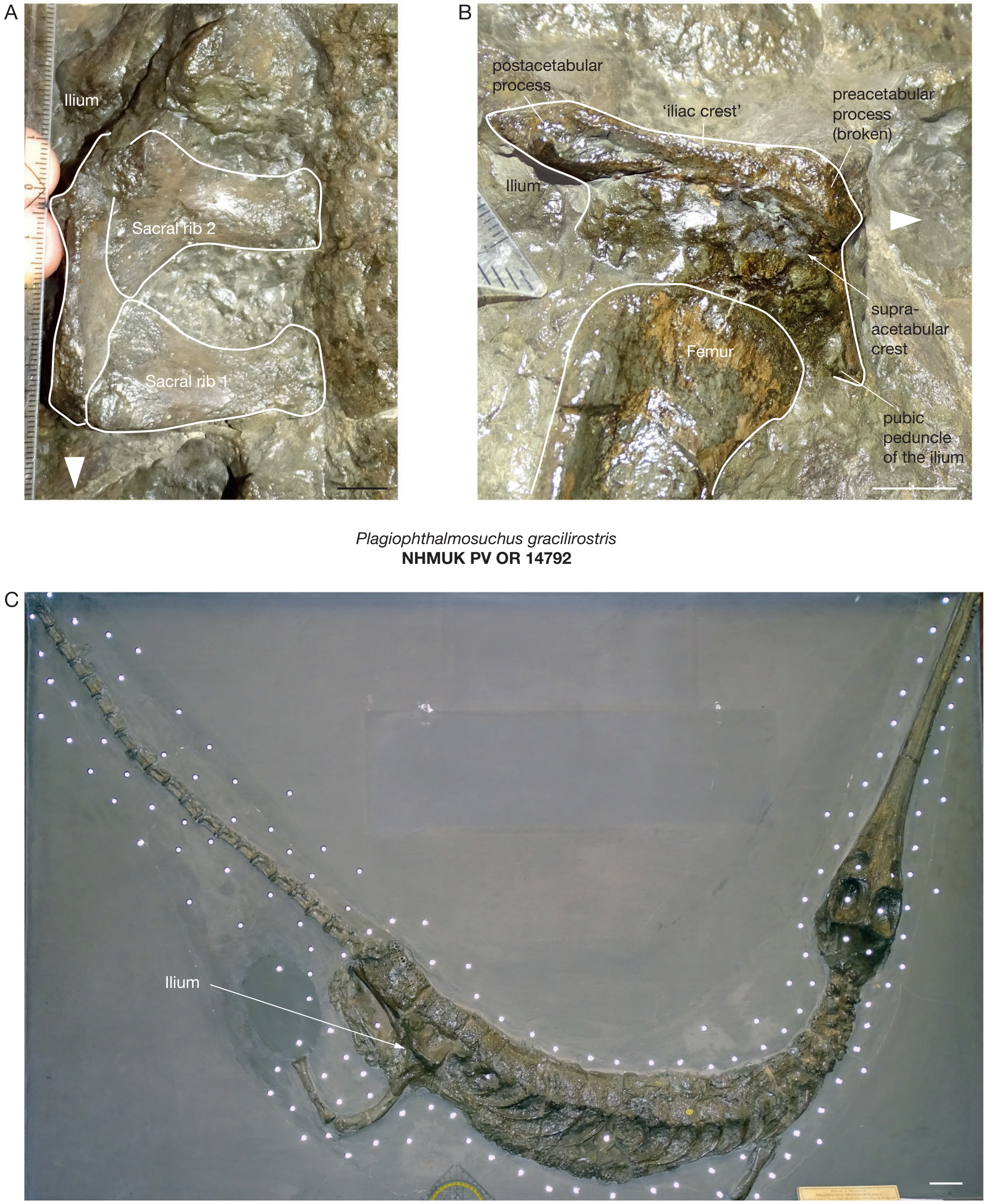


Fig. 36. — Pelvic girdle elements and overview of *Plagiophthalmosuchus gracilirostris* (Westphal, 1961), NHMUK PV OR 14792 (holotype): **A**, right ilium in dorsal view; **B**, right ilium in lateral view; **C**, overview of *Plagiophthalmosuchus gracilirostris*. Arrow points anteriorly. Scale bars: A, B, 1 cm; C, 5 cm.

MNHN.F.CNJ78 thus increasing its total dorsoventral height and giving it a more slender appearance. In MNHN.F.CNJ78, the posterior margin of the ischium displays a more subtle concavity but with a greater amplitude. Hence, the posterior margin of the ischium of *Aeolodon priscus* MNHN.F.CNJ78 appears almost entirely concave, and culminates posteriorly to form a dorsoventrally thinner posterior process compared to *Aeolodon priscus* NHMUK PV R 1086.

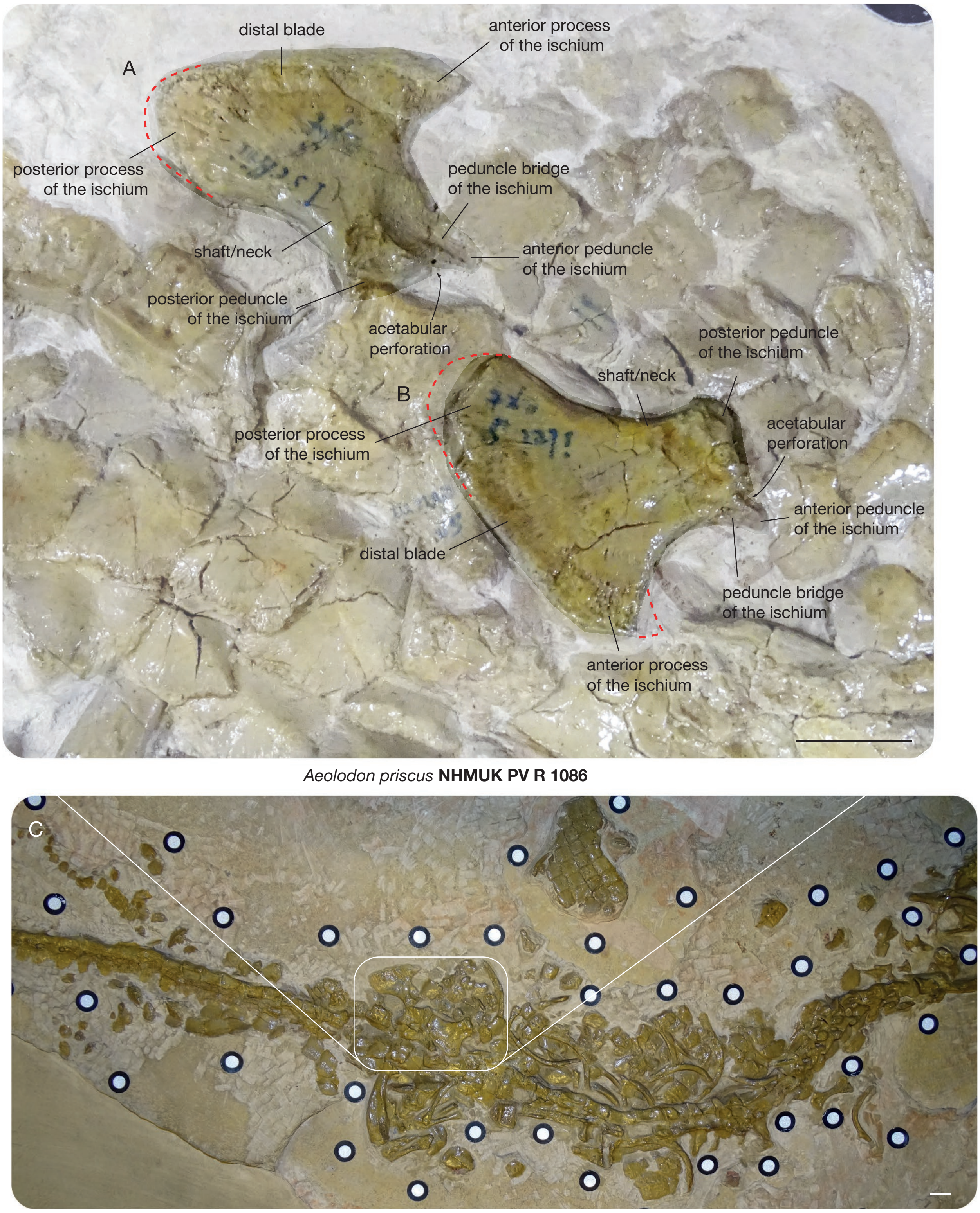


FIG. 37. — Pelvic girdle elements of *Aeolodon priscus* (Von Sömmerring, 1815), NHMUK PV R 1086 (holotype): **A**, right ischium in medial view; **B**, left ischium in lateral view; **C**, overview of *Aeolodon priscus*. Scale bars: 1 cm.

In *Aeolodon priscus*, the ventral margin of the ischium is straight over most of its surface. Unlike in MNHN.F.CNJ78, the linearity of the margin of *Aeolodon priscus* NHMUK PV R 1086 is ruptured by a bent of about 160° located where the anterior process starts (i.e. the portion of the bone anterior and ventral to the thinnest portion of the shaft), similar to the metriorhynchoid *Thalattosuchus superciliosus*. The anterior process of *Aeolodon priscus* is a sharp bony process constituted by a ventral straight margin and a slightly curved (concave) dorsal one, as in most teleosauroids (like in *Teleosaurus* sp. [Geoffroy Saint Hilaire 1825], *Macrospondylus bollensis*, and *Proexochokefalos* cf. *bouchardi*). It points anterodorsally as in other thalattosuchians (i.e. *Thalattosuchus superciliosus*, *Cricosaurus albersdoerferi*, *Lemmysuchus obtusidens*, etc.). The anterior process of *Aeolodon priscus* (Fig. 37) does not appear to protrude anteriorly further than the anterior peduncle, as in some metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Thalattosuchus superciliosus* NHMUK PV R 2054).

The anterior margin of the ischium of *Aeolodon priscus* (Figs 37; 38) is concave underneath the peduncles. The degree of concavity of the anterior margin in *Aeolodon priscus* NHMUK PV R 1086 is comparable to that of *Geosaurus giganteus* and thus also takes the shape of a Lancet arch. Dorsally, the anterior margin culminates to form the anterior peduncle but this portion is partially obstructed. The dorsal portion of the anterior peduncle and the peduncle bridge of *Aeolodon priscus* NHMUK PV R 1086 are visible on the right ischium, and the outline of the anterior peduncle appears to be circular in medial view, as in other thalattosuchians (i.e. *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus albersdoerferi*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Proexochokefalos* cf. *bouchardi*, *Teleosaurus* sp., etc.). The dorsal border of the peduncle bridge appears relatively straight or faintly concave. Globally, the anterior peduncle appears short, especially in relation to the posterior peduncle as in *Sericodon jugleri* but unlike in *Cricosaurus suevicus*. A small notch marks the transition between the anterior and posterior peduncles; it corresponds to the acetabular perforation. The latter is smaller than in *Sericodon jugleri* and *Macrospondylus bollensis*, but appears to have the same mediolateral orientation which is uncommon in teleosauroids. The posterior peduncle sticks out from the rest of the shaft as it protrudes in all directions. Still, the shaft of the ischium of *Aeolodon priscus* is not significantly longer anteroposteriorly than the posterior peduncle unlike in *Lemmysuchus obtusidens*, and thus resembles those of *Neosteneosaurus edwardsi*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Torvoneustes carpenteri*, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus* NHMUK PV R 2054, or even *Dakosaurus maximus*. The posterior peduncle is located more ventrally than the anterior peduncle, which overhangs the ischium dorsally as in other thalattosuchians.

On the medial side of the ischia of *Aeolodon priscus* NHMUK PV R 1086, there is a crescent-shaped area underneath the anterior peduncle extending as far ventrally as the base of the shaft (i.e. anteroposterior narrowing) and as far posteriorly as the beginning of the posterior peduncle. The latter displays a drastic slimming down mediolaterally from the surrounding areas. Such a hollowed area on the medial side of the ischium is commonly found in thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus albersdoerferi*, *Torvoneustes carpenteri*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, etc.). On the medial side of the bone, the distal blade of *Aeolodon priscus* NHMUK PV R 1086 (Fig. 37) is deeply scarred with perpendicular grooves as in other thalattosuchians. This region presumably bore cartilaginous structures *in vivo* assuring, most notably, the connection between both ischia.

SERICODON JUGLERI VON MEYER, 1845
For measurements, see Tables 7-9.

The bone referred to the pubis of *Sericodon jugleri* MJSN SCR010-312 in Schaefer *et al.* (2018) is not included in our description. Indeed, the bone displays all the characteristics of a derived teleosauroid humerus: shortening of humeral shaft; posterior deflection of the articular proximal head; distal torsion of the condyles in relation to the coronal plane; continuous surface between the deltopectoral crest and the proximal articular head.

Ilium

The ilium of *Sericodon jugleri* (Figs 39; 40) stand out with its combination of a long and mediolaterally thick preacetabular process with a proportionally short and broad postacetabular process. Indeed, the preacetabular process of *Sericodon jugleri* slightly flares out anteriorly as it increases in thickness mediolaterally, which contrasts with other teleosauroids (e.g. *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*). The apex of the preacetabular process of *Sericodon jugleri* is semi-circular in dorsal view. In lateral view, the preacetabular process forms a relatively long (about 26% of total dorsal length) and sharp apex: its ventral margin is concave whereas its dorsal margin is slightly convex, similar to other teleosauroids. However, in *Sericodon jugleri*, the preacetabular process is oriented anterodorsally which further contrasts with other teleosauroids (e.g. *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*). Posteriorly, the junction between the preacetabular process and the dorsal margin of the ilium – the iliac crest – forms a shallow recess.

Overall, the postacetabular process of *Sericodon jugleri* stands out from that of other teleosauroids in displaying the following combined traits: 1) two convex margins forming a Lancet arch; 2) two apparent hollows marking its base dorsally and posteriorly; and 3) a posterodorsal orientation. Similarly to the preacetabular process, the postacetabular process of *Sericodon jugleri* possesses a dorsal component in its orientation so that its apex points posterodorsally, as in *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, and *Neosteneosaurus edwardsi*. The dorsal and posterior margins of the postacetabular process of *Sericodon jugleri* are both slightly convex with the same degree, giving the posterior process the shape of a Lancet arch. In comparison, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens* and *Machimosaurus* also have a posterior process in the overall shape of a Lancet arch, although with relatively differing degrees of convexity. Anteriorly, the first half of the lateral surface of the iliac crest is finely striated and so is the apex of the posterior process, indicating the presence of a

Fig. 38. — Pelvic girdle elements of *Aeolodon priscus* (Von Sömmerring, 1815), MNHN.F.CNJ78: **A**, left ischium in lateral view; **B**, overview of *Aeolodon priscus*. Scale bars: 1 cm.

cartilage cap *in vivo*. Ventrally, around ⅔ of its length, the concave posterior margin of the ischium becomes slightly concave for the remaining of its length. The inflection point marks the base of the postacetabular process, like the recess along the dorsal margin of the ischium. In comparison, only *Machimosaurus* and *Lemmysuchus obtusidens* appear to display two shallow recesses bordering the base of the postacetabular process, whereas other teleosauroids either displays none (e.g. *Platysuchus multiscrobiculatus* and *Macrospondylus bollensis*) or only one (e.g. *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Proexochokefalos* cf. *bouchardi*).

The anterior margin underneath the preacetabular process is straight throughout most of its length. Indeed, the supraacetabular crest follows the outline of the anterior margin of the ilium without brimming over the edge (like in *Pelagosaurus typus*). Ventrally, the anterior margin of the ilium of *Sericodon jugleri* forms a slight bulge corresponding to the anterior edge of the pubic peduncle. The ventral margin of the ilium of *Sericodon jugleri* is strongly undulating as the ventral surfaces of the peduncles are not aligned, as in other teleosauroids. However, *Sericodon jugleri* differs from most teleosauroids in displaying a strongly ventrally protruding pubic peduncle as well as a marked acetabular perforation. In comparison, the pubic peduncle of *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens* is also ventrally prominent but their acetabular perforation is shallower. In *Sericodon jugleri*, the acetabular perforation forms a relatively deep notch with a semi-circular outline.

Laterally, the bony acetabulum of the ilium of *Sericodon jugleri* forms a relatively large and deep recess almost spherical in shape and the bony acetabulum is almost as long anteroposteriorly as dorsoventrally tall as in most teleosauroids. The bony acetabulum is bordered anteriorly and dorsally by an arched structure: the supracetabular crest. The latter forms a thin ridge anteriorly which gradually widens dorsally to form a wedged-shape scarred area, which contrasts with the thinner supraacetabular crest of *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*. Laterally, the supraacetabular crest of *Sericodon jugleri* faintly protrudes throughout its length, as in most teleosauroids (except *Proexochokefalos* cf. *bouchardi*).

On the lateral surface of the ilium, the outline of the pubic and ischial peduncle of *Sericodon jugleri* are similar to *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*. The pubic peduncle of *Sericodon jugleri* forms two major dorsal peaks slightly posteriorly titled and separated by a deep depression. The anterior peak is isosceles-shaped whereas the posterior one possesses a circular top. In addition, the pubic peduncle of *Sericodon jugleri* is dorsoventrally taller than the ischial peduncle as in *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*. Still, in *Sericodon jugleri*, both peaks of the pubic peduncle are similarly sized which contrasts with *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*. Ventrally, the surface of the pubic peduncle of *Sericodon jugleri* displays a wedged outline similar to other teleosauroids: the lateral margin is concave as it borders the acetabulum, whereas the medial margin is convex. However, unlike in *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*, the posterior margin of the pubic peduncle of *Sericodon jugleri* does not form a pointed tip but is rather concave (which is similar to *Charitomenosuchus leedsi*, and *Proexochokefalos* cf. *bouchardi*). Like in *Neosteneosaurus edwardsi* and *Proexochokefalos* cf. *bouchardi*, the mediolateral thickness of the pubic peduncle is relatively constant throughout its length.

Laterally, the outline of the ischial peduncle of *Sericodon jugleri* has a more common shape as in other teleosauroids: it is crescent-shaped with its dorsal apex being posteriorly shifted. As it borders the acetabulum posteriorly, the ischial peduncle protrudes laterally and hence is mediolaterally thicker posteriorly. In ventral view, the ischial peduncle displays a triangular outline with its longest axis anteroposteriorly oriented. Like for the pubic peduncle, the lateral margin of the ischial peduncle of *Sericodon jugleri* is slightly concave whereas its medial margin is slightly convex. Like in *Charitomenosuchus leedsi* and *Proexochokefalos* cf. *bouchardi*, the ischial peduncle of *Sericodon jugleri* is markedly longer anteroposteriorly than the pubic peduncle (about ⅓ of the pubic peduncle's length). This contrasts with *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens* in which the difference is more subtle.

The attachment sites for the sacral ribs of *Sericodon jugleri* are found on the medial side of the ilium, and are overall similar to most teleosauroids (except *Lemmysuchus obtusidens* and *Machimosaurus* which possess a third attachment site for the first caudal). Indeed, the attachment sites for the sacral ribs form two distinct imprints located at the mid-height of the bone. They share a margin around the centre of the ilium, then gradually flare out in opposing directions (i.e. anteriorly and posteriorly) like a pair of almost symmetrical wings. The attachment site for the second sacral rib is the largest. The dorsal edge of the attachment site for the first sacral rib splits the preacetabular process in two along its greatest length, and extends up to its apex. Similarly, the dorsal edge of the attachment site for the second sacral rib reaches the apex of the postacetabular process through its mid-line. However, the ventral edge of the attachment site of the second sacral rib reaches the posteroventral corner of the ilium whereas the ventral edge of the attachment site for the first sacral rib forms a semi-circular shape which stretches to the base of the preacetabular process. The medial surface of both attachment sites are deeply scarred with radiating ridges, and also possess large medial excrescences located around their top (for the second) and centre (for the first). The attachment site for the second sacral rib also forms a small bump along the edge of the posterior margin of the ischium, which is partly visible in anterior view. This small bump differs from the marked pointed corner found along the posterior margin of *Neosteneosaurus edwardsi* (underneath the postacetabular process).

Ischium

Proximally, the ischium of *Sericodon jugleri* (Figs 39; 40) bears the distinctive combination of a proportionally short peduncle bridge as well as a marked acetabular perforation. The former trait – short peduncle bridge – is also found in *Aeolodon priscus* in which it is proportionally smaller in relation to the posterior peduncle. The peduncle bridge of *Sericodon jugleri* appears distantly set from the posterior peduncle, as in *Macrospondylus bollensis* and *Charitomenosuchus leedsi* (which also have a large acetabular perforation). The dorsal margin of the peduncle bridge is slightly concave whereas the anterior margin is relatively straight. Anterodorsally, the peduncle bridge of *Sericodon jugleri* is proportionally thick – a trait emphasized by its short length – but still decreases in dorsoventral thickness towards the anterior peduncle. Mediolaterally, the peduncle bridge increases in width towards the articular facet of the anterior peduncle. The junction between

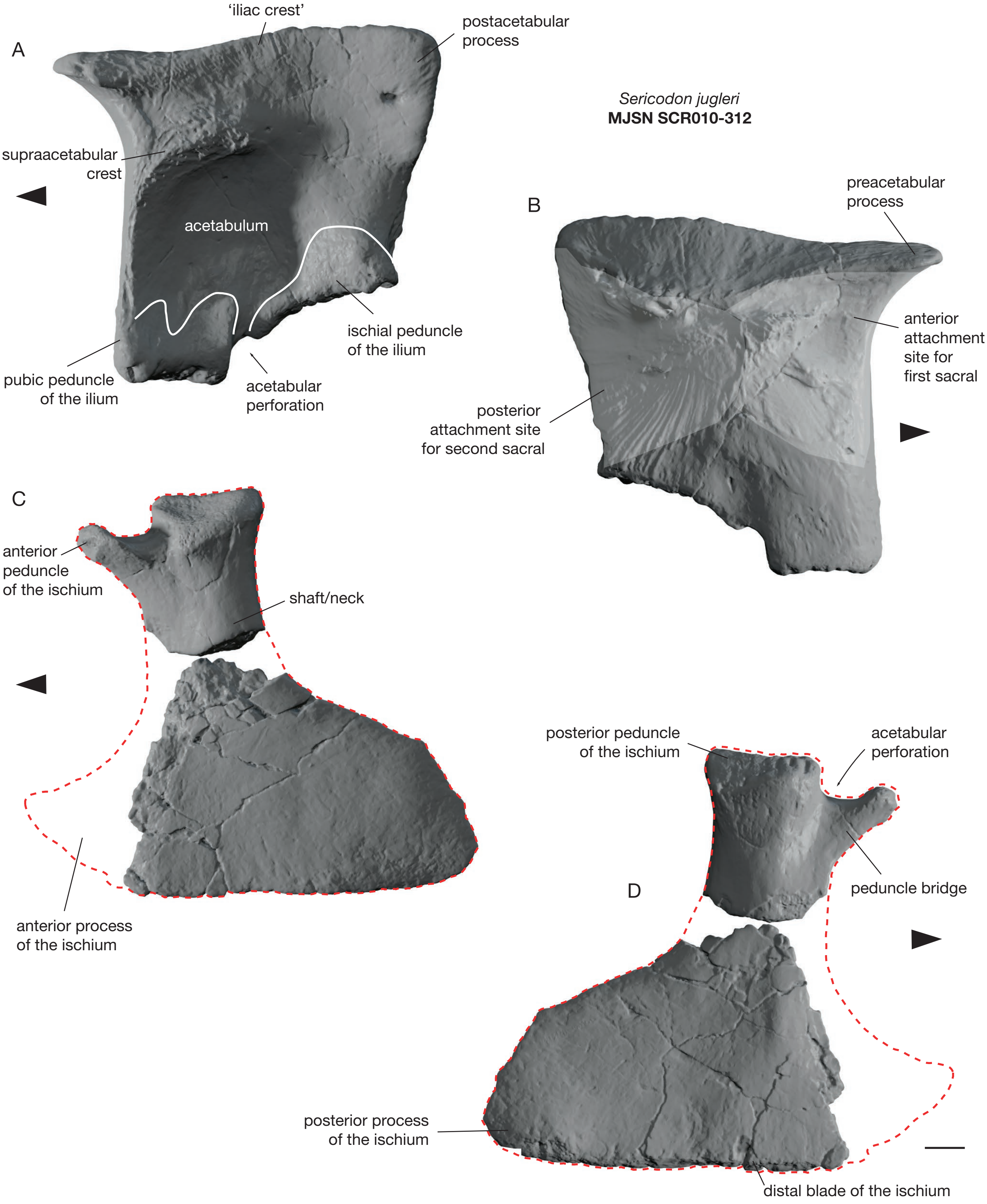


FIG. 39. — Pelvic girdle elements of *Sericodon jugleri* Von Meyer, 1845, MJSN SCR010-312: **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, left ischium in lateral view; **D**, left ischium in medial view. Cross indicates posterior. Original models courtesy of Dr. Jeremy Anquetin (Jurassica Museum-MJSN). Scale bar: 1 cm.

the articular facet of the anterior peduncle and the peduncle bridge is marked dorsally and ventrally by a small depression, whereas mediolaterally it is marked by a peak in width. The articular facet of the anterior peduncle is convex and displays the typical crescent-shape found in other teleosauroids: dorsally concave, ventrally convex, and pointed mediolaterally. Like in other thalattosuchians, the anterior peduncle of *Sericodon jugleri* appears laterally offset when looking at the posterior peduncle as a whole, but it is actually centred in relation to the lateral articular facet.

In *Sericodon jugleri*, the shape of the acetabular perforation is uncommon among teleosauroids: it is large, is sub-circular in shape and is mediolaterally oriented as in extant crocodylians and dyrosaurids. In comparison, the acetabular perforation of *Aeolodon priscus* and *Macrospondylus bollensis* display the same mediolateral orientation, but in *Charitomenosuchus leedsi* it is slightly tilted medially (see below). In *Sericodon jugleri*, the pronounced depth of the acetabular perforation coupled with the shortness of the peduncle bridge make the posterior peduncle stand out dorsally. The overall shape of the posterior peduncle of *Sericodon jugleri* is similar to other teleosauroids. About ⅓ of the posterior peduncle is oriented medially and displays a strongly scarred surface as it was connected to the ischial peduncle of the ilium. The remaining portion of the posterior peduncle is laterally oriented, has a subquadrangular outline and a slightly concave surface. The junction between the two surfaces forms a slightly protruding ridge also concave. The lateral edge of the posterior peduncle forms a thick rounded rim (e.g. *Teleosaurus* sp., *Macrospondylus bollensis*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens* and presumably *Machimosaurus*), which becomes more tenuous on the other sides. In comparison, *Mycterosuchus nasutus*, *Indosinosuchus potamosiamensis* Martin, Suteethorn, Lauprasert, Tong, Buffetaut, Liard, Salaviale, Deesri, Suteethorn & Claude, 2019, and *Platysuchus multiscrobiculatus* display a thin rim marking the edge of the posterior peduncle.

Distally, the ischium of *Sericodon jugleri* is distinct due to its bulky posterior process; it bears a dorsoventrally thick and rounded posterior process so that its entire posterior margin presumably displayed a strong sinusoidal shape (with the inflection point located around its mid-length). Other teleosauroids with a similarly undulating posterior margin include *Aeolodon priscus*, *Proexochokefalos* cf. *bouchardi*, *Machimosaurus*, and *Lemmysuchus obtusidens*, all of which display a relatively thick posterior process. Compared to the more derived teleosauroids *Proexochokefalos* cf. *bouchardi*, *Machimosaurus*, and *Lemmysuchus obtusidens*, the aeolodontines *Sericodon jugleri* and *Aeolodon priscus* display an anteroposteriorly shorter posterior process which contributes to their bulkier aspect. The ischial blade of *Sericodon jugleri* is relatively straight, and the ischial suture surface is restricted to its ventral margin (i.e. does not expand on the medial surface of the bone) as in the other aeolodontines *Aeolodon priscus* and *Mycterosuchus nasutus*. This feature is also present in in *Pelagosaurus typus*, *Proexochokefalos* cf. *bouchardi*, and *Neosteneosaurus edwardsi*.

MYCTEROSUCHUS NASUTUS (ANDREWS, 1909)

For measurements, see Tables 7-9.

Ischium

The most distinguishing feature of the ischium of *Mycterosuchus nasutus* (Fig. 41) is the combination of a thin and elongated shaft with a long and narrow posterior process. Indeed, the ischium of *Mycterosuchus nasutus* (Fig. 41) displays strongly concave anterior and posterior margins, resulting in a slender shaft as in *Teleosaurus* sp. (NHMUK PV R 238 and OUMNH. J1638) and *Charitomenosuchus leedsi* (NHMUK PV R 3806). Comparatively, the ischium of *Proexochokefalos* cf. *bouchardi* (MJSN SCR010-374) also displays a slender shaft and an overall slender ischium. The slender shaft of *Mycterosuchus nasutus* strongly contrasts with the thicker shaft of the other aeolodontines *Aeolodon priscus* and, presumably, *Sericodon jugleri*.

Dorsally and ventrally to the maximum constriction of the shaft, the ischium of *Mycterosuchus nasutus* drastically flares out which gives it a very distinctive aspect like *Charitomenosuchus leedsi* and *Teleosaurus* sp. (NHMUK PV R 238 and OUMNH. J1638). However, the posterior margin of the ischium of *Mycterosuchus nasutus* stands out in rapidly displaying a change in concavity directly dorsally to the constriction. As a result, the posterior margin of the ischium underneath the posterior peduncle forms a marked bulged, rather than being straight as in *Teleosaurus* sp. (NHMUK PV R 238 and OUMNH. J1638) or concave throughout as in *Charitomenosuchus leedsi*. The edge of the posterior peduncle of *Mycterosuchus nasutus* forms a thin ridge on both its lateral and medial sides, which appears similar to *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Platysuchus multiscrobiculatus* but contrasts with *Sericodon jugleri* , *Teleosaurus* sp., *Macrospondylus bollensis*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens* and presumably *Machimosaurus*. Only the base of the peduncle bridge of *Mycterosuchus nasutus* is preserved, which shows a partially obstructed acetabular perforation laterally as in most teleosauroids (except *Sericodon jugleri*, *Charitomenosuchus leedsi* and *Macrospondylus bollensis*).

Underneath the shaft, the posterior margin of the ischium of *Mycterosuchus nasutus* is relatively straight until it reaches the apex of the posterior process, as in most teleosauroids (e.g. *Teleosaurus* sp. (NHMUK PV R 238 and OUMNH. J1638), *Macrospondylus bollensis*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*). It contrasts with the irregular posterior margin of *Charitomenosuchus leedsi*, and also with the other aeolodontines *Aeolodon priscus* and *Sericodon jugleri* which have a straight but shortened posterior margin. Like in most thalattosuchians, the ventral margin of the ischium of *Mycterosuchus nasutus* – corresponding to the ischial blade – is relatively straight throughout its length, although it shows a subtle bulge around its mid length. Due to the shape and relative inclination of the posterior and ventral margin of the ischium, the posterior process of *Mycterosuchus nasutus* displays a proportionality long and narrow outline compared to other aeolodontines *Aeolodon priscus* and *Sericodon jugleri*. Still, the posterior process of *Mycterosuchus nasutus* is less extended than in *Teleosaurus* sp. (NHMUK PV R 238 and OUMNH.J1638) and *Macrospondylus bollensis* among teleosauroids, and it is also dorsoventrally thicker than in *Platysuchus multiscrobiculatus*. Posteriorly, the posterior process of *Mycterosuchus nasutus* extends to form a slightly rounded apex with the greatest axis of the concavity being parallel to the ventral margin of the ischium, giving it a dorsoventrally symmetrical aspect as in *Pelagosaurus typus*,

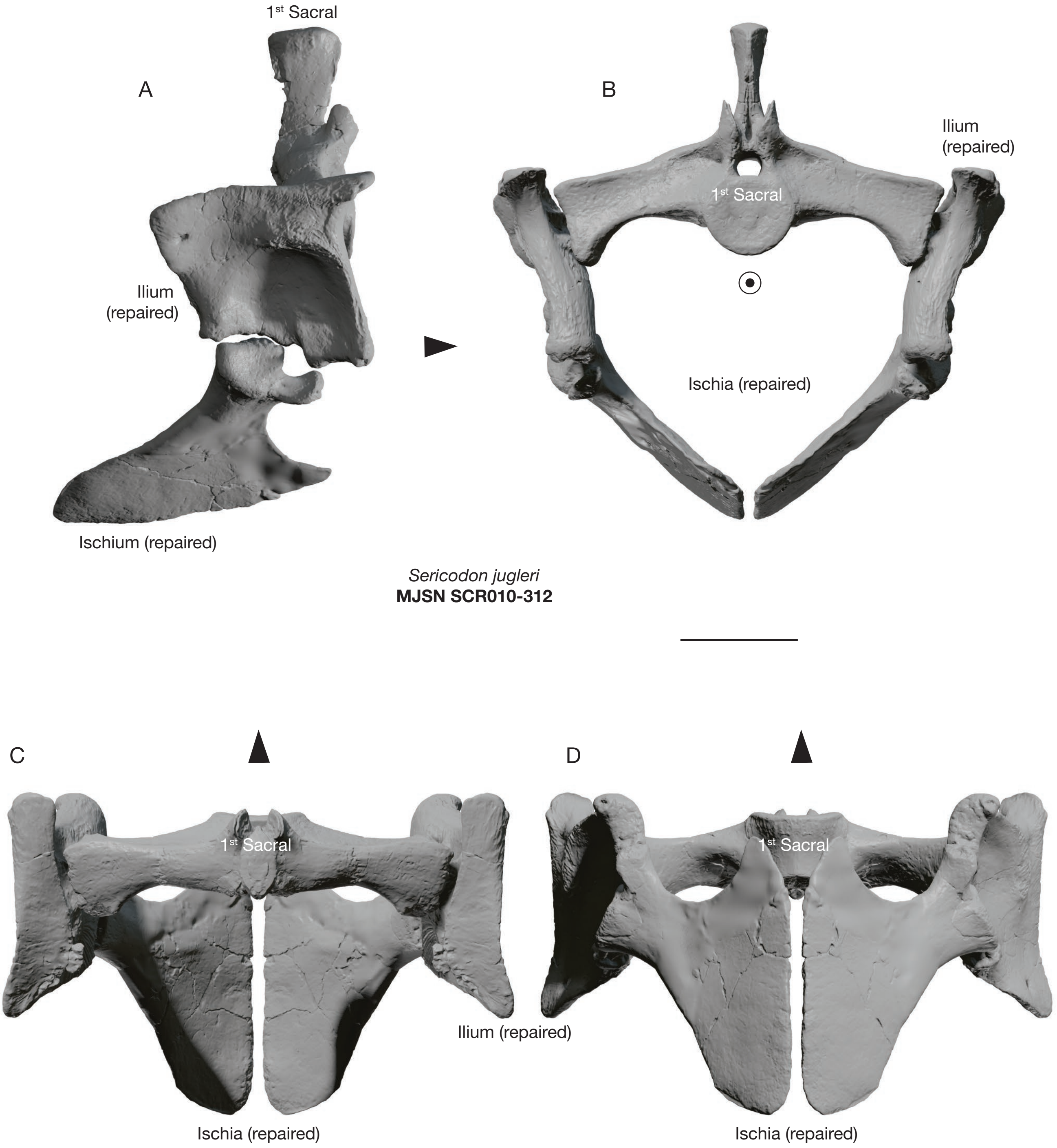


Fig. 40. — Reconstruction of the pelvic girdle of *Sericodon jugleri* Von Meyer, 1845, MJSN SCR010-312: **A**, right lateral view; **B**, anterior view; **C**, ventral view. Target indicates anterior. Arrow points anteriorly. The right ilium and ischium are mirrored. Original models courtesy of Dr. Jeremy Anquetin (Jurassica Museum-MJSN). Scale bar: 5 cm.

Teleosaurus sp. (NHMUK PV R 238 and OUMNH.J1638), *Platysuchus multiscrobiculatus*, *Proexochokefalos* cf. *bouchardi*, and *Lemmysuchus obtusidens*. The slightly convex apex of *Mycterosuchus nasutus* contrasts with the angular shapes of *Aeolodon priscus*, *Sericodon jugleri*, *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*, and the marked semi-circular apex of *Pelagosaurus typus*, *Platysuchus multiscrobiculatus* and *Macrospondylus bollensis*. In this way, the degree of convexity of the apex of *Mycterosuchus nasutus* is similar to those of *Proexochokefalos* cf. *bouchardi* and *Lemmysuchus obtusidens*, but at a smaller size.

In *Mycterosuchus nasutus*, the ischial suture is mainly oriented ventrally as in the other aeolodontines (*Aeolodon priscus* and *Sericodon jugleri*), and also as in *Pelagosaurus typus*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and hence is not clearly visible on the medial side of the ischial blade.

Pubis

The pubis of *Mycterosuchus nasutus* (Figs 41; 42) is distinguished from that of other thalattosuchians in possessing a prominent posterior bulge or protuberance at the intersection between the distal blade and the lateral margin of the pubis (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Cricosaurus bambergensis*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Machimosaurus*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*). The taxa '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 also possesses a posterior protuberance but it is more subtle than in *Mycterosuchus nasutus*. Among dyrosaurids, only *Cerrejonisuchus improcerus* possesses a strongly protruding posterior protuberance.

The lateral and medial margins of the pubis of *Mycterosuchus nasutus* forming the entirety of the pubic apron are not symmetrical. Indeed, the medial margin of *Mycterosuchus nasutus* is concave throughout whereas its lateral margin is concave proximally but starts undulating distally, similar to what is observed in *Suchodus durobrivensis* and also *Machimosaurus* to a lesser extent. The lateral margin of *Mycterosuchus nasutus* starts to bulge (and thus forms an undulation) at the same time as the pubic apron expands distally. Hence, the bulge of the lateral margin marks the beginning of the distal flare out of the pubic plate similar to *Suchodus durobrivensis* but unlike *Machimosaurus*.

Overall, *Mycterosuchus nasutus* appears to possess a well-developed pubic symphysis, but its size relative to the total length of the pubis cannot be calculated. However, the intuition of a relatively long pubic symphysis for *Mycterosuchus nasutus* comes from the fact that the total length of the pubic symphysis (reconstructed as on Fig. 41) almost equals the remaining mediolateral length of the distal blade of the pubis. The junction between the medial margin of the pubis and the pubic symphysis of *Mycterosuchus nasutus* is unknown, but was presumably forming a right-angled corner as in other thalattosuchians with a well-developed pubic symphysis (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Lemmysuchus obtusidens*, *Machimosaurus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.). In *Mycterosuchus nasutus*, the pubic symphysis is set at an angle of approximately 27° with the median of the shaft (and upper portion of the pubic apron), which is close to the value of *Charitomenosuchus leedsi* but slightly lesser than the 30° of *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi*. Despite this, the inclination of the pubic symphysis of *Mycterosuchus nasutus* falls within the same overall range as *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*.

The pubic symphysis of *Mycterosuchus nasutus* laterally transitions to the distal blade of the pubis through an angle of approximately 150°, which is greater than in *Neosteneosaurus edwardsi*, but is similar to *Lemmysuchus obtusidens* and especially *Charitomenosuchus leedsi*. The exact shape of the distal blade of *Mycterosuchus nasutus* is unknown but appears to have been convex based on the preserved portions. as in other thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Machimosaurus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.). The thickness of the distal blade of the pubis of *Mycterosuchus nasutus* in the anteroposterior direction is greater than that of the pubic symphysis (Fig. 42), similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Lemmysuchus obtusidens*, and *Neosteneosaurus edwardsi*. Like in other thalattosuchians, the pubic apron of *Mycterosuchus nasutus* (Fig. 42) is concave anterodorsally (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 3804, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.).

TELEOSAURUS GEOFFROY SAINT-HILAIRE, 1825

For measurements, see Tables 7-9.

Ischium

The ischium of *Teleosaurus* sp. (NHMUK PV R 238 [Fig. 43]) stands out with its combination of both a slender shaft and posterior process. Indeed, the ischium of *Teleosaurus* sp. displays a strongly concave anterior margin which partly accounts for the strong shaft constriction. In comparison, the shaft of *Teleosaurus* sp. OUMNH.J1638 is slightly more chunky due to a proportionally shorter shaft (dorsoventrally). Among teleosauroids, *Mycterosuchus nasutus*, *Charitomenosuchus leedsi*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a) and *Proexochokefalos* cf. *bouchardi* also display an anteroposteriorly thin shaft, but the shaft of *Proexochokefalos* cf. *bouchardi* is proximodistally shorter. Among metriorhynchoids, *Pelagosaurus typus* BRLSI M.1410 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 show a slender shaft as well. In comparison, the posterior margin of the ischium of *Teleosaurus* sp. is subtly concave: its apex is located relatively proximally (around onefourth of total posterior length) and its concavity shows a greater amplitude so that the posterior margin of the ischium underneath the shaft appears straight. Compared to the other teleosauroids with a thin shaft, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Charitomenosuchus leedsi* and *Proexochokefalos* cf. *bouchardi* also display a more subtly concave posterior margin in relation to the anterior one, whereas *Mycterosuchus nasutus* possesses a markedly concave posterior margin.

Proximally, the shaft of the ischium of *Teleosaurus* sp. flares out asymmetrically to form the anterior and posterior peduncles. Laterally, the base of the peduncle bridge is borne close to the rim of the posterior peduncle which partly obstructs the acetabular perforation as in most teleosauroids, as opposed to *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Charitomenosuchus leedsi* and *Macrospondylus bollensis*. In *Teleosaurus* sp., the peduncle bridge retains most of its base height throughout its lengths which give it a thick aspect as in *Aeolodon priscus*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Neosteneosaurus edwardsi* and *Lemmysuchus*

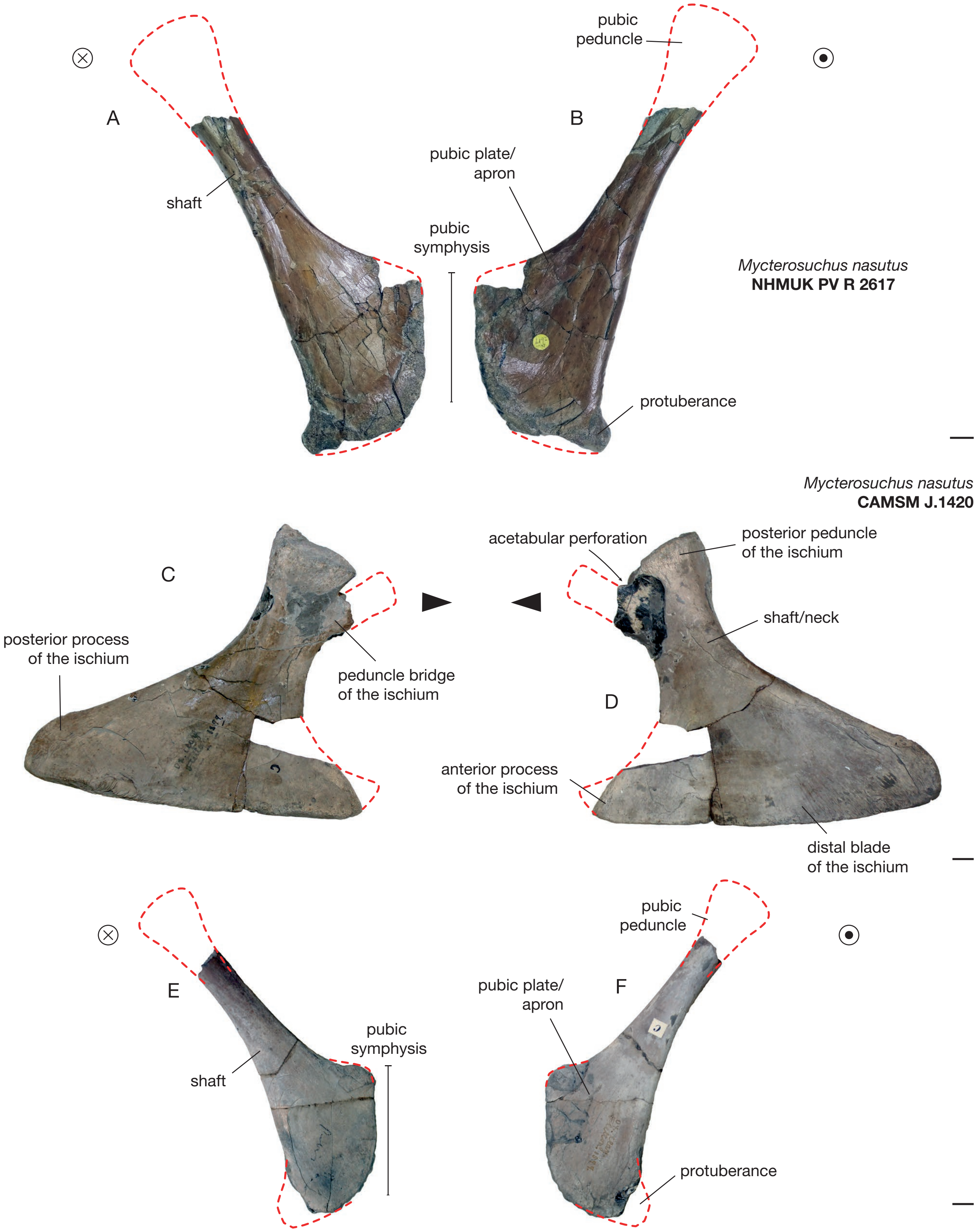


Fig. 41. — Pelvic girdle elements of *Mycterosuchus nasutus* (Andrews, 1909): **A**, **B**, NHMUK PV R 2617, holotype; **C**, **D**, CAMSM J.1420 (referred); **A**, left pubis in anterior view; **B**, left pubis in posterior view; **C**, left ischium in medial view; **D**, left ischium in lateral view; **E**, left pubis in posterior view; **F**, left pubis in anterior view. Target indicates anterior. Cross indicates posterior. Pictures of CAMSM J.1420 courtesy of Dr. Michela Johnson. Scale bars: 1 cm.

obtusidens. Overall, the peduncle bridge of *Teleosaurus* sp. is moderately long as its total length (including the anterior peduncle) is comparable to that of the posterior peduncle. The anterior peduncle of *Teleosaurus* sp. is not preserved in its entirety, but it does not ventrally protrude from the ventral margin of the peduncle bridge.

The posterior peduncle of *Teleosaurus* sp. is typically divided between the slightly concave articular facet participating in the hip acetabulum, and the rough articular facet connecting with the ischial peduncle of the ilium. The edge of the posterior peduncle forms a thick rounded rim which contrasts with the thinner rim of the other teleosaurids *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a) and *Platysuchus multiscrobiculatus*.

Distally, the shaft of the ischium of *Teleosaurus* sp. also flares out asymmetrically to form the anterior and posterior processes. The latter is strongly expanded posteriorly with an overall tubular shape, as in *Pelagosaurus typus*, *Macrospondylus bollensis*, and *Platysuchus multiscrobiculatus*. It is possible that *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a) displayed a tubular posterior process similar to *Teleosaurus* sp. and *Platysuchus multiscrobiculatus*, however it is not preserved. The dorsal margin of the posterior process of *Teleosaurus* sp. possesses a low slope angle in relation to the ischial blade and, as a result, the dorsoventral thickness of the posterior process subtly decreases in size posteriorly. In addition, the posterior process of *Teleosaurus* sp. displays a thick and rounded apex, which contributes to the tubular aspect of the process, as in *Platysuchus multiscrobiculatus* but unlike *Macrospondylus bollensis*.

In contrast, the anterior process of the ischium of *Teleosaurus* sp. forms a short and sharp hook pointing anterodorsally. Hence, the anterior process is not in line with the ischial blade, as in *Aeolodon priscus*. The dorsal margin of the anterior process is slightly concave (as it follows the curve of the anterior margin of the ischium) whereas the ventral margin is more straight. Overall, the dorsal and ventral margins of the anterior process appear to display the same length and inclination. As a consequence, the anterior process has a strong symmetrical aspect dorsoventrally, similar to an isosceles triangle. This strongly contrasts with the other teleosaurids *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a) and *Platysuchus multiscrobiculatus* in which the anterior process is directly in line with the ischial blade.

The ischial blade of *Teleosaurus* sp. connects the anterior and posterior processes along the ventral margin of the ischium. It displays an overall straight surface with a wide ischial suture on its medial side, as in *Platysuchus multiscrobiculatus* (and *Charitomenosuchus leedsi* but to a lesser extent). The ischial suture is identifiable as its surface is bevelled in relation to the medial surface of the ischium, and is also scarred throughout. In addition, the edge of the ischial suture forms a rim where it connects with the medial surface of the bone.

Pubis

The pubis of *Teleosaurus* sp. (OUMNH.J1638; Fig. 43) shows a relatively large peduncle proximally, which contrasts with *Platysuchus multiscrobiculatus* and *Charitomenosuchus leedsi*, but is similar to *Macrospondylus bollensis* and *Neosteneosaurus edwardsi*. The marked constriction of the shaft of *Teleosaurus* sp. also emphasizes the proximal flaring of the pubis to form the peduncle (which is more than twice as wide). However, the minimum constriction of the shaft of *Teleosaurus* sp. is slightly proportionally larger than what is observed in *Macrospondylus bollensis* and *Neosteneosaurus edwardsi*. In *Teleosaurus* sp. the shaft is moderately long as the maximum mediolateral constriction is set at around ⅓ of the total proximodistal length of the bone, which is similar to *Macrospondylus bollensis* and *Neosteneosaurus edwardsi*. In comparison, the shaft of *Charitomenosuchus leedsi* and *Lemmysuchus obtusidens* are proportionally shorter and reach 27.5% and 22.13% of the total length of the pubis, respectively.

In *Teleosaurus* sp., the concavity of the medial and lateral margins is relatively similar, which contrasts with most teleosauroids (e.g. *Mycterosuchus nasutus*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*). This is due to the slow and gradual widening of the pubic apron underneath the shaft, which only shows a marked increase in width around the beginning of the pubic symphysis as in *Machimosaurus*. Indeed, around the level of the pubic symphysis, the medial margin of the pubis of *Teleosaurus* sp. forms a marked bent towards the medial side, so that the angle produced externally between the two surfaces of the medial margin reaches around 138°. As a result, the portion of the pubic apron bearing the pubic symphysis medially appears to strongly protrude from the rest of the pubic apron, hence forming a medial protuberance or flange (like in *Machimosaurus*).

The pubic symphysis of *Teleosaurus* sp. is well-developed as in most thalattosuchians, and reaches around 33% of the total proximodistal length of the bone. Dorsally, the pubic symphysis forms an almost right-angled corner with the medial margin (corresponding to the medial corner of the protuberance), whereas its transition with the distal margin of the pubic apron is achieved through an obtuse angle. In *Teleosaurus* sp., the distal margin of the pubic apron is relatively straight which contrasts with other teleosauroids (e.g. *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, and *Machimosaurus*). Laterally, the distal margin of the pubic apron forms a semi-circular corner at its junction with the lateral margin of the bone, which stands out from other teleosauroids. There is an indentation between the semi-circular corner and the lateral margin of the pubis which emphasizes its bulbous shape. This rounded-corner also slightly protrudes laterally from the rest of the lateral margin of the bone, forming a small lateral protuberance. In comparison, the lateral protuberance of *Mycterosuchus nasutus* is more laterally prominent, but less dorsoventrally thick than in *Teleosaurus* sp.

Platysuchus multiscrobiculatus (Berckhemer, 1929)

For measurements, see Tables 7-9.

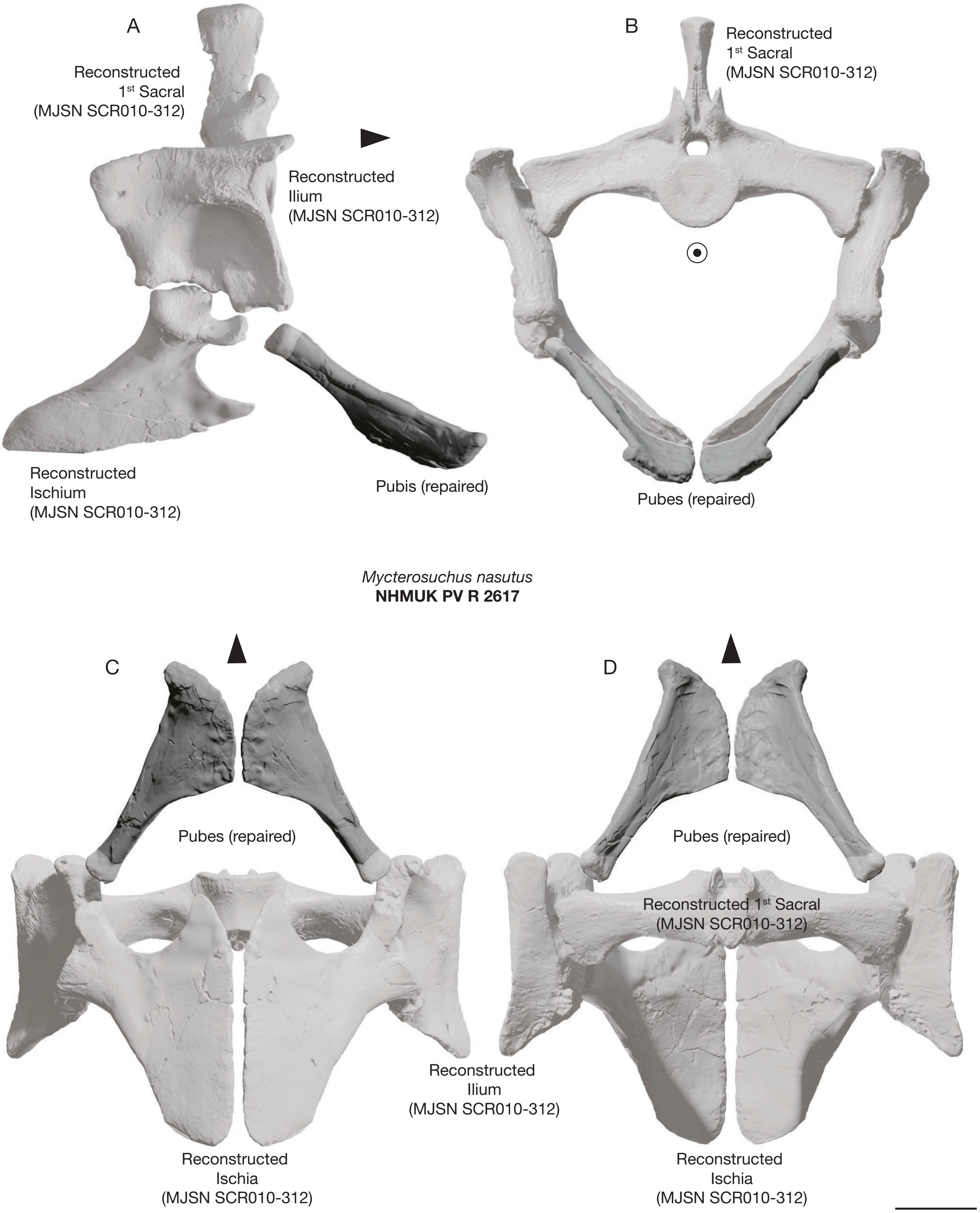


FIG. 42. — Reconstruction of the pelvic girdle of *Mycterosuchus nasutus* (Andrews, 1909), NHMUK PV R 2617: **A**, right lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Target indicates anterior. Arrow points anteriorly. The right pubis is mirrored. The ilium, ischium and first sacral are reconstructed from *Sericodon jugleri* Von Meyer, 1845, MJSN SCR010-312, and only serve as a qualitative representation to better highlight the remains of *Mycterosuchus nasutus* NHMUK PV R 2617. Scale bar: 5 cm.

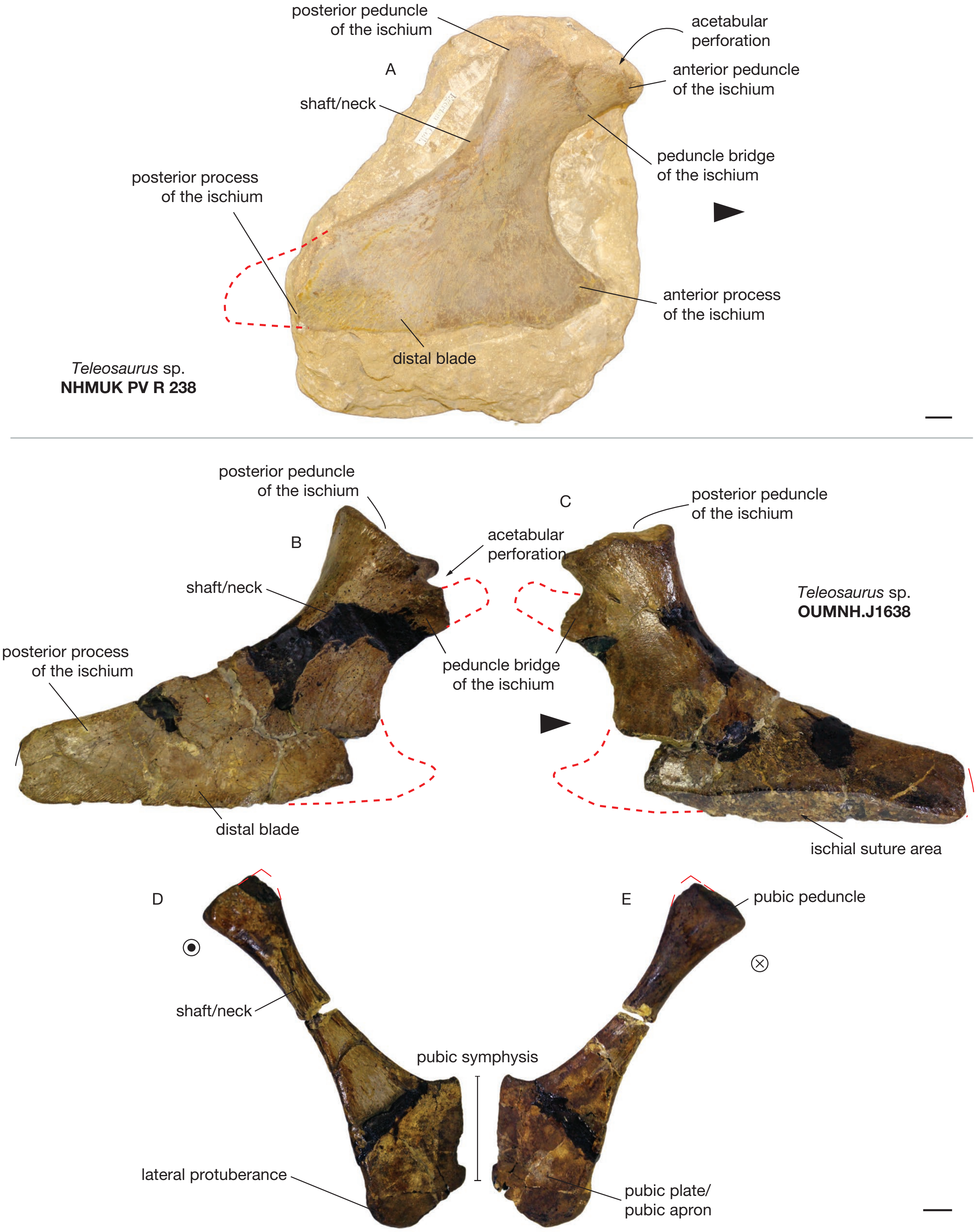


FIG. 43. — Pelvic girdle elements of *Teleosaurus* sp., NHMUK PV R 238 (**A**) and OUMNH.J1638 (**B**-**E**): **A**, right ischium in lateral view; **B**, right ischium in lateral view; **C**, right ischium in medial view; **D**, right pubis in anterior view; **E**, right pubis in posterior view. Arrow points anteriorly. Target indicates anterior. Pictures courtesy of Dr. Michela Johnson. Scale bars: 1 cm.

Ilium

The ilium of *Platysuchus multiscrobiculatus* (Fig. 44) displays an anteroposteriorly elongated shape due to the presence of a postacetabular process as in other telesauroids (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Plagiophthalmosuchus gracilirostris*, etc.). The postacetabular process of *Platysuchus multiscrobiculatus* differs from those of most teleosauroids in being relatively slender: the postacetabular process almost retains the same dorsoventral height throughout its anteroposterior length, giving it a tubular shape. *Plagiophthalmosuchus gracilirostris* and *Macrospondylus bollensis* display a relatively slender postacetabular process as well. Posteriorly, the postacetabular process of *Platysuchus multiscrobiculatus* culminates in a blunt hemispherical peak whose diameter is not significantly smaller than the overall dorsoventral height of the process (i.e. there is no major decrease in the size of the process posteriorly).

The dorsal margin of the postacetabular process is slightly undulating with a small depression around its mid-length. On either side of this recess, the dorsal margin of the postacetabular process is convex. Anteriorly, the postacetabular process gradually moves on to the iliac crest, which corresponds to the dorsal border of the ilium. The latter is convex throughout its length, with the vertex being shifted posteriorly towards the iliac crest-postacetabular process junction. The transition to the preacetabular process is marked by a shallow recess along the dorsal margin of the ilium.

The shape of the preacetabular process grossly mirrors that of the postacetabular process but at a smaller scale: overall, the preacetabular process is relatively elongated anteroposteriorly as well as dorsoventrally thick. Indeed, the dorsoventral height of the preacetabular is retained throughout its anteroposterior length. Also, the peak of the preacetabular process is rather smooth and rounded, but definitely sharper than that of the postacetabular process giving it the appearance of a Lancet arch. Such a combination of shape for the preacetabular and postacetabular processes differs from other thalattosuchians (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 3804, ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, *Charitomenosuchus leedsi*, etc.). The preacetabular process of *Platysuchus multiscrobiculatus* is in line with the iliac crest and the postacetabular process as in other teleosauroids (e.g. *Macrospondylus bollensis*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Plagiophthalmosuchus gracilirostris*, etc.). The global orientation of the ilium is uncertain since the position and shape of the sacral rib attachment sites of *Platysuchus multiscrobiculatus* are unknown. Hence it is unsure if it pointed anteroventrally as in *Lemmysuchus obtusidens* or more anteriorly as in *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*.

The junction between the preacetabular process and the anterior margin of the ilium is achieved through a smooth acute angle due to the leaning anterior margin of the ilium, as in *Lemmysuchus obtusidens contra Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*. Indeed, the anterior margin of the ilium of *Platysuchus multiscrobiculatus* is anteriorly tilted starting from its junction with the preacetabular process. Overall, the anterior margin of the ilium displays a straight outline, and culminates ventrally in an almost hemispherical shape to form the pubic peduncle. In *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi*, this junction also forms a rounded corner, but is less marked.

The posterior margin of the ilium of *Platysuchus multiscrobiculatus* almost reaches the length of the anterior margin underneath the preacetabular process due to the shortness of the postacetabular process in the dorsoventral direction. Overall, the posterior margin of the ilium appears to be parallel to the anterior margin of the ilium and thus is anteriorly inclined. The junction between the ventral margin of the postacetabular process and the posterior margin of the ilium forms an angle closer to 90° than to an obtuse angle as in *Plagiophthalmosuchus gracilirostris contra Lemmysuchus obtusidens*, *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi*. The only difference between *Platysuchus multiscrobiculatus* and the other teleosauroids resides in the global orientation of the margins involved in the aforementioned junction.

The bony acetabulum of *Platysuchus multiscrobiculatus* (Fig. 44) forms a shallow depression on the lateral surface of the ilium. As in most thalattosuchians (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, etc.), the acetabulum is bordered by the pubic peduncle anteriorly, the ischial peduncle posteriorly, and the supraacetabular crest dorsally. Proportionally, the bony acetabulum occupies a large area of the ilium as in other crocodyliforms (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Macrospondylus bollensis*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*, etc.). But in *Platysuchus multiscrobiculatus* this effect is even more emphasized by the shape of the postacetabular process. The supraacetabular crest corresponds to a curved and prominent ridge, located ventrally to the preacetabular and postacetabular processes. Like in *Lemmysuchus obtusidens*, the supraacetabular crest of *Platysuchus multiscrobiculatus* extends over almost the totality of the anteroposterior length of the bony acetabulum.

Ischium

The ischium of *Platysuchus multiscrobiculatus* (Fig. 44) stands out from that of most thalattosuchians (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.) in displaying an overall T-shape. Indeed, the combination of slender anterior and posterior processes, added to the perpendicularity between the distal blade and the shaft and the overall similar thickness of the anterior and posterior processes, give the ischium of *Platysuchus multiscrobiculatus* an atypical look. *Cricosaurus bambergensis* also possesses a perpendicular relation between its distal blade and shaft, and *Pelagosaurus typus* displays similarly slender anterior and posterior processes almost perpendicular to the shaft.

The anterior and posterior margins of the ischium connecting the proximal peduncles with the distal blade are both strongly concave similar to other teleosauroids (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*). In *Platysuchus multiscrobiculatus*, the vertex of each margin are relatively facing each other similar to *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, and also *Cricosaurus bambergensis* and *Cricosaurus araucanensis* (but not *Cricosaurus suevicus*). The position of the vertex of each concavity also marks the end of the shaft, together forming maximum constriction. In *Platysuchus multiscrobiculatus*, the maximum concavity of the anterior and posterior margins is set proportionally far from the peduncles, resulting in a long shaft (about 44% of the total dorsoventral height of the bone), adding to the distinctive shape of the bone. Moreover, another particularity of the ischium (Fig. 44) resides in the thickness of the shaft: the anteroposterior length of the shaft reaches about 90% of its dorsoventral length, giving it a stout look.

Distally, the anterior margin of the ischium culminates in a relatively sharp peak: the anterior process of the ischium. The anterior process of *Platysuchus multiscrobiculatus* does not appear to protrude much anteriorly; indeed, the anteroposterior length of the anterior process is inferior to that of the shaft as opposed to *Lemmysuchus obtusidens*, for which it is slightly greater. Comparatively, *Aeolodon priscus* and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 also possess a relatively short anterior process. The axis of the anterior process of *Platysuchus multiscrobiculatus* is parallel to the margin of the distal blade, as in *Lemmysuchus obtusidens* as opposed to *Aeolodon priscus*. This effect is imputable to the shape of the ventral margin of the anterior process which is aligned with the ventral margin of the distal blade. Hence, there is no rupture along the distal blade of the ischium in *Platysuchus multiscrobiculatus*, which forms a straight border ventrally. Posteriorly, the distal blade moves on to build the posterior process of the ischium. The latter largely contributes to the T-shape of the ischium due to its narrow configuration. Indeed, the posterior process of the ischium takes a shape similar to that of the postacetabular process of the ilium of *Platysuchus multiscrobiculatus*: its dorsoventral thickness is almost constant throughout its anteroposterior length. Moreover, the posterior process of the ischium is not significantly taller than the anterior process (only about ⅓ taller dorsoventrally), giving a certain continuity in the appearance of the T-bar. The peak of the posterior process of the ischium of *Platysuchus multiscrobiculatus* is hemispherical. Comparatively, *Macrospondylus bollensis*, *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Cricosaurus bambergensis* show similarly shaped posterior processes.

The posterior peduncle of the ischium of *Platysuchus multiscrobiculatus* appears to be significantly shorter than the shaft at its shortest anteroposterior portion, as in *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Pelagosaurus typus*, *Cricosaurus suevicus* or *Thalattosuchus superciliosus* NHMUK PV R 2054.

Pubis

The pubis of *Platysuchus multiscrobiculatus* (Fig. 44) is very distinctive among teleosauroids as it shows both a relatively long shaft and flared pubic apron. Comparatively, *Machimosaurus* also display a long shaft but with a narrow pubic apron, whereas *Lemmysuchus obtusidens* (Fig. 59) possesses a large pubic apron for a shorter shaft. *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi* also have a moderately long shaft with a wide pubic plate like that of *Platysuchus multiscrobiculatus*, but the distal shapes are different. In *Platysuchus multiscrobiculatus*, the thinnest portion of the shaft mediolaterally almost accounts for about half of the mediolateral width of the pubic peduncle, similar to several other thalattosuchians (e.g. *Cricosaurus suevicus* [Fig. 19], *Geosaurus giganteus* [Fig. 30], *Machimosaurus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). In comparison, this value is even lesser for *Macrospondylus bollensis* and *Pelagosaurus typus*.

The pubic peduncle of *Platysuchus multiscrobiculatus* is flared proximally. In relation to the median of the shaft, the pubic peduncle is relatively asymmetrical with its medial half being larger than the lateral one. Indeed, the lateral margin of the pubis leading to the peduncle shows a line break in the smooth overall concavity which decreases the size of the peduncle laterally.

The lateral and medial margins of the pubis of *Platysuchus multiscrobiculatus* are overall concave, with the medial margin of the bone showing several undulations rupturing the harmony of the curve similar to what is observed in *Machimosaurus*. The distal blade of the pubis drastically flares out from the narrow width of the shaft. The exact shape of the distal blade is uncertain, but the distal blade appears to have been relatively asymmetrical. Indeed, the pubic apron is wider medially than laterally compared to the median of the shaft. In addition, the pubic blade displays a relatively rounded but asymmetrical appearance as it is more expanded medially.

MACROSPONDYLUS BOLLENSIS (JÄGER, 1828)

For measurements, see Tables 7-9.

Ilium

The ilium of *Macrospondylus bollensis* SMNS 17484a (Fig. 45) resembles those of basal teleosauroids *Platysuchus multiscrobiculatus* and *Plagiophthalmosuchus gracilirostris* in displaying a slender postacetabulum process. Indeed, the posterior margin of the ilium of *Macrospondylus bollensis* joining the ischial peduncle to the ventral base of the postacetabulum is relatively long as it almost reaches the length of the anterior margin of the ilium. This trait contrasts with the more derived *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*. In addition, the posterior and anterior margins of the ilium of *Macrospondylus bollensis* are parallel to one another as in *Platysuchus multiscrobiculatus* and supposedly *Plagiophthalmosuchus gracilirostris*. The lat-

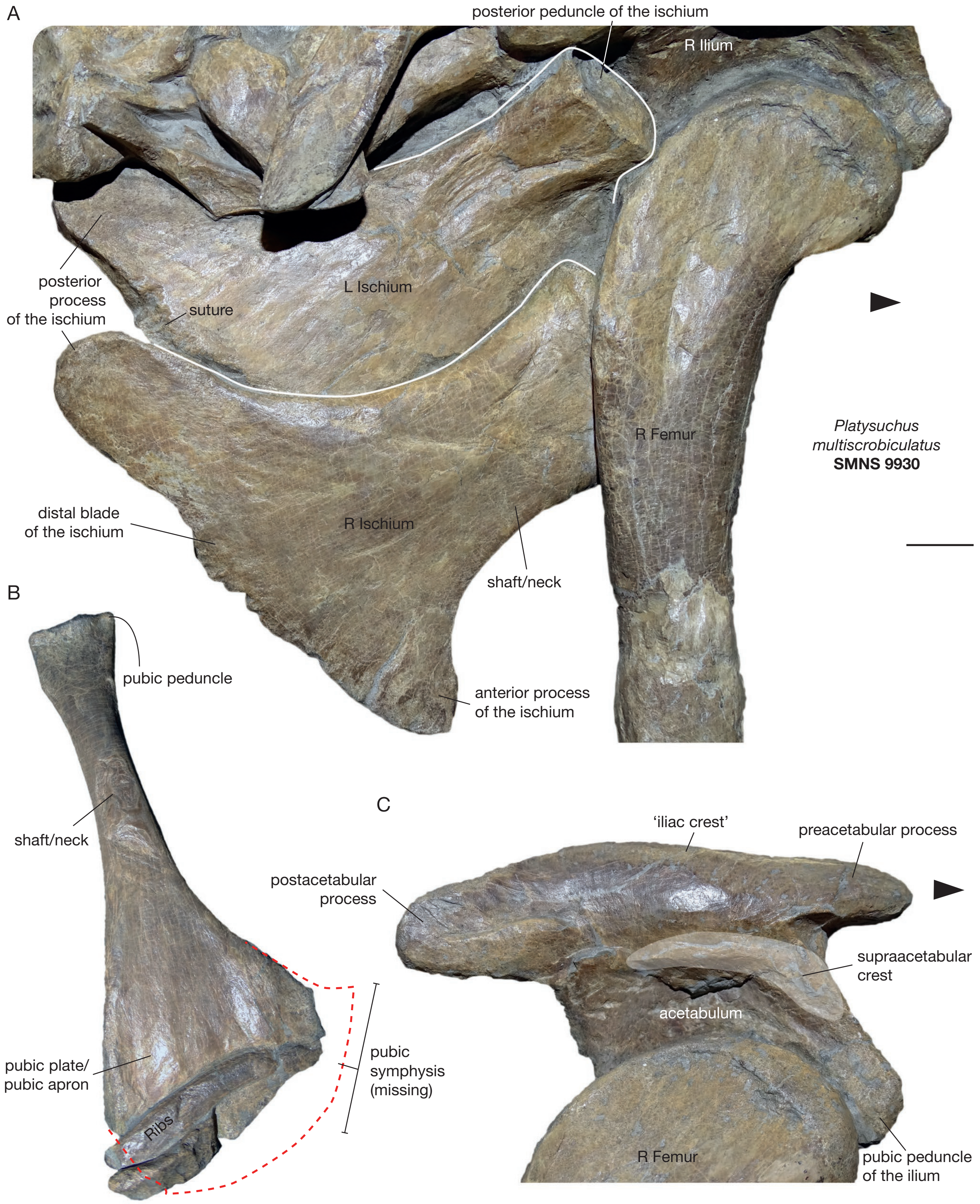


FIG. 44. — Right and left pubes of *Platysuchus multiscrobiculatus* (Berckhemer, 1929), SMNS 9930 (holotype): **A**, right ischium in lateral view and left ischium in medial view; **B**, right pubis in anterior view; **C**, right ilium in lateral view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

ter condition is also recovered in *Charitomenosuchus leedsi* although both margins are curved and of differing length. As a consequence, the dorsal and ventral margins of the postacetabular process of the ilium of *Macrospondylus bollensis* are located close to one another as in *Platysuchus multiscrobiculatus* and *Plagiophthalmosuchus gracilirostris*, but unlike the other more derived teleosauroids (i.e. *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*). Still, *Charitomenosuchus leedsi* displays a proportionally narrower postacetabular process compared to *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*.

The preacetabular process of the ilium of *Macrospondylus bollensis* displays a relatively stout aspect as in *Platysuchus multiscrobiculatus*: its base height almost reaches its total anteroposterior length, and its thickness only slightly decreases anteriorly. The preactebular process of *Macrospondylus bollensis* culminates in a rounded tip similar to *Platysuchus multiscrobiculatus*. Comparatively, more derived teleosauroids display a slender preacetabular process that appears hook-shaped. The junction between the preacetabular process and the dorsal margin of the ilium forms a shallow recces as in other teleosauroids (i.e. *Plagiophthalmosuchus gracilirostris*, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*). The dorsal margin of the ilium of *Macrospondylus bollensis* appears to have been convex like that of other teleosauroids. Comparatively, the anterior margin of the ilium of *Macrospondylus bollensis* seems relatively straight as in *Platysuchus multiscrobiculatus* and *Plagiophthalmosuchus gracilirostris*, but it is possible that it were slightly convex following the arc of the supraacetabular crest similar to what is observed in *Lemmysuchus obtusidens*. The junction between the preacetabular process and the anterior margin of the ilium of *Macrospondylus bollensis* is achieved through an acute angle as in *Platysuchus multiscrobiculatus* and *Lemmysuchus obtusidens* only.

Ventrally, the margin of the ilium of *Macrospondylus bollensis* is slightly undulating similar to other teleosauroids (i.e. *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*): the ventral surface of each peduncle are slightly concave and the junction between them is achieved through a small notch (i.e. the acetabular perforation). Both peduncle are titled mesially towards the centre of the ilium to form the borders of the bony acetabulum (Fig. 45). The ischial peduncle is anteroposteriorly longer than the pubic peduncle, but their lateral facet shows a similar dorsal extension unlike in *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi* (in *Lemmysuchus obtusidens* the extension of the ischial peduncle is unknown). The bony acetabulum of *Macrospondylus bollensis* proportionally occupies most of the lateral surface of the ilium, notably due to the small size of the postacetabular process. It also extends as far anteriorly and posteriorly as the margins of the bone, and occupies about ⅔ of the dorsoventral height of the ilium. The bony acetabulum of the ilium is ventrally bordered by the peduncles (of which the ischial peduncle also forms a portion of the posterior border), and anterodorsally by the supraacetabular crest. The supraacetabular crest of the ilium of *Macrospondylus bollensis* appears relatively shallow and smooth (i.e. not markedly pitted) as in *Platysuchus multiscrobiculatus* and *Lemmysuchus obtusidens*. The acetabular perforation of the ilium of *Macrospondylus bollensis* is strongly reduced as in other thalattosuchians (e.g. *Pelagosaurus typus*, *Thalattosuchus superciliosus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, etc.). However, the counterpart of the acetabular perforation on the ischium of *Macrospondylus bollensis* is one of the largest among teleosauroidea, along with that of *Charitomenosuchus leedsi*.

Ischium

Overall, the ischium of *Macrospondylus bollensis* (Figs 46; 47) displays a proportionally thick shaft as well as a deep acetabular perforation in all specimens (NHMUK PV R 5703, SMNS 17484a and SMNS 16848). In this way, it resembles the proximal portion of the ischium of *Pelagosaurus typus*. Indeed, in *Macrospondylus bollensis*, the anteroposterior thickness of the shaft at its constriction is greater than that of the posterior peduncle (similar to *Cricosaurus suevicus*, *Dakosaurus maximus*, *Aeolodon priscus*, and *Lemmysuchus obtusidens*) of about ¼ in this case. In addition, the shaft of *Macrospondylus bollensis* is relatively short with its dorsoventral height reaching the same length as anteroposterior constriction, as in *Dakosaurus maximus* or *Lemmysuchus obtusidens*. The anterior and posterior margins of the ischium of *Macrospondylus bollensis* are strongly concave with their apex parallel, similar to most thalattosuchians (with the exception of *Thalattosuchus superciliosus* NHMUK PV R 2054 and *Cricosaurus suevicus*). The posterior margin of the ischium of *Macrospondylus bollensis* shows a strong posterior bulge located underneath the posterior peduncle. This bulge is not found in other teleosauroids.

The anterior peduncle of the ischium of *Macrospondylus bollensis* NHMUK PV R 5703 and SMNS 17484a is relatively ovoid in shape with its greatest axis being oriented lateromedially rather than dorsoventrally (SMNS 16848 is flattened mediolaterally). The dorsal-most surface of the anterior peduncle is not significantly taller than the dorsal-most surface of the posterior peduncle and thus appears on the same level, unlike in metriorhynchoids (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, etc.) but similar to other teleosauroids (i.e. *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). The anterior peduncle is borne by the peduncle bridge, which is an anteriorly protruding process. The latter displays a concave dorsal margin and a convex ventral one which slightly diverge posteriorly thus widening the process as it connects with the main body of the ischium. Similar to other thalattosuchians, the dorsal surface of the peduncle bridge is uneven and leans medially (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, etc.). This surface corresponds to the ventral border of the acetabular perforation.

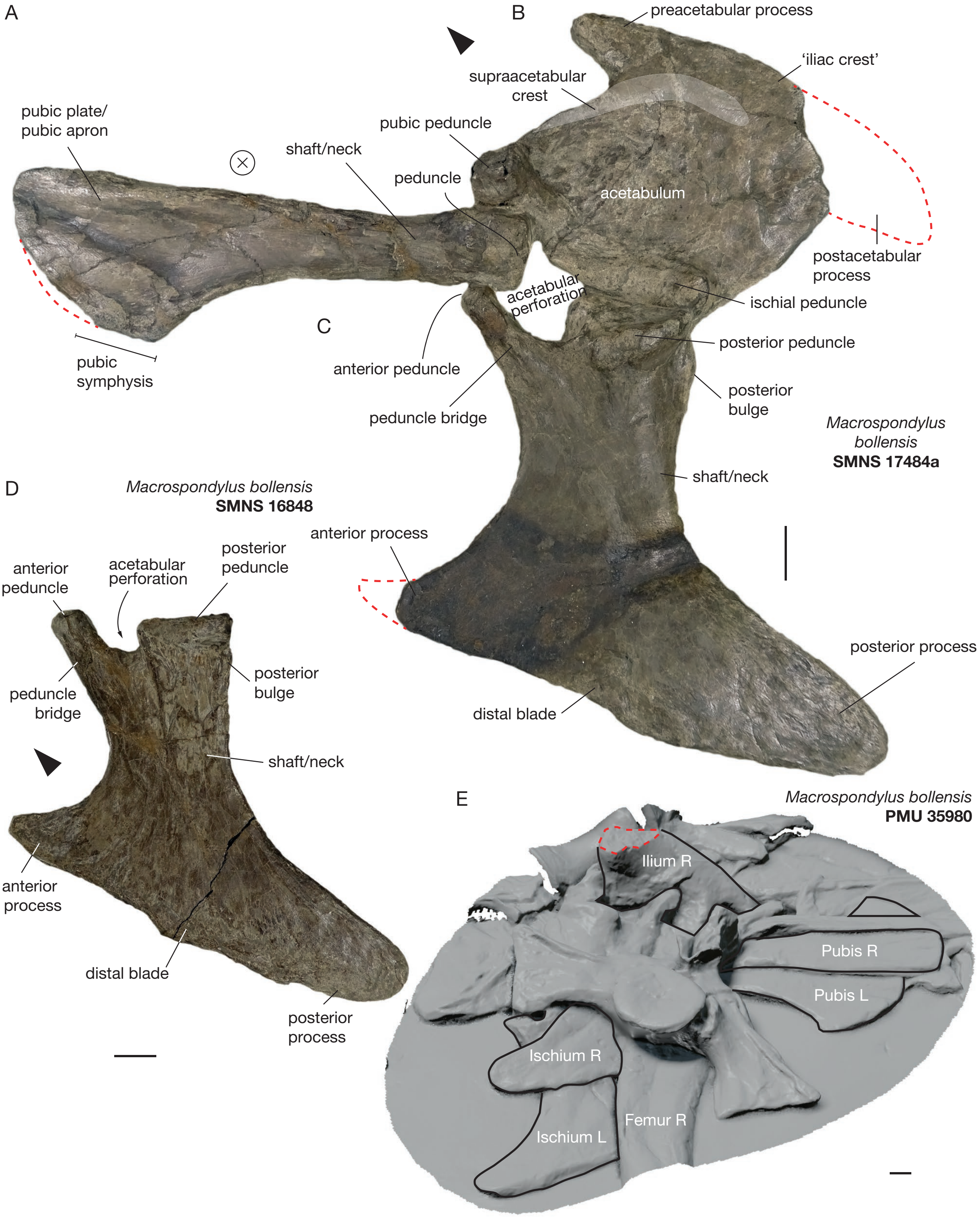


FIG. 45. — Pelvic girdle elements of *Macrospondylus bollensis* (Jäger, 1828): **A**, left pubis in posterior view of SMNS 17484a; **B**, left ilium in lateral view of SMNS 17484a; **C**, left ischium in lateral view of SMNS 17484a; **D**, left ischium in lateral view of SMNS 16848; **E**, overview of the pelvic girdle of PMU 35980. Arrow points anteriorly. Target indicates anterior. Scale bars: 1 cm.

The posterior peduncle of *Macrospondylus bollensis* (NHMUK PV R 5703, SMNS 17484a and SMNS 16848) differs from that of most thalattosuchians in being markedly prominent dorsally (i.e. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Dakosaurus maximus*, *Tyrannoneustes lythrodectikos*, *Torvoneustes carpenteri*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*). This unusual shape can partly be explained through a deeper and larger indentation for the acetabular perforation at the junction between the peduncle. Indeed, the acetabular perforation of *Macrospondylus bollensis* (Figs 46; 47) is almost as deep as the peduncle bridge is anteroposteriorly long. This trait is not usually recovered in thalattosuchians, but rather in dyrosaurids (e.g. *Hyposaurus natator*, or *Dyrosaurus maghribensis*). The articular surface of the posterior peduncle of *Macrospondylus bollensis* is wedge-shaped, with the iliac suture occupying about ⅓ of the surface medially. The second facet of the posterior peduncle of *Macrospondylus bollensis* (SMNS 17484a) corresponding to the ventral border of the bony acetabulum displays a triangular shape and is slightly concave as in other teleosauroids.

The distal blade of the ischium of *Macrospondylus bollensis* SMNS 17484a, SMNS 16848 and PMU 35980 is relatively slender, especially compared to the broadness of the overhanging shaft. Indeed, the slender aspect of the distal blade is mainly caused by the shape of the posterior process, whose anteroposterior length greatly exceeds its dorsoventral height (and accounts for about 150% of its base height).

In addition, the posterior process appears to retain most of its thickness throughout its length. The tip of the posterior process is rather rounded or slightly elliptic. In this way, the ischium of *Macrospondylus bollensis* strongly resembles that of *Platysuchus multiscrobiculatus* and *Pelagosaurus typus*. The anterior process of the ischium of *Macrospondylus bollensis* forms a short and thin hook with a slightly undulating ventral margin and a convex dorsal one. The anterior process extends anteriorly as further as the anterior peduncle similar to other thalattosuchians (i.e. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, etc.). The ventral margin of the distal blade is overall straight but forms a wave around its mid-length.

Pubis

The pubis of *Macrospondylus bollensis* NHMUK PV R 5703, SMNS 17484a, and PMU 35980 (Figs 46; 47) displays an overall singular shape highly resembling that of *Pelagosaurus typus*, with the main difference residing in the relative size of the pubic apron (which is proportionally shorter and larger for *Macrospondylus bollensis*). Indeed, the pubis of *Macrospondylus bollensis* is relatively slender due to an elongated but narrow pubic apron whose maximum proximodistal height reaches about 67% of the total height of the pubis.

The shaft of *Macrospondylus bollensis* is relatively straight, as opposed to *Pelagosaurus typus*. The lateral and medial margins of the pubic apron of *Macrospondylus bollensis* follow the same curve, with the medial one being concave and the lateral one convex. Distally, the lateral and medial margins connect to the distal blade, which is slightly convex like that of *Pelagosaurus typus*. The pubic symphysis is found along this convex margin, near the medial corner of the pubic apron. The pubic symphysis of *Macrospondylus bollensis* is not as well developed as in some other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Lemmysuchus obtusidens*, *Machimosaurus*, etc.), but reaches about 35% of the total perimeter of the distal blade (Fig. 47). In addition, the pubic apron of *Macrospondylus bollensis* does not display a wide flaring, which is similar to *Pelagosaurus typus* and *Plagiophthalmosuchus gracilirostris*.

Like other thalattosuchians (except rhacheosaurines and *Geosaurus giganteus*), the pubic apron of *Macrospondylus bollensis* (Fig. 46) is strongly asymmetrical (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Machimosaurus*, etc.). Indeed, the majority of the surface of the pubic apron lies on the medial side of the median of the shaft.

The constriction of the pubis, delimiting the shaft distally, is relatively narrow leading to impressive proximal and distal widening of the bone. Indeed, the thickness of the constriction represents about ⅓ of the mediolateral width of the peduncle. The latter is composed of a convex margin laterally and a concave one medially. The articular surface of the peduncle appears to be slightly convex as well, but also medially tilted as in *Suchodus durobrivensis* or *Thalattosuchus superciliosus*.

CHARITOMENOSUCHUS LEEDSI (Andrews, 1909)

For measurements, see Tables 7-9.

Ilium

Overall, the ilium of *Charitomenosuchus leedsi* (Figs 48; 49) stands out from that of most thalattosuchians in displaying a parallelepiped shape (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, etc.). Indeed, the different surfaces of *Charitomenosuchus leedsi* (Fig. 48) are parallel two by two (i.e. dorsal and ventral, anterior and posterior), and their angular relations are different from 90°. In this way, it strongly resembles that of *Neosteneosaurus edwardsi* NHMUK PV R 3701, NHMUK PV R 3898, and NHMUK PV R 2076. However, the curvature of the anterior margin of *Charitomenosuchus leedsi* is not present in any specimens of *Neosteneosaurus edwardsi*.

The ilium of *Charitomenosuchus leedsi* (Fig. 48) possesses a well-developed postacetabular process like other teleosauroids (i.e. *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Neosteneosaurus edwardsi*, *Macrospondylus bollensis*, *Plagiophthalmosuchus gracilirostris*). Overall, the postacetabular process of *Charitomenosuchus leedsi* takes the shape of a Lancet arch like that of *Lemmysuchus obtusidens*: its dorsal (i.e. the iliac crest) and ventral margins are both convex, with the latter showing

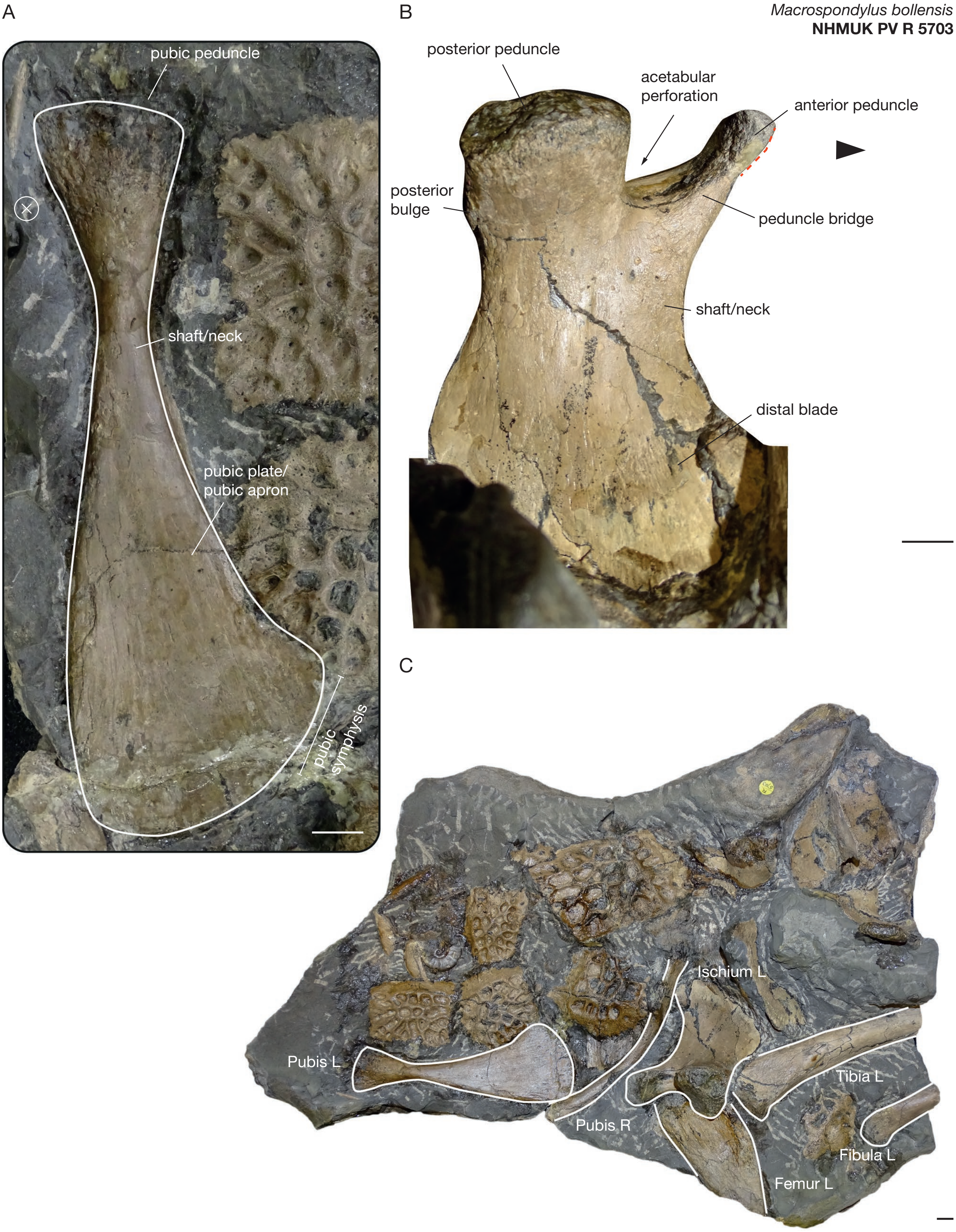


FIG. 46. — Pelvic girdle elements of *Macrospondylus bollensis* (Jäger, 1828), NHMUK PV R 5703: **A**, left pubis in posterior view; **B**, left ischium in medial view; **C**, overview of the pelvic girdle elements. Arrow points anteriorly. Target indicates anterior. Scale bars: 1 cm.

the greatest intensity. However, at about its mid-length, the concavity of the ventral margin of the postacetabular process switches to become concave. The total anteroposterior length of the iliac crest (i.e. dorsal margin of the postacetabular process) reaches that of the ilium around the peduncles, similar to *Lemmysuchus obtusidens*. Posteriorly, the postacetabular process culminates in a sharp apex oriented dorsoposteriorly and thus differs from those of *Lemmysuchus obtusidens* and *Platysuchus multiscrobiculatus* for which the axis of the postacetabular process is in line with that of the preacetabular process. This dorsal component in the orientation of the postacetabular process of *Charitomenosuchus leedsi* renders its junction with the preacetabular process more pronounced than in *Lemmysuchus obtusidens* or *Platysuchus multiscrobiculatus*, and gives *Charitomenosuchus leedsi* a distinctive look. The lateral surface of the postacetabular process is relatively flat near its margins, but forms a shallow depression around its base and centre.

The preacetabular process of *Charitomenosuchus leedsi* (Fig. 48) is proportionally large as its anteroposterior length reaches about half of the total anteroposterior length of the postacetabular process. Comparatively, *Plagiophthalmosuchus gracilirostris*, *Platysuchus multiscrobiculatus* and *Macrospondylus bollensis* also possess an elongated preacetabular process. Overall, the shape of the preacetabular process of *Charitomenosuchus leedsi* is that of a slender peak whose ventral margin is concave and its dorsal margin is subtlety convex. The preacetabular process of *Charitomenosuchus leedsi* appears to be pointing anteriorly with a small ventral component, like that of *Lemmysuchus obtusidens*, *Macrospondylus bollensis* SMNS 17484a and *Neosteneosaurus edwardsi* NHMUK PV R 3898. Underneath the preacetabular process, the anterior margin of the ilium strongly bulges not unlike that of *Suchodus durobrivensis*, which contrasts with those of *Lemmysuchus obtusidens* or *Platysuchus multiscrobiculatus*. The junction between the preacetabular process and the anterior margin is achieved through a smooth rounded corner.

Ventrally, the margin of the ilium is strongly undulating with each indentation marking the position of each peduncle, as in other thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, *Macrospondylus bollensis*, etc.). The junction between the anterior margin of the ilium and the pubic peduncle forms a protruding bulge, as in *Thalattosuchus superciliosus* NMI F21731 or *Lemmysuchus obtusidens*. Laterally, the facet of the pubic peduncle of *Charitomenosuchus leedsi* is not well defined but appears to be wedge-shaped as in *Macrospondylus bollensis* and *Neosteneosaurus edwardsi*, with its dorsoventral height reaching almost ⅓ of its anteroposterior length. The ventral surface of the pubic peduncle possesses a strong indentation along its midline whose intensity is greater than what is observed in *Lemmysuchus obtusidens*. Ventrally, the pubic peduncle is also wedge-shaped with its medial and anterior margins being relatively flat and the junction between both taking the form of a rounded right-angle corner. Mediolaterally, the pubic peduncle is the thickest at its anterior-most portion, as in all other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Dakosaurus maximus*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*).

The ischial peduncle of *Charitomenosuchus leedsi* (Fig. 48) also contributes to the ventral margin of the ilium along with the pubic peduncle and the acetabular perforation (Fig. 49). The facet of the ischial peduncle is shaped similar to an isosceles triangle with one of its summit pointing strictly dorsally similar to many other crocodyliforms (e.g. *Caiman crocodilus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Dyrosaurus maghribensis*, etc.). Likewise, the facet of the ischial peduncle is also tilted towards the centre of the acetabulum as its posterior corner is set further away from the ilium than its anterior corner. The ischial peduncle greatly protrudes from the ilium posteriorly and in this way forms a bony barrier posteriorly to the acetabulum. Ventrally, the surface of the ischial peduncle is strongly concave and wedge-shaped like the pubic peduncle but with smoother corners. Comparatively, the ischial peduncle is dorsoventrally taller than the pubic peduncle but both display similar lengths anteroposteriorly. Both peduncles are physically separated by the acetabular perforation as in other teleosauroids (e.g. *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*). Compared to *Lemmysuchus obtusidens*, the acetabular perforation of *Charitomenosuchus leedsi* appears relatively reduced as its anteroposterior extension is more limited. In depth, the acetabular perforation of *Charitomenosuchus leedsi* is relatively shallow, as in *Pelagosaurus typus* or *Lemmysuchus obtusidens*.

The bony acetabulum of *Charitomenosuchus leedsi* (Fig. 48) accounts for about half of the total lateral surface of the bone, which contrasts with both *Lemmysuchus obtusidens* and *Platysuchus multiscrobiculatus* in which the acetabulum covers a wider portion of the lateral surface of the ilium. Due to the shape of the anterior margin of the ilium, the bony acetabulum of *Charitomenosuchus leedsi* (Fig. 48) is placed directly underneath the preacetabular process as in *Pelagosaurus typus* or *Suchodus durobrivensis*, not posteriorly to it as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, and *Lemmysuchus obtusidens*.

Medially, the ilium of *Charitomenosuchus leedsi* (Fig. 48) bears two distinct scars marking the position of the sacral rib attachment sites for both sacrals. The sacral rib attachment sites are adjacent and are located around the mid-height of the bone as in *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi*. In *Charitomenosuchus leedsi*, the posterior attachment site takes the shape of a droplet and is overall greater than the anterior one as it extends posteriorly almost until the tip of the postacetabular process. The area of the posterior attachment site expanding over the postacetabular process presumably received the winglet of the second sacral whereas the more rounded portion next to the anterior attachment site bore the main body of the second sacral rib. The anterior attachment site displays a rather bilobate silhouette with the ventral margin of the scar being more circular than the dorsal one. Each scar is delimited by a thin rim and forms a relatively shallow indentation similar to *Suchodus durobrivensis* or

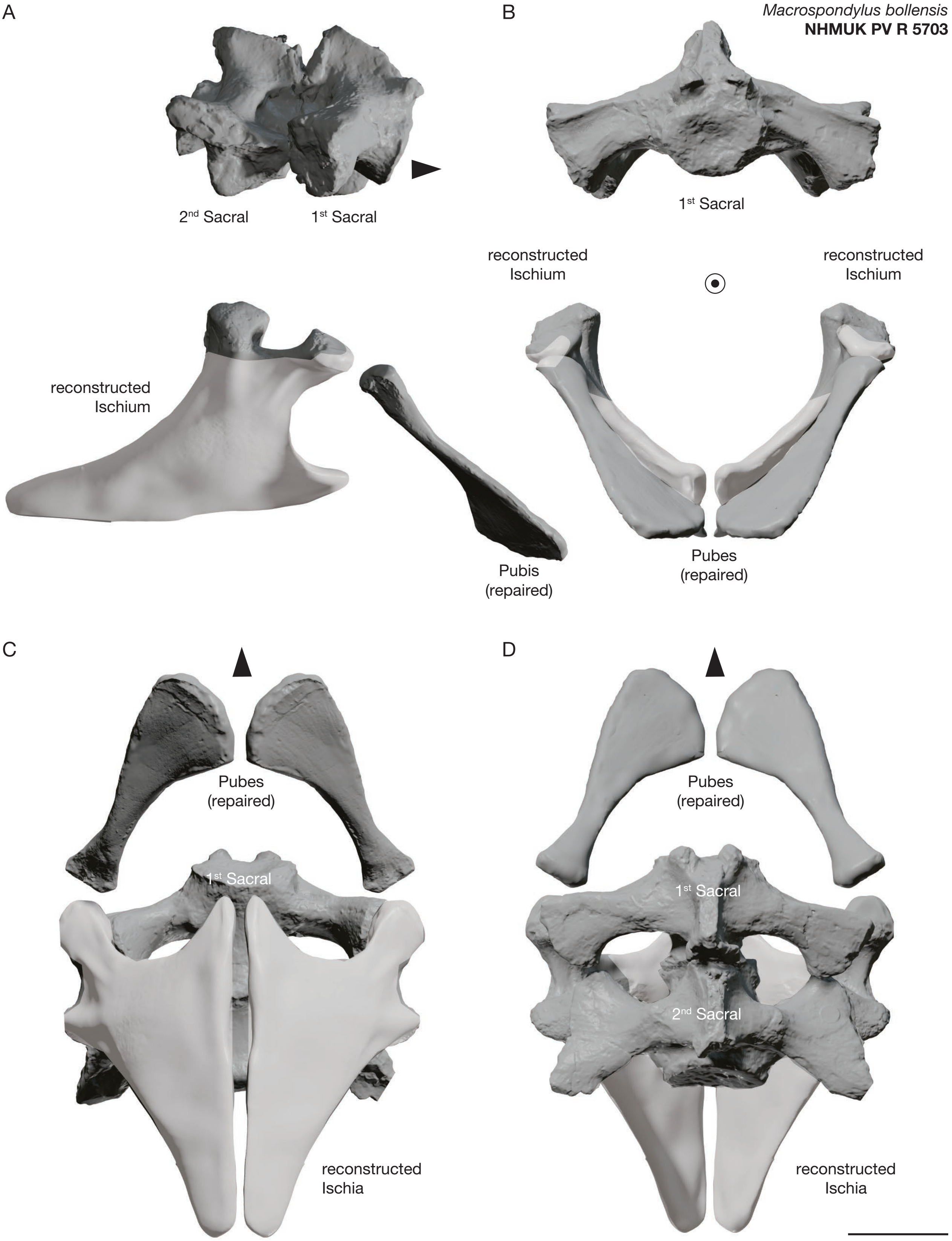


FIG. 47. — Pelvic reconstruction of *Macrospondylus bollensis* (Jäger, 1828), NHMUK PV R 5703 (holotype): **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right ischium and left pubis are mirrored. Reconstruction of the ischium based on *Macrospondylus bollensis,* SMNS 16848. Scale bar: 5 cm.

Lemmysuchus obtusidens. However, *Charitomenosuchus leedsi* drastically stands out from the latter and other thalattosuchians by displaying a thick elevation directly underneath the dorsal border of each attachment site.

Ischium

The ischium of *Charitomenosuchus leedsi* (Fig. 48) displays an overall thin shaft, an elongated peduncle bridge and a rather unusual shape for its posterior process. Like other thalattosuchians the anterior peduncle of *Charitomenosuchus leedsi* is drastically smaller than the posterior peduncle (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, etc.). In anterior view, the anterior peduncle has an isosceles triangular outline whose greatest axis is oriented mediolaterally. The overall articular surface of the anterior peduncle is also truncated so that the base of the triangle (about ⅓ of its height) faces anteriorly whereas the remaining portion of the peduncle is posteriorly deflected. The base of the triangular articular surface is presumably where the peduncle of the pubis was anchored to the ischium through soft tissues (Fig. 49). The anterior peduncle is borne by the peduncle bridge, which elevates the latter slightly over the posterior peduncle dorsally and also subtlety places it more medially. The peduncle bridge of *Charitomenosuchus leedsi* is relatively long as it is almost as long anteroposteriorly as the posterior peduncle similar to *Macrospondylus bollensis* but unlike *Lemmysuchus obtusidens*. The ventral surface of the peduncle bridge of *Charitomenosuchus leedsi* is relatively straight whereas its dorsal surface is deeply concave. The latter, combined with the position of the peduncle bridge in relation to the posterior peduncle creates an overall deep acetabular perforation between the peduncles, as in *Macrospondylus bollensis* and *Sericodon jugleri*. Unlike metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, etc.), the acetabular perforation of *Charitomenosuchus leedsi* does not form a sulcus on the medial side of the bone, since it is well defined dorsally to the peduncle bridge. However, the acetabular perforation of *Charitomenosuchus leedsi* is slightly titled medially compared to *Macrospondylus bollensis* and *Sericodon jugleri*.

The posterior peduncle of *Charitomenosuchus leedsi* corresponds to the mediolaterally widest portion of the ischium. It is almost positioned on the same level dorsally as the anterior peduncle which contrasts with several metriorhynchoids (e.g. *Pelagosaurus typus*, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Geosaurus giganteus*, etc.). Yet, there are some thalattosuchians that also display similar dorsal extensions for their peduncle but those possess a more reduced acetabular perforation laterally (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Lemmysuchus obtusidens*). Dorsally, the posterior peduncle displays two distinct facets: the articular facet connecting to the ilium, and the facet forming the ventral border of the bony acetabulum. The latter accounts for almost ⅔ of the total dorsal surface of the posterior peduncle and is slightly concave. Its silhouette is that of a rounded triangle with its anterior margin being concave and its lateral one being strongly convex up to the point of being almost hemispherical. The limit between the two sub-surfaces of the posterior peduncle is relatively straight. The medial articular facet of the posterior peduncle is overall triangular in shape. It is oriented medially rather than laterally and its surface is strongly pitted. The posterior peduncle of *Charitomenosuchus leedsi* appears to be slightly elevated from the shaft as in *Macrospondylus bollensis*, which is presumably caused by the overall position of the peduncle bridge (which is relatively more ventral in both *Charitomenosuchus leedsi* and *Macrospondylus bollensis*).

Overall, the anterior and posterior margins of the ischium are both concave, with the anterior one displaying a greater intensity and almost appearing hemispherical. The shaft of the ischium of *Charitomenosuchus leedsi* (Fig. 48), located directly underneath the peduncles, is proportionally long and thin as its total dorsoventral height greatly exceeds (of about 140 %) the anteroposterior length of its constriction. In parallel, the anteroposterior constriction of the shaft (which corresponds to its ventral limit) is not significantly longer than the posterior peduncle, unlike in *Macrospondylus bollensis*. Ventrally to the shaft, the ischium of *Charitomenosuchus leedsi* drastically flares out to form the distal blade. Within Thalattosuchia, *Cricosaurus suevicus* and *Lemmysuchus obtusidens* also possess the combination of a thin shaft and large distal blade. Posteriorly, the subtle concavity of the posterior margin of the ischium of *Charitomenosuchus leedsi* is disrupted by a series of undulations before culminating in the posterior process. These undulations in the vicinity of the posterior process appear unique to *Charitomenosuchus leedsi* (i.e. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*). The shape of the posterior process of *Charitomenosuchus leedsi* is also singular: it consists in a relatively straight surface connected to the posterior margin of the ilium and the distal through rounded corners (almost right-angled). *Thalattosuchus superciliosus* also displays a relatively straight surface for its posterior process, but with a different inclination and size. The posterior process of *Charitomenosuchus leedsi* is also moderately well-developed as its dorsoventral height reaches about 27% of the total dorsoventral height of the ischium unlike those of *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, *Thalattosuchus superciliosus*, or *Platysuchus multiscrobiculatus*. Comparatively, *Aeolodon priscus* and *Lemmysuchus obtusidens* display a proportionally thicker posterior process than *Charitomenosuchus leedsi*.

The posterior process of the ischium is connected to the anterior process through the ventral margin, which also corresponds to the distal blade. The latter is not straight unlike in several other thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, *Cricosaurus bambergensis*, *Dakosaurus maximus*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, etc.)

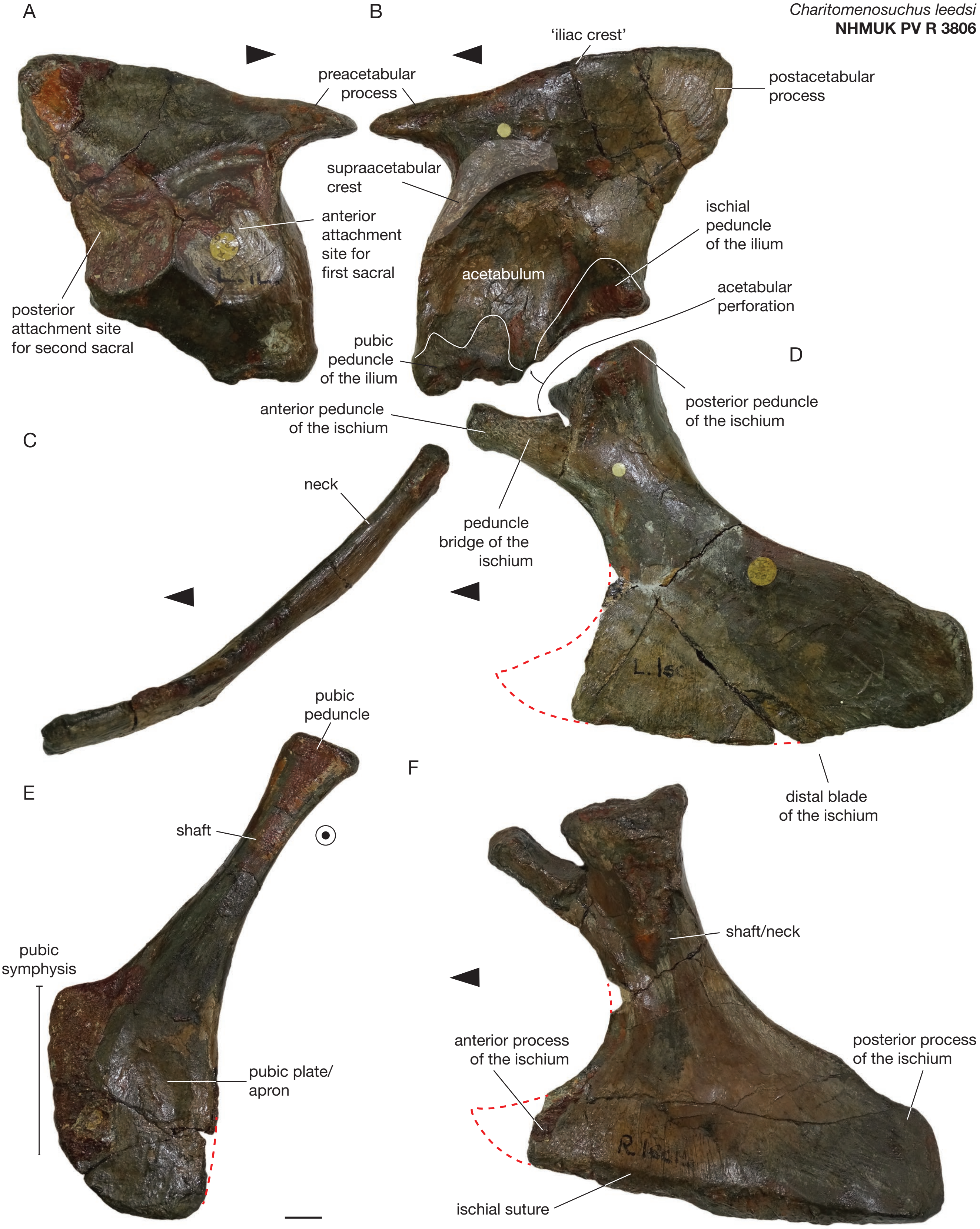


FIG. 48. — Pelvic girdle elements of *Charitomenosuchus leedsi* (Andrews, 1909), NHMUK PV R 3806: **A**, left ilium in medial view; **B**, left ilium in lateral view; **C**, left pubis in lateral view; **D**, left ischium in lateral view; **E**, left pubis in anterior view; **F**, right ischium in medial view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

but is highly undulating similar to *Neosteneosaurus edwardsi*. *Thalattosuchus superciliosus* NHMUK PV R 2054 also displayed a singular distal blade due to an anterior bending. Mediolaterally, the distal blade of the ischium is relatively thick, unlike the anterior and posterior processes. Indeed, on the medial side of the ischium, the distal blade displays a strongly pitted area which corresponds to the ischial suture where both ischia met *in vivo* (Fig. 49). The anterior process of *Charitomenosuchus leedsi* (Fig. 48) appears to have been relatively sharp as both the ventral and anterior margins of the ischium are strongly convergent.

Pubis

The pubis *Charitomenosuchus leedsi* (Fig. 48) shows the combination of a relatively short shaft and a long pubic symphysis, similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Machimosaurus*, *Lemmysuchus obtusidens*, and *Neosteneosaurus edwardsi*. Overall, the lateral and medial margins of the pubis are concave. However, the concavity of the lateral margin is less harmonious than the lateral one, as it displays undulations along its length similar to *Machimosaurus*.

The shaft of *Charitomenosuchus leedsi* accounts for about ¼ of the total proximodistal length of the pubis. The mediolateral width of the thinnest portion of the shaft (i.e. the constriction) is drastically lesser than that of the pubic peduncle, similar to *Pelagosaurus typus*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*. In *Charitomenosuchus leedsi*, the mediolateral width of the constriction of the shaft corresponds to half of the mediolateral width of the pubic peduncle. From the base of the constriction up until the pubis peduncle, the medial and lateral margins of the shaft are concave but not symmetrical, so that the median of the pubic peduncle is shifted laterally compared to that of the shaft. The pubic peduncle is set on top of the shaft proximally. It displays an oval outline whereas its articular surface is curving, with its centre being concave and its medial corner being set more distally that the lateral corner.

The pubic apron of *Charitomenosuchus leedsi* is relatively slender up until the apparition of the pubic symphysis, as in *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 3804, *Cricosaurus albersdoerferi*, *Cricosaurus bambergensis*, *Machimosaurus*, *Platysuchus multiscrobiculatus*. Medially, the margin of the pubis bends at an angle of approximately 153° which drastically expands the size of the pubic apron medially before the pubic symphysis (Fig. 49). The junction between the medial margin of the shaft and the pubic symphysis forms a right angle, as in other thalattosuchians with elongated pubic symphysis regardless of the orientation of the pubic symphysis (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Lemmysuchus obtusidens*, *Machimosaurus*, *Macrospondylus bollensis*, etc.). The pubic symphysis of *Charitomenosuchus leedsi* (Fig. 48) is well developed as it accounts for about 31% of the total proximodistal height of the bone. The transition between the pubic symphysis and the distal margin of the pubis is well marked as opposed to *Pelagosaurus typus*, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, and *Macrospondylus bollensis*. In *Charitomenosuchus leedsi*, the distal margin of the pubis and the pubic symphysis form an angle of approximately 150°, similar to *Lemmysuchus obtusidens* and *Mycterosuchus nasutus*. The distal margin of the pubis appears to be overall convex, even though there is a relatively angular bent around its mid-length. Laterally, the distal margin of the pubic apron forms a smooth corner in line with the lateral margin of the pubis (i.e. it does not protrude laterally as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804).

The entire pubic apron of *Charitomenosuchus leedsi* is slightly twisted so that the medial corner is also pointing ventrally whereas the lateral one also points dorsally. In addition, the posteroventral surface of the pubic apron is slightly concave, emphasizing the curve of the pubic apron (Fig. 49). The pubic apron of other thalattosuchians may show other configurations similarly turning the pubic apron into a shallow spatula (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Lemmysuchus obtusidens*, *Machimosaurus*, etc.).

Overall, the pubis of *Charitomenosuchus leedsi* (Fig. 48) bears a resemblance to those of *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi* among other teleosauroids (i.e. *Machimosaurus*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, etc.). The resemblance between *Charitomenosuchus leedsi*, *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi* is mainly driven by the shape of the pubic apron (including the pubic symphysis) and its relation with the shaft. The shape of the pubic apron is strongly influenced by the size and orientation of the pubic symphysis and both display similar values in *Charitomenosuchus leedsi*, *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi*, and *Mycterosuchus nasutus* (the lowest value): the pubic symphysis corresponds to about 28-35% of the total height of the bone, and forms an angle of approximately 28-30° with the median of the shaft. In addition, the distal margin of the pubic apron joining the pubic symphysis and the posterior margin of the pubis is slightly convex in both *Charitomenosuchus leedsi* and *Lemmysuchus obtusidens*.

PROEXOCHOKEFALOS CF. *BOUCHARDI* (SAUVAGE, 1872)

For measurements, see Tables 7-9.

The bone referred to the pubis of *Proexochokefalos* cf. *bouchardi* MJSN SCR010-374 in Schaefer *et al.* (2018) is not included in our description. Indeed, the bone displays all the characteristics of a derived teleosauroid humerus: shortening of humeral shaft; posterior deflection of the articular proximal head; distal torsion of the condyles in relation to the coronal plane; continuous surface between the deltopectoral crest and the proximal articular head.

Ilium

The ilium of *Proexochokefalos* cf. *bouchardi* (Figs 50; 51) stands out from that of other teleosauroids with the bulged shape of its preacetabular process and dorsal margin as a whole. Indeed, the dorsal margin of the ilium of *Proexochokefalos* cf. *bouchardi* is almost entirely convex, with a shallow recess

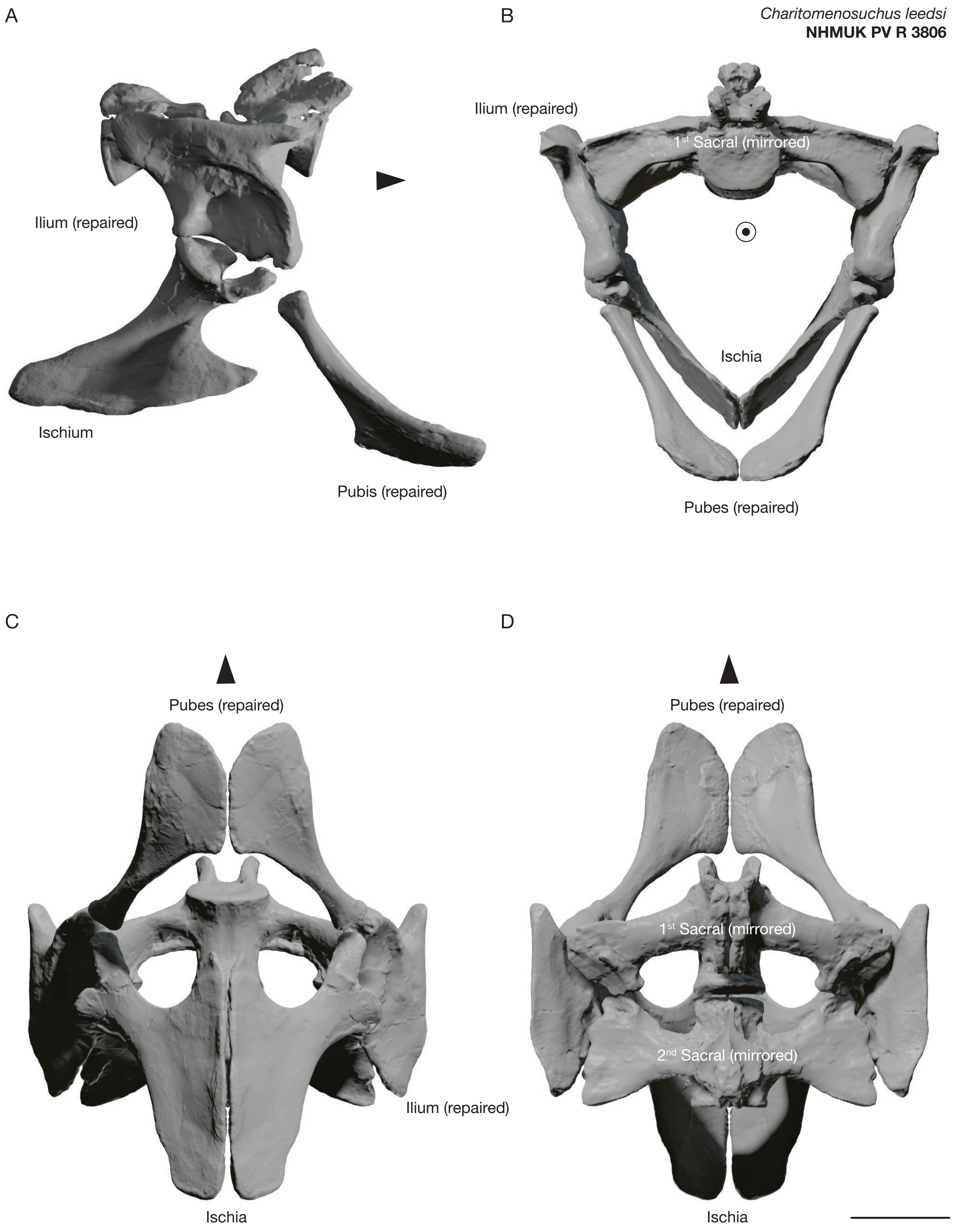


FIG. 49. — Pelvic reconstruction of *Charitomenosuchus leedsi* (Andrews, 1909), NHMUK PV R 3806: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right ilium, ischium and pubis are mirrored. Scale bar: 5 cm.

located at ⅔ of its length posteriorly rather than at the base of the preacetabular process as in other teleosauroids (e.g. *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*). As a result, the preacetabular process of *Proexochokefalos* cf. *bouchardi* is dorsoventrally thick, and the area of the ilium extending from the supraacetabular crest to the dorsal margin is enlarged compared to other teleosauroids. Still, the preacetabular process of *Proexochokefalos* cf. *bouchardi* rapidly slims down anteriorly to form a sharp apex, thanks to its strongly concave ventral margin. Like in *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*, the preacetabular process of *Proexochokefalos* cf. *bouchardi* is, in general, oriented anteriorly and is mediolaterally thin.

In comparison, the postacetabular process of *Proexochokefalos* cf. *bouchardi* possesses a dorsal component in its orientation, so that its apex is oriented dorsoventrally as in *Sericodon jugleri*, *Charitomenosuchus leedsi*, and *Neosteneosaurus edwardsi*. The postacetabular process of *Proexochokefalos* cf. *bouchardi* takes the shape of a Lancet arch as in most teleosauroids (except *Macrospondylus bollensis* and *Platysuchus multiscrobiculatus*), despite possessing a slightly concave dorsal margin. The posterior margin of the ilium of *Proexochokefalos* cf. *bouchardi* forms a symmetrical sine curve, with a convex portion dorsally switching to a more concave shape ventrally at about its mid length. The inflexion point marks the base of the postacetabular process of *Proexochokefalos* cf. *bouchardi*, which is proportionally short as it only reaches about 36% of the total dorsal length (anteroposteriorly) of the ilium. The concave portion of the posterior margin of the ilium may have presented a short spike around its centre as in *Neosteneosaurus edwardsi*. Indeed, the centre presents a broken portion whose sides constitute two slightly emerging surfaces.

The anterior margin of the ilium of *Proexochokefalos* cf. *bouchardi* underneath the preacetabular process is relatively straight throughout its length. Still, the rim of the supraacetabular crest of *Proexochokefalos* cf. *bouchardi*, although broken, hangs over the edge of the anterior margin, making it slightly convex as in *Pelagosaurus typus* and *Charitomenosuchus leedsi*. In *Proexochokefalos* cf. *bouchardi*, the supraacetabular crest forms a thin and convex ridge, which strongly protrudes laterally which contrasts with *Sericodon jugleri*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*. In comparison, *Charitomenosuchus leedsi* also has a markedly convex supraacetabular crest, but instead of laterally protruding, the later is noticeable due to the deep indentation of the acetabulum directly underneath it. The bony acetabulum of *Proexochokefalos* cf. *bouchardi* is large (i.e. both dorsoventrally tall and anteroposteriorly long) as in other teleosauroids, but only forms a relatively shallow indentation as in *Lemmysuchus obtusidens* (as opposed to *Sericodon jugleri*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, and possibly *Macrospondylus bollensis*). This is partly due to the relatively thin mediolateral thickness, and subsequent small lateral protrusion, of both pubic and ischial peduncles.

The pubic peduncle of *Proexochokefalos* cf. *bouchardi* only forms a subtle bulge along the anterior margin of the ilium, as in *Sericodon jugleri*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Platysuchus multiscrobiculatus*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*. Like in other teleosauroids, the pubic peduncle of *Proexochokefalos* cf. *bouchardi* is more ventrally located than the ischial peduncle, which gives an undulating aspect to the ventral margin of the ilium. In ventral view, the pubic peduncle of *Proexochokefalos* cf. *bouchardi* shows an overall constant thickness throughout its length, and displays the typical lunate or wedge-shaped outline found in other teleosauroids but with a smaller concavity. Like in *Sericodon jugleri*, the posterior edge of the pubic peduncle of *Proexochokefalos* cf. *bouchardi* is concave where is transitions to the acetabular perforation. On the lateral side of the ilium, the outline of the pubic peduncle of *Proexochokefalos* cf. *bouchardi* draws two adjacent triangular shapes with the posterior one being the greatest, as in other teleosauroids. However, unlike in *Neosteneosaurus edwardsi*, *Charitomenosuchus leedsi* and *Sericodon jugleri*, the posterior triangular shape of the pubic peduncle of *Proexochokefalos* cf. *bouchardi* is comparatively dorsoventrally squashed, and hence is shorter than the ischial peduncle.

Laterally, the ischial peduncle of *Proexochokefalos* cf. *bouchardi* displays an overall triangular outline, with the dorsal apex posteriorly shifted as in other teleosauroids (*e.g Sericodon jugleri*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*). Posteriorly, the ischial peduncle gradually protrudes laterally from the rest of the ilium, forming the posterior barrier of the acetabulum. The ventral surface of the ischial peduncle of *Proexochokefalos* cf. *bouchardi* forms a sinusoidal shape which dealigns it with the ventral margin of the pubic peduncle and gives the ventral margin of the ilium its undulating aspect. In ventral view, the ischial peduncle of *Proexochokefalos* cf. *bouchardi* also shows a subtly lunate outline like the pubic peduncle. Its mediolateral thickness is overall constant for the first anterior ⅔ of its lengths, then it gradually increases posteriorly to reach 150% of its anterior thickness at its peak. The maximum mediolateral thickness and anteroposterior length of the ischial peduncle of *Proexochokefalos* cf. *bouchardi* exceed the dimensions of the pubic peduncle.

The acetabular perforation of *Proexochokefalos* cf. *bouchardi* forms a shallow notch (about five times longer anteroposteriorly than deep) separating the pubic and ischial peduncles, similarly to most teleosauroids (except *Sericodon jugleri* in which it is enlarged). The acetabular perforation of *Proexochokefalos* cf. *bouchardi* is most similar to *Charitomenosuchus leedsi* in terms of size (and possibly *Macrospondylus bollensis*). However, it contrasts with *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens* in being less extented anteroposteriorly, which brings the pubic and ischial peduncles close to one another.

The attachment sites for the sacral ribs form two distinct impressions on the medial side of the ilium of *Proexochokefalos* cf. *bouchardi*, as in most teleosauroids (except *Lemmysuchus obtusidens* and *Machimosaurus* in which there are three). Their

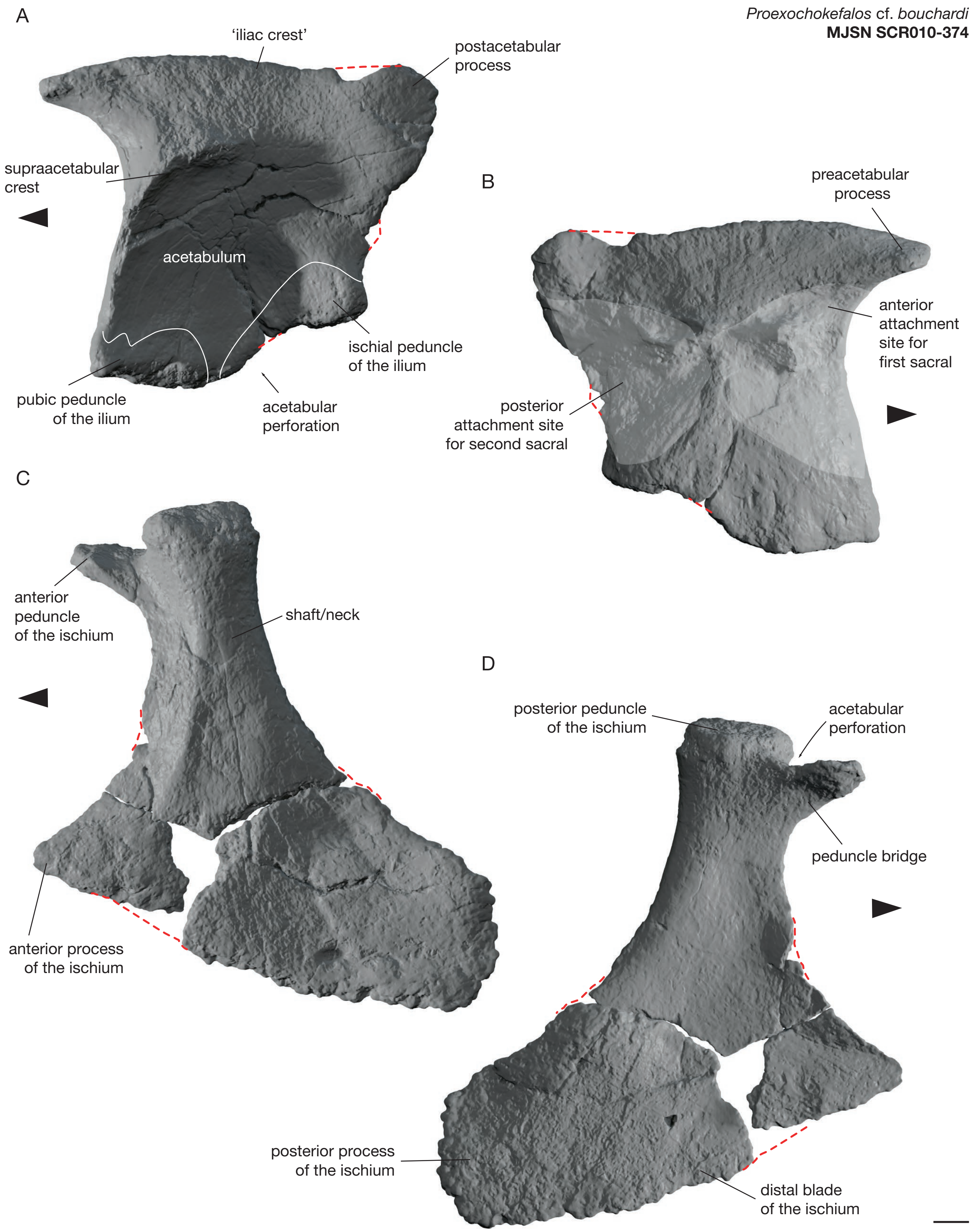


FIG. 50. — Pelvic girdle elements of *Proexochokefalos* cf. *bouchardi* (Sauvage, 1872), MJSN SCR010-374: **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, right ischium in medial view; **D**, right ischium in lateral view. Arrow points anteriorly. Original models courtesy of Dr Jeremy Anquetin (Jurassica Museum-MJSN). Scale bar: 1 cm.

shape is also similar to what is observed in most teleosauroids; the attachment sites for the sacral ribs are bell-shaped (i.e. their dorsal and ventral margins are convex) with their apex meeting around the centre of the ilium and their greatest axis oriented anteroposteriorly. Each print possesses a strongly protruding excrescence near its apex, which was inserted in the hollow tip of the sacral rib. The dorsal margin of the attachment site of the second sacral rib reaches the apex of the postacetabular process and divides it in half, whereas the dorsal margin of the attachment site of the first sacral rib is in line with the ventral margin of the preacetabular process. In comparison, the ventral margin both attachment sites reach each ventral corner of the ilium.

Ischium

The ischium of *Proexochokefalos* cf. *bouchardi* (Figs 50; 51) displays a relatively slender shaft, similar to *Mycterosuchus nasutus*, *Teleosaurus* sp., and *Charitomenosuchus leedsi*.

However, the ischium of *Proexochokefalos* cf. *bouchardi* drastically differs from these taxa (and other teleosauroids) in displaying a rather gracile outline. The anterior and posterior margins of the ischium of *Proexochokefalos* cf. *bouchardi* are both concave with a relatively great amplitude, resulting in a more ventrally stretched ischium. Furthermore, both anterior and posterior margins have their apex located around their mid-length which contributes to their symmetrically concave aspect throughout their length and overall stretched look. The anterior margin of other teleosauroids is often symmetrically concave (i.e. the apex is located at the mid-length of the margin; e.g. *Aeolodon priscus*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*), but it is not always the case for the posterior margin. Comparatively, *Platysuchus multiscrobiculatus* and *Macrospondylus bollensis* also display a symmetrically concave posterior margin like *Proexochokefalos* cf. *bouchardi*.

Proximally, the shaft of *Proexochokefalos* cf. *bouchardi* widens to form the anterior and posterior peduncles. The latter has an overall circular outline and has a bulged rim around its lateral edge whereas the rim becomes thinner medially. The dorsal surface of the posterior peduncle is separated into a wedgeshaped surface medially and a trapezoid-shaped surface laterally through a faintly protruding ridge. The lateral surface – which is involved in the hip acetabulum– is dorsally facing, which is similar to the Machimosaurinae members *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*. Another common trait between *Proexochokefalos* cf. *bouchardi* and *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens* is the relative size of each dorsal surface of the posterior peduncle: both surfaces appear to have similar dimensions, although the medial one is slightly smaller.

The anterior peduncle of *Proexochokefalos* cf. *bouchardi* strongly differs from that of other teleosauroids as it presents a sharp extremity pointing strictly anteriorly, which resembles an isosceles triangle in lateral and dorsal views. Furthermore, the articular facet of the anterior peduncle of *Proexochokefalos* cf. *bouchardi* is mainly oriented dorsally, with an additional small surface present on the underside, laterally, which presumably met with the peduncle of the pubis. This strongly contrasts with the slightly convex articular surface mainly anteriorly facing found in other teleosauroids (e.g. *Aeolodon priscus*, *Teleosaurus* sp., *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*). Such a sharp anterior peduncle was found in some metriorhynchoids, like '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5 and *Thalattosuchus superciliosus*.

The anterior and posterior peduncles are separated by the acetabular perforation. Like in most teleosauroids, the acetabular perforation of *Proexochokefalos* cf. *bouchardi* is partially obstructed laterally by the peduncle bridge and, as a result, it is medially tilted. The dorsal margin of the peduncle bridge is markedly concave as it forms the base of the acetabular perforation. In comparison, the ventral margin of the peduncle bridge is straight. Laterally and medially, the peduncle bridge gradually widens and reaches its maximum width at its junction with the anterior peduncle.

Like *Platysuchus multiscrobiculatus* and *Teleosaurus* sp., the posterior process of *Proexochokefalos* cf. *bouchardi* displays a tubular to subquadrangular shape, yet less slender. The posterior process of *Proexochokefalos* cf. *bouchardi* is dorsoventrally thick throughout its length and its apex is rectangular with rounded corners and a subtly convex posterior edge. The ventral margin of the ischium of *Proexochokefalos* cf. *bouchardi* appears to have been relatively straight but is not entirely preserved. The anterior process of *Proexochokefalos* cf. *bouchardi* is relatively short and extends as far anteriorly as the anterior peduncle as in other teleosauroids. The anterior process of *Proexochokefalos* cf. *bouchardi* points mainly anteriorly and forms an isosceles triangle with its slightly concave dorsal margin and straight ventral margin.

NEOSTENEOSAURUS EDWARDSI (EUDES-DESLONGCHAMPS, 1868)

For measurements, see Tables 7-9.

The specimen NHMUK PV R 3701 is supposedly a juvenile or subadult individual.

Ilium

The ilium of *Neosteneosaurus edwardsi* (Figs 52-55; 57; 58) is proportionally large like that of other teleosauroids, notably due to the presence of a well-developed postacetabular process and a greater bony acetabulum (e.g. *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*, etc.). Overall, the relative parallelepiped shape of the ilium of *Neosteneosaurus edwardsi* is similar in appearance to *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi* than to *Platysuchus multiscrobiculatus*, *Plagiophthalmosuchus gracilirostris*, and *Macrospondylus bollensis*. Still, the ilium of *Neosteneosaurus edwardsi* (PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898) differs from that of *Charitomenosuchus leedsi* in displaying a flat anterior margin, and from that of *Lemmysuchus obtusidens* in possessing a proportionally larger preacetabular process. In parallel, the ilia of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701 and NHMUK PV R 2076 are oriented

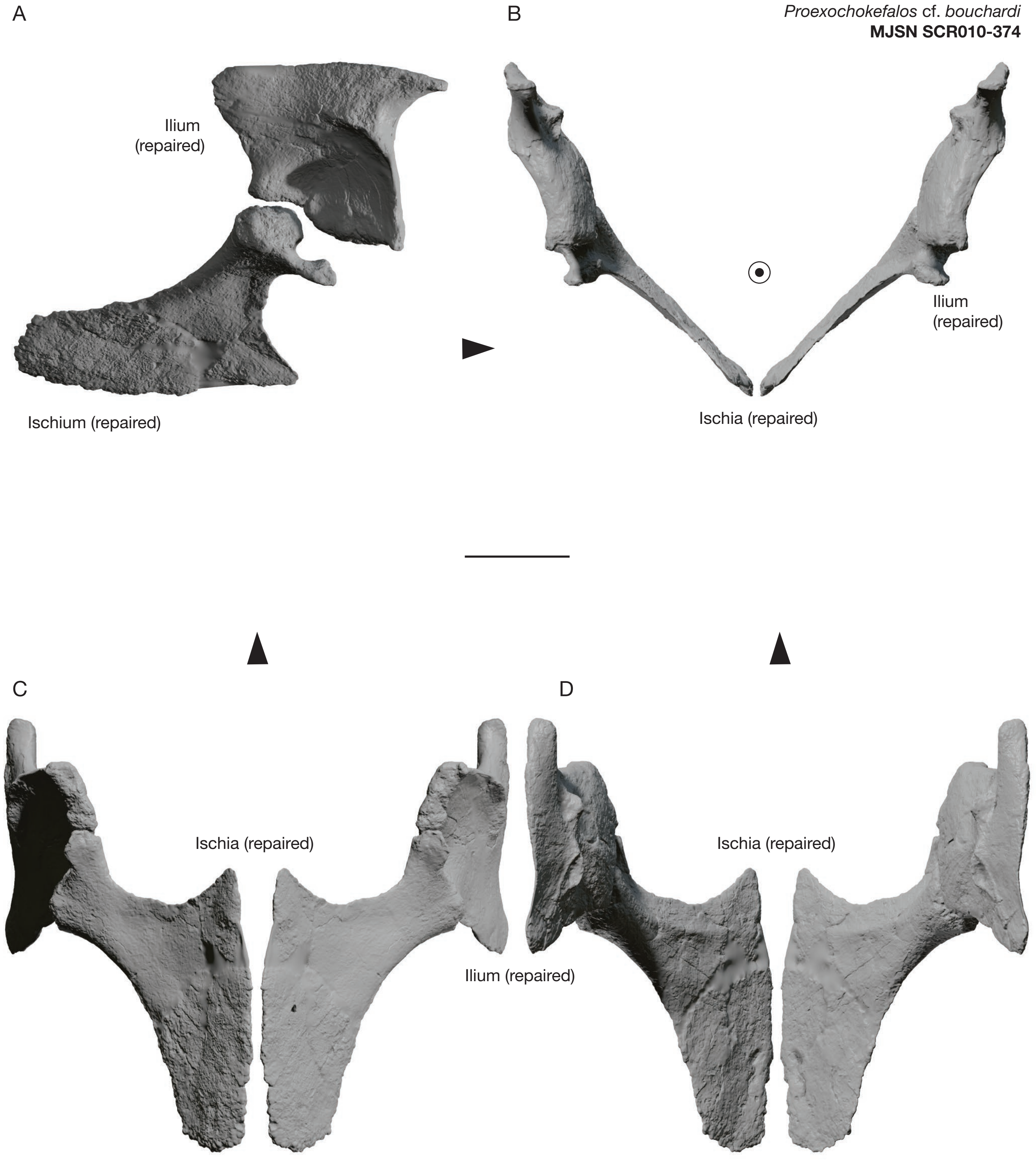


FIG. 51. — Pelvic reconstruction of *Proexochokefalos* cf. *bouchardi* (Sauvage, 1872), MJSN SCR010-374: **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The right ilium and left ischium mirrored. Original models courtesy of Dr Jeremy Anquetin (Jurassica Museum-MJSN). Scale bar: 5 cm.

differently than those of *Lemmysuchus obtusidens* (Fig. 59) and *Charitomenosuchus leedsi*, which appear closer to *Neosteneosaurus edwardsi* NHMUK PV R 3898.

The preacetabular process of *Neosteneosaurus edwardsi* (Figs 52-55) is proportionally long as its anteroposterior length approximately reaches that of the pubic peduncle, unlike that of *Lemmysuchus obtusidens* which is slightly shorter. In all specimens (PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898), the preacetabular process of *Neosteneosaurus edwardsi* is slender: the size of its mid-section dorsoventrally and mediolaterally is lesser or equal to half of its anteroposterior length. Moreover, the preacetabular processes of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898 display an overall constant mediolateral and dorsoventral thickness (approximating that of the mid-section) throughout their anteroposterior length. For this reason, the ventral and dorsal margins of the preacetabular process almost appear mirrored with one another whereas the dorsal margin is overall straight and the ventral one subtlety concave. The dorsal margin of the ilium of *Neosteneosaurus edwardsi* (PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898) corresponding to the iliac crest is aligned with the dorsal border of the preacetabular process. The junction between the two is achieved through a subtle depression at the base of the preacetabular process in PETMG R178, NHMUK PV R 2076 and NHMUK PV R 3898. In NHMUK

PV R 3701, the junction is even less visible, presumably due to the deformation of the bone. The anterior margin of the ilium underneath the supraacetabular process is straight, unlike *Charitomenosuchus leedsi*.

The iliac crest of *Neosteneosaurus edwardsi* is relatively straight for about three-quarters of its length, then becomes gently convex posteriorly as it forms the apex of the postacetabular process. The latter takes the shape of an asymmetrical Lancet arch, as the convexity of its posteroventral margin displays a greater amplitude. The dorsal surface of the iliac crest of PETMG R178, NHMUK PV R 2076 and NHMUK PV R 3898 is not entirely flat but presents some low amplitude undulations throughout (Figs 54; 55). The peak of the postacetabular process is almost in line with the iliac crest so that it points in the exact opposite direction of the preacetabular process. Comparatively, the ilia of *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi* display relatively similar dorsal margins and apex for their postacetabular process, but differ in the shape of their posterior margin. Indeed, the posteroventral margin of the postacetabular process of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 2076 and NHMUK PV R 3898 (Figs 54; 55) forms a global sinusoid curve with the convex and concave portions showing equal shares. In addition, the concave part of the posterior margin of the ilium displays a small crest around its mid-length which is a feature not found in other teleosauroids (i.e. *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*). On the lateral surface of the ilium, the area bordering the margins of the postacetabular process shows a series of ridges indicating the presence of a cartilage cap *in vivo*. The ridges are perpendicular to the margin of the ilium dorsally, but those become more tilted along the second half of the postacetabular process.

The ventral margin of the ilium of *Neosteneosaurus edwardsi* (Figs 53-55) is strongly undulating with the pubic peduncle extending more ventrally than the ischial peduncle, as in other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, etc.). In *Neosteneosaurus edwardsi*, the large difference in the dorsoventral position of the peduncles and their global anteroposterior extension is typical of teleosauroids (i.e. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*). Indeed, in teleosauroids, the pubic peduncle is positioned more ventrally unlike in metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Geosaurus giganteus*, etc.). Similar to other crocodyliforms, the posterior corner of the ischial peduncle of *Neosteneosaurus edwardsi* (PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898) greatly protrudes from the lateral surface of the ilium, whereas its anterior corner is set in the wall of the bony acetabulum. In NHMUK PV R 3898, the ischial peduncle also protrudes posteriorly and extends over the posterior margin of the ilium, masking its junction with the posterior margin. The ischial peduncle of the ilium forms the posterior border of the bony acetabulum, and was presumably the anchoring site for a structure similar to the antitrochanter of extant crocodylians (Tsai & Holliday 2015). The facet of the ischial peduncle on the lateral surface of the ilium is wedge-shaped and not triangular similar to *Lemmysuchus obtusidens*, *Macrospondylus bollensis* and *Charitomenosuchus leedsi*, which contrasts with most metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, etc.). The facet of the ischial peduncle is also dorsoventrally shorter than the pubic peduncle in PETMG R178,NHMUK PV R 2076, and NHMUK PV R 3898 (like in *Pelagosaurus typus*), whereas both are about the same height in NHMUK PV R 3701. The ventral surface of the ischial peduncle is mainly flat, but becomes concave anteriorly before its junction with the acetabular perforation as in *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi*. In ventral view, the ischial peduncle takes the shape of an isosceles triangle, with its greatest axis oriented anteroposteriorly.

Similar to other teleosauroids (i.e. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*), the acetabular perforation of *Neosteneosaurus edwardsi* (PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898) forms an anteroposteriorly long but shallow indentation which completely separates both peduncle. The pubic peduncle of the ilium of *Neosteneosaurus edwardsi* NHMUK PV R 3701 and NHMUK PV R 2076 displays an anteroposterior length similar to that of the ischial peduncle, as in *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, and *Charitomenosuchus leedsi*. In PETMG R178 and NHMUK PV R 3898, the ischial peduncle largely exceeds the pubic peduncle in length anteroposteriorly (as in for example *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, or *Lemmysuchus obtusidens*). But on the other hand, the ischial peduncle of NHMUK PV R 3898 is drastically thinner mediolaterally whereas this is not seen in the other specimens. Indeed, in NHMUK PV R 3701 and NHMUK PV R 2076, the maximal mediolateral thickness reached by the pubic peduncle is either similar (NHMUK PV R 2076) or slightly greater (NHMUK PV R 3701) than that of the ischial peduncle. Compared to NHMUK PV R 2076 and NHMUK PV R 3701, PETMG R178 and NHMUK PV R

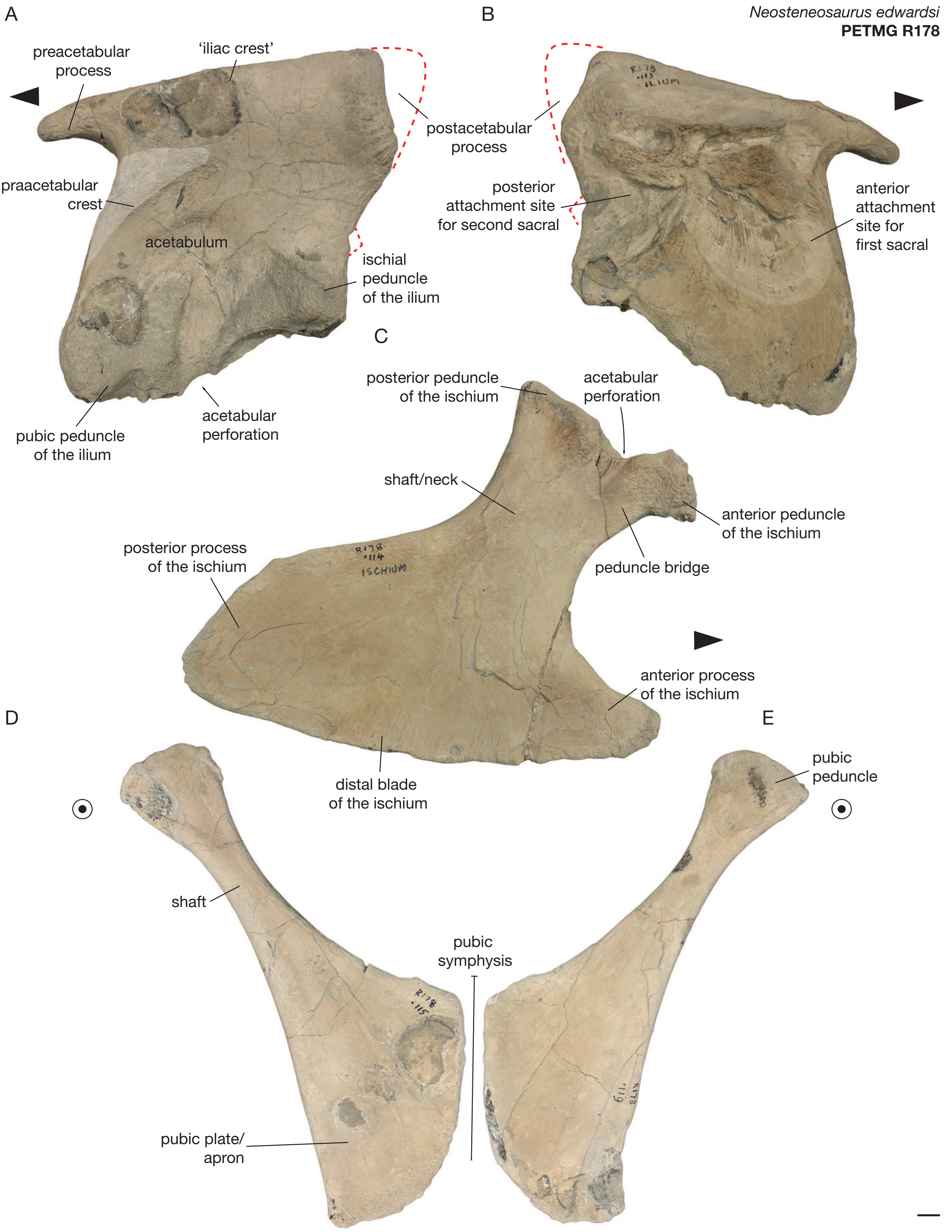


FIG. 52. — Pelvic girdle elements of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), PETMG R178: **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, right ischium in lateral view; **D**, right pubis in anterior view; **E**, left pubis in anterior view. Arrow points anteriorly. Target indicates anterior. Pictures courtesy of Dr Michela Johnson. Scale bar: 1 cm.

3898 are significantly larger and it is possible that it accounts for the difference in the size and shape of the ischial peduncle (Figs 52-55). In all four specimens, the ventral surface of the pubic peduncle is slightly concave, similar other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*). In NHMUK PV R 2076 and NHMUK PV R 3701, the outline of the pubic peduncle ventrally is crescent-shaped (i.e. smoothly curved lateral and medial margins) with its tips begin rounded rather than sharp. In NHMUK PV R 3898 the ventral outline of the pubic peduncle is different as the anterior and medial side form a right-angled corner. The facet of the pubic peduncle on the lateral surface of the ilium displays a greater dorsal extension than the ischial peduncle in PETMG R178 (partially altered anteriorly), NHMUK PV R 2076 and NHMUK PV R 3898; the ilium of NHMUK PV R 3701 is too strongly altered to observe the exact shape of the pubic peduncle laterally. The silhouette the pubic peduncle draws on the lateral surface of the ilium of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 2076 and NHMUK PV R 3898 forms two triangular shapes pointing dorsally. There are other thalattosuchians (mainly metriorhynchoids) whose pubic peduncle forms two triangular shapes (e.g. *Proexochokefalos* cf. *bouchardi*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763), but those of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 2076 and NHMUK PV R 3898 drastically differs from the latter in displaying an exceedingly large posterior shape (more than three times the height of the anterior one). In comparison, the pubic peduncle of *Sericodon jugleri* and *Charitomenosuchus leedsi* also possesses two large triangular shapes, but the posterior one is rather elliptical.

Medially, the ilium of *Neosteneosaurus edwardsi* (Figs 52-55) displays two distinct scars marking the position of the sacral rib attachment sites for each sacral, similar to *Sericodon jugleri*, *Proexochokefalos* cf. *bouchardi*, *Charitomenosuchus leedsi*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), but unlike *Lemmysuchus obtusidens* which possesses three scars. The sacral attachment sites occupy the whole anteroposterior length of the bone are positioned at the mid dorsoventral height of the bone. PETMG R178, NHMUK PV R 2076, NHMUK PV R 3898, and NHMUK PV R 3701 all share the same shape for each of their attachment sites, but their relative size varies across the specimens. Each attachment site is quadrangular in shape and appears like the mirrored version of the other. Indeed, both their dorsal and ventral borders converge towards the centre of the ilium, and their exterior side – either anterior or posterior – is parallel but drastically larger than the shared central margin. The linearity of the shared central delimitation contrasts with the curved one of *Charitomenosuchus leedsi*. The sacral rib attachment sites are delimited by a shallow rim ventrally which gradually increases in intensity to reach its maximal height dorsally. This effect is partly provoked by the relative inclination of the sacral rib attachment sites, which are dorsally sinking towards the ilium. Comparatively, in *Charitomenosuchus leedsi* and *Lemmysuchus obtusidens* the sacral rib attachment sites only form a shallow depression on the medial side of the ilium and thus present a steady border throughout. Similar to other teleosauroids, the sacral rib attachment sites of *Neosteneosaurus edwardsi* possess medially protruding bony insertions located near their dorsal border (Figs 52-55). These processes presumably convey the existence of a matching concave shape on each sacral rib.

Ischium

The ischium of *Neosteneosaurus edwardsi* (Figs 52; 53; 55-58) displays the typical hook-shaped anterior process of thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Torvoneustes carpenteri*, *Aeolodon priscus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, etc.). Indeed, the anterior margin of the ischium underneath the peduncles is markedly concave and culminates ventrally in a sharp process. The later extends slightly further anteriorly than the anterior peduncle does as in *Aeolodon priscus*, *Proexochokefalos* cf. *bouchardi* and *Lemmysuchus obtusidens*. The anterior peduncle of *Neosteneosaurus edwardsi*, which is borne by the peduncle bridge, is larger mediolaterally than it is anteroposteriorly long similar to other teleosauroids (e.g. *Proexochokefalos* cf. *bouchardi*, *Lemmysuchus obtusidens*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, etc.) but unlike metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Torvoneustes carpenteri*, etc.). Furthermore, the articular facet of the anterior peduncle of *Neosteneosaurus edwardsi* (Figs 52; 53; 55; 56) has a slightly convex surface mainly anteriorly oriented as in *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Sericodon jugleri* and *Macrospondylus bollensis*. Hence, in anterior view, the anterior peduncle of *Neosteneosaurus edwardsi* displays a triangular outline pointing ventrally, like *Charitomenosuchus leedsi* and possibly *Macrospondylus bollensis*. In comparison, *Lemmysuchus obtusidens* has its ventral apex slightly truncated so that the articular facet appears more like a parallelepiped. In *Proexochokefalos* cf. *bouchardi*, the anterior peduncle is strongly pointed anteriorly so that the articular facet is oriented strictly dorsally, with however a small articular surface on the underside (but only laterally) for the pubis. In *Sericodon jugleri* the articular facet is incomplete, and it is too obstructed in *Teleosaurus* sp. NHMUK PV R 238.

The peduncle bridge of *Neosteneosaurus edwardsi* is proportionally short as its anteroposterior length reaches that of the posterior peduncle, as in *Lemmysuchus obtusidens*, but unlike *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Macrospondylus bollensis* and *Charitomenosuchus leedsi*. *Sericodon jugleri*, *Proexochokefalos* cf. *bouchardi* and *Aeolodon priscus* also show a short peduncle bridge, but it is proportionally shorter than in *Neosteneosaurus edwardsi*. The relative length of the peduncle bridge of *Neosteneosaurus edwardsi*, like for *Lemmysuchus obtusidens*, is induced by the relative position of the base of the peduncle bridge. Indeed, in both *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens* the peduncle bridge

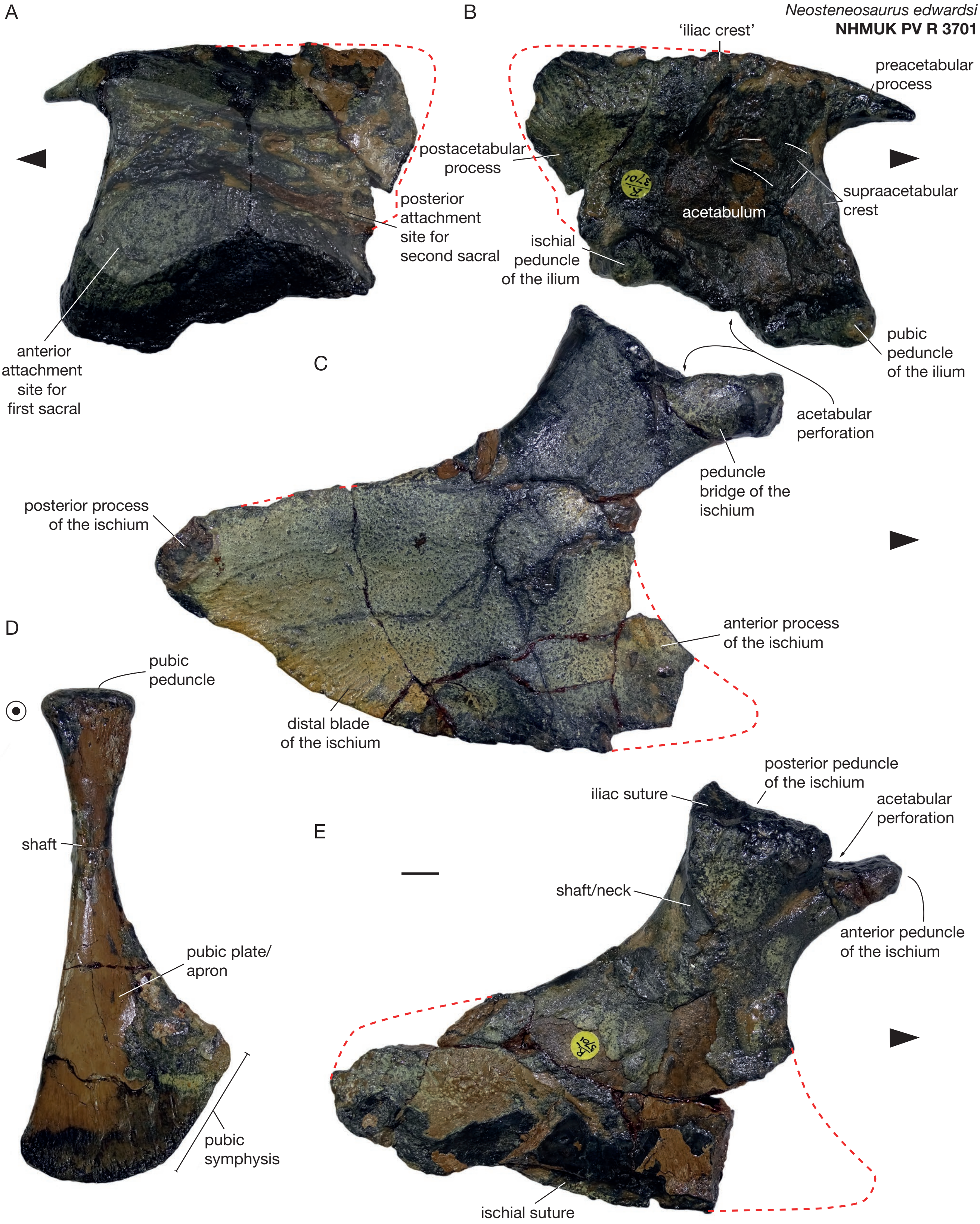


Fig. 53. — Pelvic girdle elements of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 3701: **A**, right ilium in medial view; **B**, right ilium in lateral view; **C**, right ischium in lateral view; **D**, right pubis in anterior view; **E**, left ischium in medial view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

appears to stem from the base of the posterior peduncle, whereas it is located more ventrally in *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a), *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Sericodon jugleri* and *Proexochokefalos* cf. *bouchardi*. For this reason, the acetabular perforation of *Neosteneosaurus edwardsi* appears almost non-existent on the lateral side of the bone. Indeed, the ventral surface of the acetabular perforation corresponds to the dorsal surface of the peduncle bridge, which is actually concave surface and tilted medially so that its medial rim is more ventral than the lateral one. Hence, the acetabular perforation appears like a burrow medially leaning as in most teleosauroids and metriorhynchoids where it is laterally obstructed. In addition, the peduncle bridge is curved medially like *Lemmysuchus obtusidens* (Figs 52; 57; 58), whereas it is more straight in for example *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, and *Sericodon jugleri*.

The posterior peduncle of the ischium of *Neosteneosaurus edwardsi* is proportionally large and displays a half-oval outline overall, with the greatest axis of this shape being aligned anteroposteriorly (Figs 52; 53; 55; 56). The posterior peduncle displays two distinct surfaces dorsally: the lateral and medial facets. The lateral facet of the posterior peduncle accounts for a little more than half of the total surface of the peduncle and is slightly concave. The medial facet is strongly pitted and oriented medially as it was fused to the ilium *in vivo*. Starting from the base of both peduncles, the anterior and posterior margins of the ischium are strongly concave, with the anterior margin displaying the greatest degree of curvature. The area extending from the base of the peduncles up until the anteroposterior constriction is known as the shaft. The shaft of the ischium of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701 and NHMUK PV R 3898 is relatively short and stout as its dorsoventral height is almost equal to its anteroposterior length, similar to *Lemmysuchus obtusidens*. The ischium of NHMUK PV R 2865 presents a bump posteriorly which undermines the identification of the exact position of the shaft constriction. For this reason, it appears slightly longer dorsoventrally than those of PETMG R178, NHMUK PV R 3701 and NHMUK PV R 3898. The shafts of *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701 and NHMUK PV R 3898 further differ from the dorsoventrally short shafts of *Aeolodon priscus* and *Proexochokefalos* cf. *bouchardi*, from the proportionally longer and thicker shaft of *Macrospondylus bollensis*, and also from the relatively more slender shafts of *Teleosaurus* sp. NHMUK PV R 238, *Platysuchus multiscrobiculatus*, *Mycterosuchus nasutus*, *Indosinosuchus potamosiamensis* (Martin *et al.* 2019a) and *Charitomenosuchus leedsi*.

The anterior process of the ischium of *Neosteneosaurus edwardsi* is sharp and points strictly anteriorly, as in *Aeolodon priscus*, *Macrospondylus bollensis*, *Proexochokefalos* cf. *bouchardi*, *Lemmysuchus obtusidens*, and *Platysuchus multiscrobiculatus*. Similar to *Charitomenosuchus leedsi*, the ventral margin of the ischium of *Neosteneosaurus edwardsi* – the ischial blade – is not flat but overall convex in PETMG R178, NHMUK PV R 3701, NHMUK PV R 3898, and NHMUK PV R 2865. In *Neosteneosaurus edwardsi*, the ischial blade almost form a right-angled with the median of the shaft, whereas the distal blade is more tilted in *Lemmysuchus obtusidens* and *Proexochokefalos* cf. *bouchardi* (angle of approximately 45° and 54° with the median of the shaft, respectively). On the medial side of the ischium, the distal blade displays a heavily scarred area over most of its length (= the ischial suture). The latter corresponds to the area where both ischia were connected *in vivo* and was presumably covered in soft tissues. At the base of the anterior process, the ischial suture becomes smooth as in *Proexochokefalos* cf. *bouchardi*, *Lemmysuchus obtusidens*, *Teleosaurus* sp. OUMNH.J1638, and the metriorhynchoids '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 and '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 as opposed to the metriorhynchoids *Thalattosuchus superciliosus* NHMUK PV R 2054 and *Torvoneustes carpenteri*. The shape of the ischial suture is rather lenticular, with its thickest portion located around the peak of the curvature of the distal blade. Like in *Torvoneustes carpenteri*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Thalattosuchus superciliosus*, the ischial suture forms an angle of approximately 45° with the lateral surface of the distal blade so that both ischia were presumably connected through a right-angled junction (Figs 57; 58).

The posterior process of the ischium of *Neosteneosaurus edwardsi* NHMUK PV R 3701, NHMUK PV R 3898, and NHMUK PV R 2865 appears relatively elongated and slender as in the subadult *Aeolodon priscus* MNHN.F.CNJ78, but not as tubular as *Platysuchus multiscrobiculatus*, *Teleosaurus* sp., *Macrospondylus bollensis*, and also *Proexochokefalos* cf. *bouchardi* (although the posterior process is quite thick throughout). The cylindrical aspect of the posterior process of *Neosteneosaurus edwardsi*

NHMUK PV R 3701, NHMUK PV R 3898, and NHMUK PV R 2865 is due to the shape of the concavity of the posterior margin of the ischium. In PETMG R178, the posterior process is bulkier due to a marked sinusoidal posterior margin of the ischium. Indeed, the posterior margin of PETMG R178 is markedly concave dorsally, and switches to strongly convex at around its mid-length, resulting in a dorsoventrally thick posterior process as in *Sericodon jugleri*. In comparison, *Lemmysuchus obtusidens* also has a thick posterior process, but the posterior margin of the latter has a different amplitude and hence presents an extended straight surface unlike in *Neosteneosaurus edwardsi* PETMG R178.

Pubis

The pubis of *Neosteneosaurus edwardsi* (Figs 52-54; 56-58) stands out from that of other teleosauroids in displaying the combination of a long and thin shaft, a large peduncle and a moderately long pubic symphysis (e.g. *Lemmysuchus obtusidens*, *Machimosaurus*, *Platysuchus multiscrobiculatus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*).

The peduncle of *Neosteneosaurus edwardsi* is mediolaterally large as it accounts for about one-fifth of the total proximodistal height of the pubis. Proximally, the outline of the peduncle of NHMUK PV R 2076 and NHMUK PV R 2865 approximates

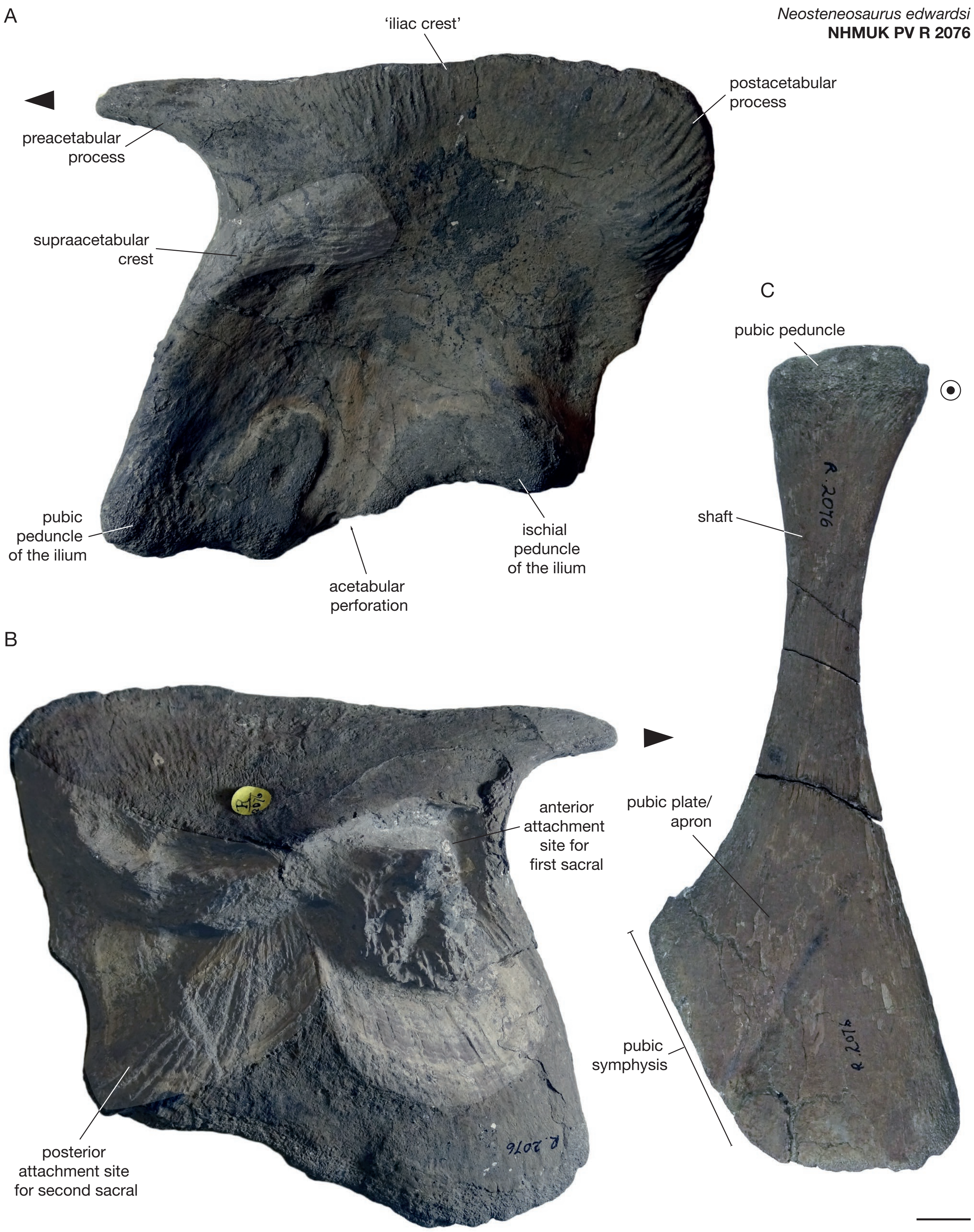


FIG. 54. — Pelvic girdle elements of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 2076: **A**, left ilium in lateral view; **B**, right ilium in medial view; **C**, right ischium in lateral view; **D**, right pubis in anterior view; **E**, left ischium in medial view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

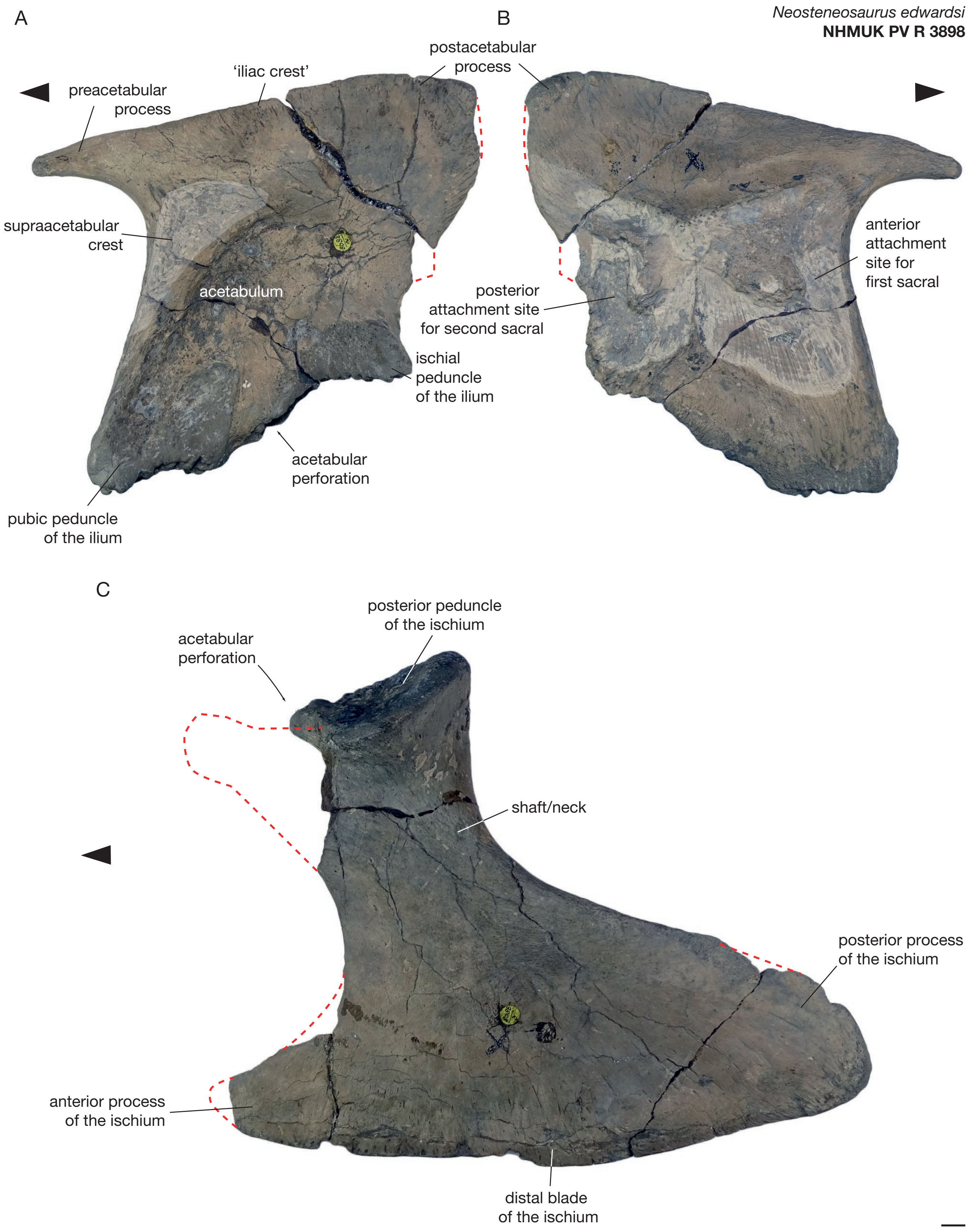


FIG. 55. — Pelvic girdle elements of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 3898: **A**, left ilium in lateral view; **B**, right ilium in medial view; **C**, left ischium in lateral view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

FIG. 56. — Pelvic girdle elements of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 2865: **A**, left ischium in lateral view; **B**, right ischium in medial view; **C**, left pubis in anterior view. Arrow points anteriorly. Target indicates anterior. Scale bar: 1 cm.

that of a droplet, with the sharp corner pointing laterally. In comparison, NHMUK PV R 3701 shows a more elliptical outline for its peduncle. The medial and lateral margins of the pubis underneath the peduncle are both concave with a similar degree of intensity. Also, the apex of each concavity is set at the same distance from the peduncle, all of which result in a relatively thin shaft mediolaterally. Indeed, the mediolateral constriction of the shaft reaches about 42% of the mediolateral width of the pubic peduncle. In addition, the shaft of *Neosteneosaurus edwardsi* is relatively elongated with the constriction being located at around 33% of the proximodistal height of the pubis, proximally (Figs 52-54; 56).

Underneath the constriction, the pubis flares out distally and forms the pubic apron or plate. The medial margin of the pubis stops its course earlier than the lateral margin as it meets with the pubic symphysis. The latter is proportionally long similar to several most thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Lemmysuchus obtusidens*, *Machimosaurus*, *Charitomenosuchus leedsi*) as opposed to *Macrospondylus bollensis*, *Pelagosaurus typus*, *Rhacheosaurus gracilis*, *Magyarosuchus fitosi* Ősi, Young, Galàcz & Rabi, 2018, *Cricosaurus* species and *Geosaurus giganteus*. In *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076 and NHMUK PV R 2865, the pubic symphysis accounts for about 29% of the total proximodistal height of the pubis of *Neosteneosaurus edwardsi* like for *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi*. However, the pubic symphysis of NHMUK PV R 2076 is proportionally slightly longer than in the other specimens (Figs 52; 57; 58). The junction between the pubic symphysis and the medial margin of the pubis is achieved through a right-angled corner as it is the case for the other thalattosuchians displaying a well-developed pubic symphysis. In *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076 and NHMUK PV R 2865, the pubic symphysis forms an angle of approximately 30° with the median of the shaft and the value reaches around 38° in PETMG R178, which are overall similar to the values of *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi*.

The pubic symphysis of *Neosteneosaurus edwardsi* is laterally connected to the distal blade of the pubis through an angle approximating 120-130°, which is lesser than in *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, and *Mycterosuchus nasutus*. As a result, the pubic apron of *Neosteneosaurus edwardsi* is not as extensive as in *Lemmysuchus obtusidens* and *Charitomenosuchus leedsi*. The distal blade of *Neosteneosaurus edwardsi* displays a convex and symmetrical outline, similar to most thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*, *Machimosaurus*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, etc.). The distal blade of *Neosteneosaurus edwardsi* increases in thickness (anteroposteriorly) towards the lateral side of the bone. Compared to the pubic symphysis, the distal blade shows an important increase in thickness, as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Lemmysuchus obtusidens*, *Mycterosuchus nasutus*, but unlike *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054 which possess a more delicate pubis. Laterally, the distal blade of *Neosteneosaurus edwardsi* transitions to the lateral margin through a rounded right-angled corner.

Lemmysuchus obtusidens (Andrews, 1909)

For measurements, see Tables 7-9.

Ilium

The ilium of *Lemmysuchus obtusidens* (Figs 59; 60) possesses the typical feature of Teleosauroidea among Thalattosuchia: the presence of a well-developed (about 36 % of the total anteroposterior length of the ilium) postacetabular process. The postacetabular process is an extension of the ilium, posterior and dorsal to the ischial peduncle. In *Lemmysuchus obtusidens*, it takes the shape of a *Lancet arch*, similar to several teleosauroids (e.g. *Sericodon jugleri*, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, and *Neosteneosaurus edwardsi*), extant crocodylians and dyrosaurids (e.g. *Mecistops cataphractus*, *Congosaurus bequaerti*, and *Hyposaurus natator*). The presence of a postacetabular process strongly influences the shape of the bone, so that ilia bearing a postacetabular process develop a long dorsal blade. Thereby, the dorsal margin of the ilium forms a convex arch posteriorly to the preacetabular process. The posterior-most portion of the ilium constitutes the peak of the *Lancet arch*, which points strictly posteriorly unlike in *Sericodon jugleri*, *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, and *Neosteneosaurus edwardsi*. The junction between the posteacetabular process and the ischial peduncle forms a smooth curve.

The ventral margin of the ilium is undulating: it is composed of the ischial peduncle posteriorly and the pubic peduncle anteriorly. The acetabular perforation separating the two peduncles is shallow, unlike that of other teleosauroids (e.g. *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, *Charitomenosuchus leedsi*, etc.), *Mecistops* or *Congosaurus bequaerti*. The small size of the acetabular perforation diminishes the space between the peduncles, and thereby renders the acetabulum of *Lemmysuchus obtusidens* relatively smaller. The ventral margins of both peduncles are oriented in the same overall direction (like in metriorhynchoids), rather than being tilted at a different angle (as in *Mecistops cataphractus* or *Congosaurus bequaerti*). Yet, the ventral border of the ischial peduncle is situated more dorsally than the pubic peduncle, and is mediolaterally thinner. This difference in relative height between the peduncles is compensated by the ischium and its protruding anterior peduncle (set on the peduncle bridge). The anterior margin of the ilium is straight (as in *Dakosaurus maximus* or *Neosteneosaurus edwardsi*) rather than convex as in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis* or *Charitomenosuchus leedsi*, and ends up with the preacetabular process dorsally. The junction between the anterior margin and the preacetabular process forms a rounded acute angle.

The preacetabular process is proportionally small in relation to the overall size of the ilium (about 16% of the anter-

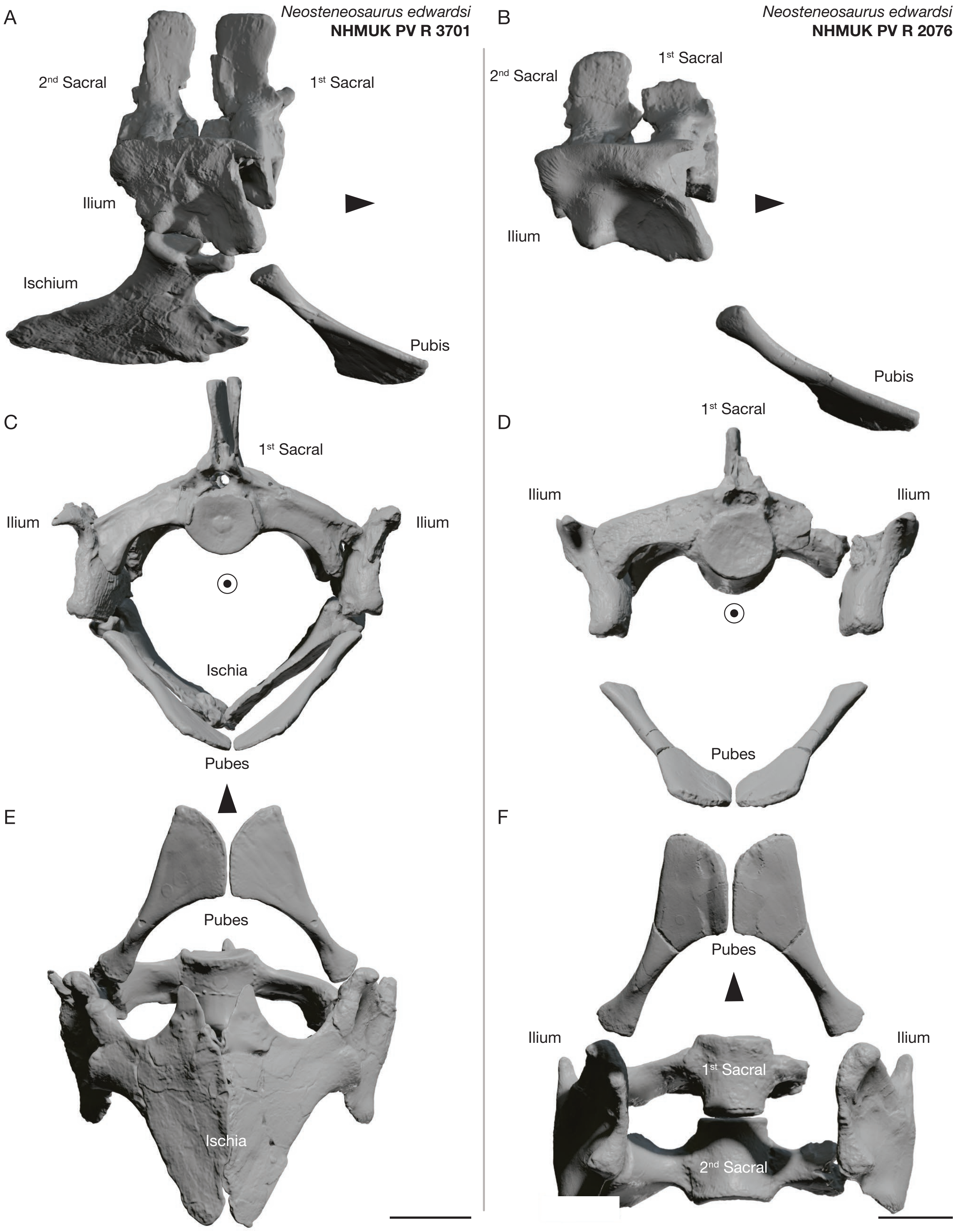


FIG. 57. — Reconstruction of the pelvic girdle of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 3701 (**A**, **C**, **E**) and NHMUK PV R 2076 (**B**, **D**, **F**): **A**, **B**, right lateral views; **C**, **D**, anterior views; **E**, **F**, ventral views. Target indicates anterior. Arrow points anteriorly. The right pubis and left ilium of NHMUK PV R 3701 are mirrored. The right pubis of NHMUK PV R 2076 is mirrored. Scale bars: 5 cm.

oposterior length of the bone), unlike what is observed in some metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Suchodus durobrivensis*) and teleosauroids (e.g. *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*). Moreover, the orientation of the preacetabular process of *Lemmysuchus obtusidens* further differs from what is observed in metriorhynchoids as it has no dorsal component in its orientation, and is facing strictly anteroventrally in the direct extension of the iliac crest (making it parallel to the ventral margins of the peduncles; Fig. 60). The shallow junction between the preacetabular process and the iliac crest emphasizes their relative linearity as in *Neosteneosaurus edwardsi*, *Plagiophthalmosuchus gracilirostris*, *Macrospondylus bollensis*, *Platysuchus multiscrobiculatus*. The preacetabular process of *Lemmysuchus obtusidens* is flattened dorsoventrally, and is wide lateromedially as in *Platysuchus multiscrobiculatus*, *Plagiophthalmosuchus gracilirostris*, or *Thalattosuchus superciliosus*. This effect is less pronounced in *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi* so that even though the ventral surface of their preacetabular process is relatively flat, their dorsal surface remains rounded thus giving a cylindrical appearance to their preacetabular process.

The acetabulum of *Lemmysuchus obtusidens* is large (about 72% of the dorsoventral height of the ilium), and encompasses almost all of the area extending from the preacetabular process through the ventral peduncles. Also, the acetabulum appears centred on the triangular surface defined by the preacetabular process and the ventral peduncles (like in *Macrospondylus bollensis*), as opposed to *Suchodus durobrivensis*, *Charitomenosuchus leedsi* and *Neosteneosaurus edwardsi* NHMUK PV R 3898. This phenomenon is imputable to the relative size of the acetabulum, but also to the position, orientation and extension of the supraacetabular crest, which is a parabolic ridge delimiting the acetabulum. Indeed, the supraacetabular crest of *Lemmysuchus obtusidens* displays a large focal width so that its anterior border closely follows the anterior margin of the ilium, while the posterior border shows a trajectory path aiming at the junction between the ischial peduncle and the base of the postacetabular process. It is also possible that the relative inclination of the anterior margin of the ilium may emphasize this phenomenon.

The configuration of *Lemmysuchus obtusidens* (i.e. large focal width) is similar to extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus* and dyrosaurids (e.g. *Congosaurus bequaerti*, and *Hyposaurus natator*), *contra* what is observed in some metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Tyrannoneustes lythrodectikos*, *Suchodus durobrivensis*, etc.) for which the supraacetabular crest is posteriorly shifted and contact the anterior margin of the ilium relatively ventrally. The supraacetabular crest of *Lemmysuchus obtusidens* also bears the typical prominent anterior ridge and the smooth posterior one, as it can be seen from many crocodyliforms (e.g. *Mecistops cataphractus*, *Congosaurus bequaerti*, *Hyposaurus natator*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Suchodus durobrivensis*, etc.).

In *Lemmysuchus obtusidens*, almost half of the surface of the acetabulum is not hollow, but is obstructed by a laterally protruding hump of bone (Figs 59; 60). This seemingly bony growth disrupts the function of the acetabulum as a cavity and presumably happened later in the life of the specimen. It is unknown if this hump is the result of a trauma or the ossification of cartilaginous (e.g. osteoarthritis of the hip) structures through ageing processes. In theory, there could have been a good dorsoventral congruence between the femoral head and acetabulum if the acetabular labrum were at least as extensive as it is for extant crocodylians (Tsai & Holliday 2015). The existence of a deeply scarred area extending from the pubic peduncle of the ischium through the preacetabular process and the supraacetabular crest in *Lemmysuchus obtusidens* (Figs 59; 60) and also other thalattosuchians (e.g. *Thalattosuchus superciliosus*, *Suchodus durobrivensis*, *Neosteneosaurus edwardsi*, etc.) teases the presence of a widely spread acetabular labrum (but does not inform on the mediolateral breath of this hypothetical structure).

The attachment sites for the sacral processes are observable on the medial side of the ilium, and take up almost half of the entire surface (Fig. 59). In some metriorhynchoids (i.e. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Tyrannoneustes lythrodectikos* or *Suchodus durobrivensis*, etc.), the areas are characterized by being slightly in relief rather than being hollow like extant crocodylians and dyrosaurids (e.g. *Mecistops cataphractus*, *Congosaurus bequaerti*, *Hyposaurus natator*, etc.). There is a thin border made of hollows and bumps drawing the general outline of the sacral rib attachment sites. The delimitation between each attachment site can be deducted from the shape of the dorsal and ventral contours, but the internal demarcation is less clear as in *Suchodus durobrivensis*. The exact contour of each attachment site is based on the careful observation of both the surface of the ilium and the distal extremities of both sacral as well as the first caudal. The general shape of the sacral rib attachment sites forms three lobes (Fig. 59), with the middle one being the greatest. The anterior lobe (the smallest) corresponds to the attachment site of the first sacral, the middle lobe belonged to the second sacral whereas the posterior one (which is cordiform) was the anchoring site for the first caudal. The anterior and middle lobes are composed of a series of radiate ridges, whereas the posterior lobe is more strongly pitted. The latter also roots deeper in the ilium than the other two, which are more superficially anchored.

Ischium

The ischium of *Lemmysuchus obtusidens* (Fig. 59) resembles that of other thalattosuchians (e.g. *Pelagosaurus typus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, *Thalattosuchus superciliosus*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, *Aeolodon priscus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.): the distal blade is elongated anteroposteriorly, giving the impression of an axe head. This shape is not found among Dyrosauridae and Crocodylia, as the shaft of the ischium is usually longer and the distal blade shorter (e.g. *Mecistops cataphractus*, *Caiman*

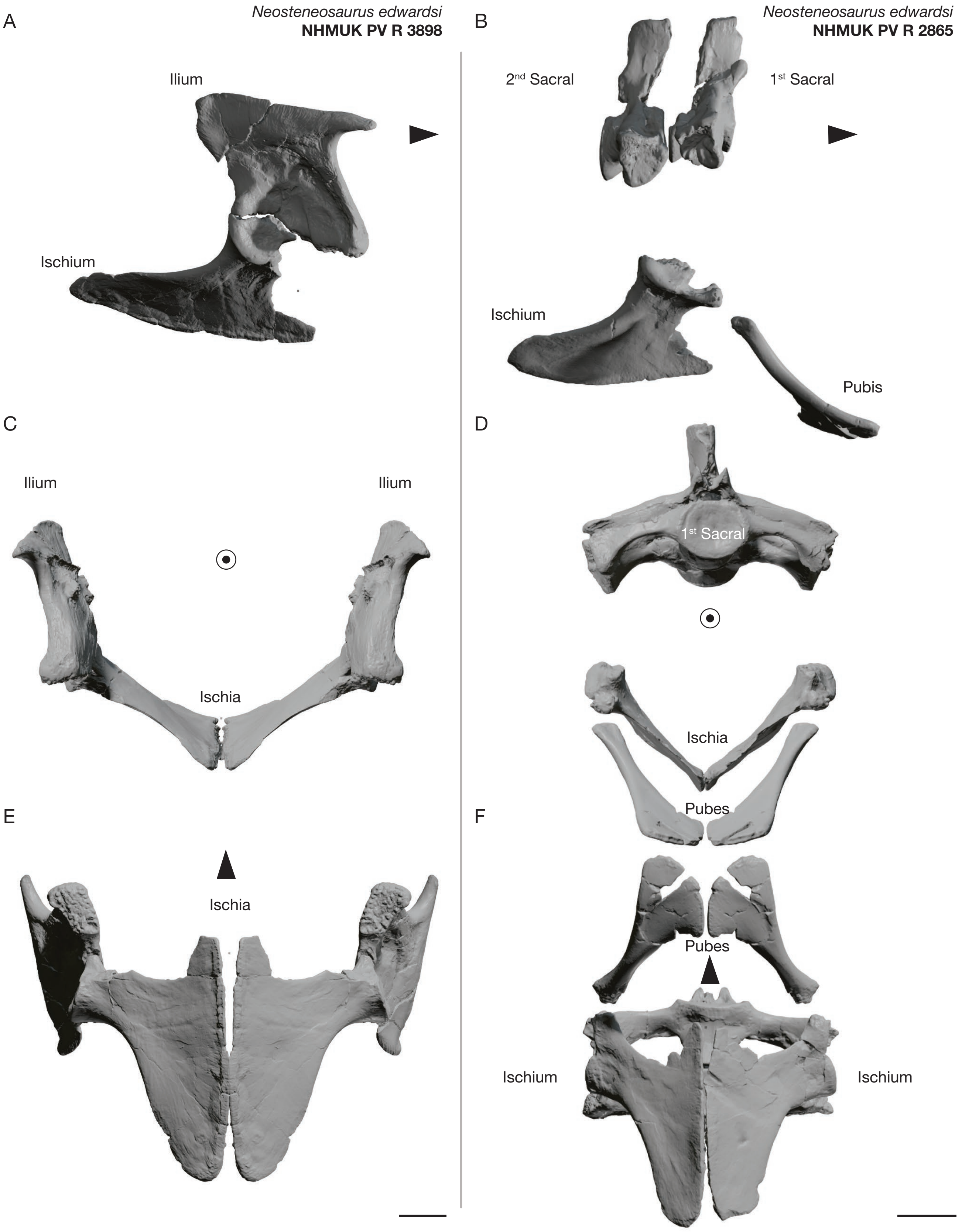


Fig. 58. — Reconstruction of the pelvic girdle of *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 3898 (**A**, **C**, **E**) and NHMUK PV R 2865 (**B**, **D**, **F**): **A**, **B**, right lateral views; **C**, **D**, anterior views; **E**, **F**, ventral views. Target indicates anterior. Arrow points anteriorly. The right ilium and ischium of NHMUK PV R 3898 are mirrored. The right pubis and left ischium of NHMUK PV R 2865 is mirrored. Scale bars: 5 cm.

crocodilus, *Hyposaurus natator*, etc.). Proximally, the ischium of *Lemmysuchus obtusidens* bears two peduncles separated by a notch: the acetabular perforation (Fig. 59). This hollow is actually tilted towards the sagittal plane and is thus entirely borne by the medial surface of the ischium, similar to several other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Torvoneustes carpenteri*, *Neosteneosaurus edwardsi*, *Proexochokefalos* cf. *bouchardi*, *Teleosaurus* sp., etc.). In extant crocodylians, this gap is covered by a membrane which protects the *ligamentum capitis* of the femur from compression, and grants it sufficient space during episodes of movements (Tsai & Holliday 2015).

The anterior peduncle is borne on an anteriorly protruding process called the peduncle bridge. Overall, the anterior peduncle of *Lemmysuchus obtusidens* does not significantly protrude from the anterior process of the ischium (Fig. 60), compared to what is observed in dyrosaurids or extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus*, *Hyposaurus natator*, etc.). Also, similar to other thalattosuchians, the anterior peduncle of *Lemmysuchus obtusidens* appears markedly reduced in size (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Torvoneustes carpenteri*, *Cricosaurus suevicus*, *Dakosaurus maximus*, *Aeolodon priscus*, *Charitomenosuchus leedsi*, *Macrospondylus bollensis*, *Neosteneosaurus edwardsi*, etc.). Yet, the anterior peduncle of *Lemmysuchus obtusidens* is more developed than metriorhynchoids, namely in being mediolaterally thicker as in other teleosauroids. The facet of the anterior peduncle is rugged, indicating the presence of a cartilage cap *in vivo*. In anterior view, the articular surface of the anterior peduncle is wedge-shaped with its concavity dorsally facing and its greatest axis oriented lateromedially. The articular facet of the anterior peduncle is however asymmetrical: its medial corner is sharp whereas its lateral one is more rounded. At about its mid-length lateromedially, the medial half of the articular surface of the anterior peduncle is posteriorly deflected similar to *Charitomenosuchus leedsi*. The lateral half of the articular surface of the anterior peduncle presumably corresponds to the anchoring site of the peduncle of the pubis (Fig. 60). The peduncle bridge of *Lemmysuchus obtusidens* (Fig. 59) stems from the shaft of the ischium and bears the anterior peduncle on its extremity. Its ventral surface is relatively straight whereas its dorsal surface is strongly concave and borders the acetabular perforation ventrally. In dorsal view, the peduncle bridge appears to be slightly curved towards the medial side of the bone. Unlike in *Charitomenosuchus leedsi*, the lateral and medial margins of the dorsal surface of the peduncle bridge of *Lemmysuchus obtusidens* (Fig. 59) are highly asymmetrical, with the lateral margin being almost on the same level as the articular surface of the posterior peduncle. As a result, the acetabular perforation of *Lemmysuchus obtusidens* (Fig. 59) appears almost non-existent in lateral view as in *Neosteneosaurus edwardsi contra Pelagosaurus typus*, *Macrospondylus bollensis* and *Charitomenosuchus leedsi*; this makes the ischium of *Lemmysuchus obtusidens* superficially appear more similar to that of metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* LEICT G .418.1956.13.5, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Torvoneustes carpenteri*, etc.) while still being more developed than the latter (among other traits). Indeed, the acetabular perforation of *Lemmysuchus obtusidens* is medially deflected like a burrow tilted towards the medial side of the bone which can be followed up until the junction between the peduncle bridge and the base of the posterior peduncle. Still, the peduncle bridge of *Lemmysuchus obtusidens* possesses a larger concave dorsal surface than in metriorhynchoids, so that the peduncle bridge creates more room for the acetabular perforation compared to that of metriorhynchoids (which almost solely relies on the burrow on the medial surface of the ischium).

The posterior peduncle is both wide lateromedially and long anteroposteriorly, and its articular surface takes the shape of an isosceles trapezoid with its long base positioned anteriorly. Comparatively, the articular surface of the anterior peduncle is downsized with its dorsoventral height reaching about 39 % of the anteroposterior length of the posterior peduncle. Indeed, the articular surface of the anterior peduncle is not dorsally facing like the posterior peduncle, but is oriented anteriorly (with dorsal and ventral components) as in many crocodyliformes, such as Dyrosauridae and Crocodylia (e.g. *Mecistops cataphractus*, *Caiman crocodilus*, *Hyposaurus natator*).

The anterior process of the ischium forms anteriorly an acute peak which is slightly pointing dorsally, and is shaped by the concave anterior margin of the ischium underneath the anterior peduncle, and the relatively straight distal blade. Both the medial and lateral surfaces of the distal blade present a rugged texture near the distal border, hinting at the existence of a cartilage cap *in vivo*. Only the medial surface of the distal blade is deeply scarred though, as it indicates the area where both ischia were joined. The ischial suture of *Lemmysuchus obtusidens* extends over the entire length of the distal blade but is the thickest around the anterior third quarter. This area also presents the deepest indentations whereas the surrounding portions are less textured. The first quarter anteriorly starts at the base of the anterior process and is entirely smooth, similar to other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Thalattosuchus superciliosus*, *Torvoneustes carpenteri*, *Neosteneosaurus edwardsi*, etc.). The ischial suture and the lateral surface of the distal blade form an acute angle of approximately 35°, unlike in '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 and *Neosteneosaurus edwardsi*.

The posterior margin of the ischium is undulated: starting from the posterior peduncle the surface is concave; at about the mid-length of the whole posterior margin, the concavity switches to convex, thus creating the rounded posterior distal extremity of the bone (which meets with the distal blade). The area extending posteriorly to the shaft is called the posterior process of the ischium. The shaft represent the thinnest portion of the ischium anteroposteriorly since it is formed by two concave margins anteriorly and posteriorly. Similar to *Macrospondylus bollensis* and *Neosteneosaurus edwardsi*, the shaft of the ischium of *Lemmysuchus obtusidens* appears relatively squared as its dorsoventral height and anteroposterior thickness reach about the same length.

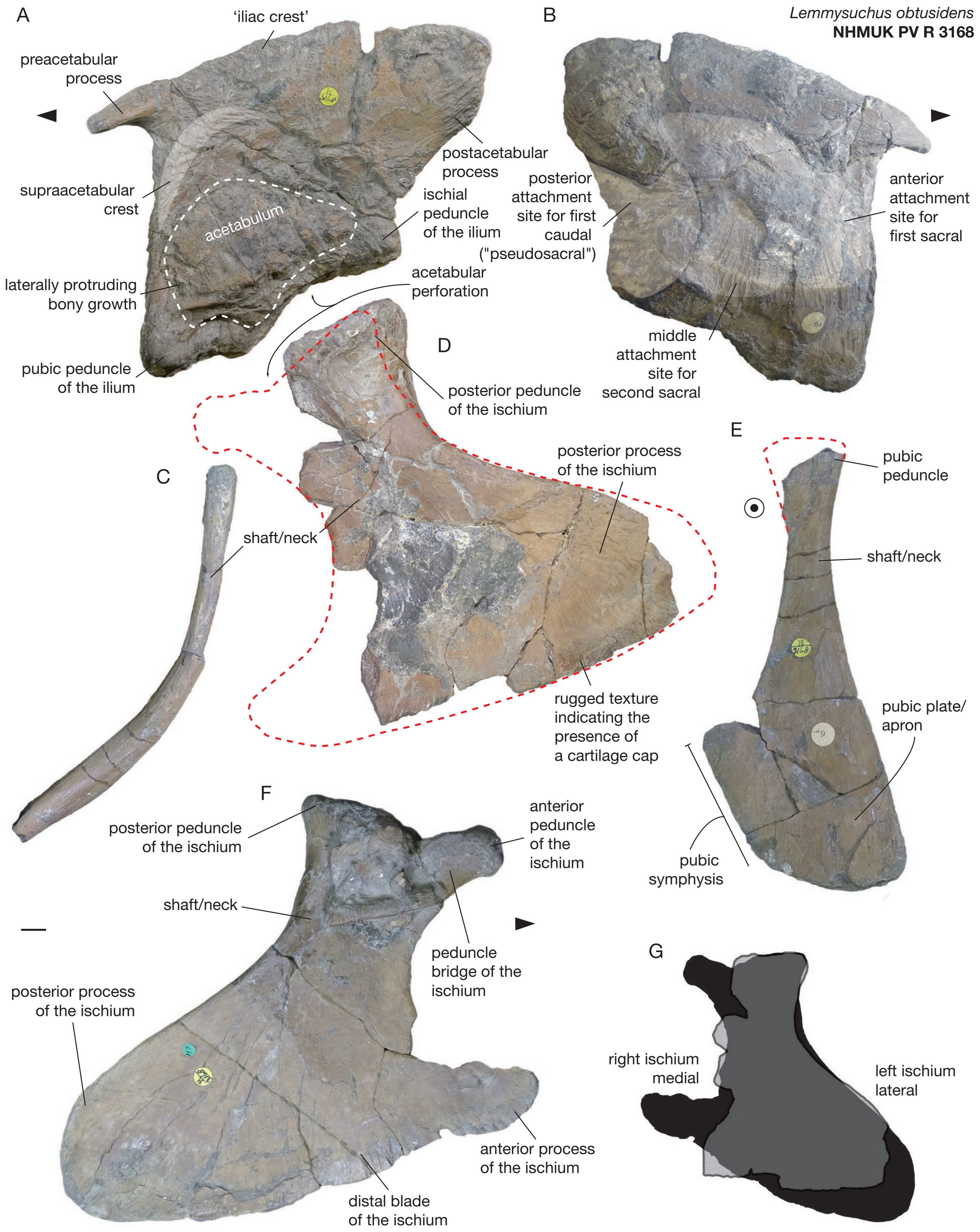


FIG. 59. — Pelvic girdle elements of *Lemmysuchus obtusidens* (Andrews, 1909), NHMUK PV R 3168 (holotype): **A**, left ilium in lateral view; **B**, left ilium in medial view; **C**, left pubis in lateral view; **D**, left ischium in lateral view; **E**, left pubis in anterodorsal view; **F**, right ischium in lateral view; **G**, surimposition of both ischia (right and left) of *Lemmysuchus obtusidens,* NHMUK PV R 3168. Target indicates anterior. Arrow points anteriorly. Scale bar: 1 cm.

When superimposed, the outline of the right and left ischia of *Lemmysuchus obtusidens* do not coincide (Fig. 59G). Indeed, there are dissimilarities in the size of the posterior peduncle, thickness of the shaft, extension of the posterior process, and inclination between the ventral margin of the distal blade and the dorsal surface of the posterior peduncle. These differences reveal an important level of intraspecific variation for *Lemmysuchus obtusidens*.

Pubis

The pubis of *Lemmysuchus obtusidens* (Fig. 59) shows an overall triangular outline, with a truncated distal extremity. In this way, the pubis of *Lemmysuchus obtusidens* resembles that of other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Cricosaurus araucanensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, etc.) and dyrosaurids (e.g. *Hyposaurus natator*, *Anthracosuchus balrogus* Hastings, Bloch & Jaramillo, 2014, *Cerrejonisuchus improcerus*, etc.), but strongly differs from that of extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus*, etc.). Indeed, this difference is due to the existence of a long pubic symphysis for *Lemmysuchus obtusidens* (and other members of Thalattosuchia and Dyrosauridae), whereas it is greatly reduced in extant crocodylians.

In *Lemmysuchus obtusidens*, the pubic symphysis is a straight margin which forms an angle of approximately 27° with the axis of the shaft, similar to *Charitomenosuchus leedsi* and *Mycterosuchus nasutus*. The angular relation in *Neosteneosaurus edwardsi* is slightly greater but overall falls within the same range. *In vivo*, the pubic symphysis of both pubes were medially connected presumably using soft tissues (Fig. 60). The pubic symphysis is proximally connected with the medial margin of the pubis, and distally with the pubic blade. The junction between the concave medial margin of the pubis and the pubic symphysis forms a right angle as in other thalattosuchians displaying a long pubic symphysis (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Machimosaurus*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, *Mycterosuchus nasutus*). In comparison, the intersection between the pubic symphysis and the pubic blade is achieved through an obtuse angle of approximately 140-150°, which is closer to *Charitomenosuchus leedsi* and *Mycterosuchus nasutus* than *Neosteneosaurus edwardsi*.

The pubic blade, which corresponds to the distal margin of the pubis, is relatively convex with its turning point slightly offset to the lateral side. The transition to the lateral margin of the pubis is smooth and rounded, but the angle between the distal and lateral margin approximates 90°. Like several other thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Dakosaurus maximus*, *Platysuchus multiscrobiculatus*, *Charitomenosuchus leedsi*, *Mycterosuchus nasutus*, etc.), the pubic plate of *Lemmysuchus obtusidens* is large, especially compared to the relatively short shaft. The extend of the pubic symphysis and distal blade contribute for the most part to the breadth of the pubis. The lateral margin of the pubis, which connects the pubic peduncle and the ventral margin of the distal blade, is lightly undulating: even though the whole lateral margin appears concave, it is actually subtly convex, with the inflexion point observable at about the mid-length of the lateral margin of the pubic plate, similar to *Machimosaurus*. The truly concave portion remains the lateral margin of the shaft. Proximally, the shaft flares out to form the peduncle of the pubis, whose articular surface presumably takes the shape of an ellipse in section (but is unfortunately not preserved; Fig. 59).

In *Lemmysuchus obtusidens* (Fig. 59), the anteroposterior thickness of the pubic apron increases laterally so that the distal blade is thicker than the pubic symphysis similar to '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Neosteneosaurus edwardsi* and *Mycterosuchus nasutus*. In comparison, the taxa *Suchodus durobrivensis* and *Thalattosuchus superciliosus* display a thinner pubis.

The pubis of *Lemmysuchus obtusidens* (Fig. 59) is deeply arched anteroposteriorly possibly as a consequence of diagenetic deformation (whereas its ilium is acutely flattened lateromedially). *In vivo*, the pubis of *Lemmysuchus obtusidens* was presumably more gently arched, in a fashion similar to Crocodylia (e.g. see *Palaeosuchus palpebrosus*).

MACHIMOSAURUS SPP. VON MEYER, 1837

For measurements, see Tables 7-9.

The number of species constituting the genus *Machimosaurus* Von Meyer 1837 is still debated (e.g. compare Young *et al.* (2014b); Fanti *et al.* (2015); Martin *et al.* (2015)). In parallel, the pelvic girdle elements associated with either species of *Machimosaurus* do not match with one another (i.e. an isolated pubis in one case, and a partial ilium and ischium in the other), preventing further comparisons. For these reasons, we chose to describe the pelvic girdle elements of *Machimosaurus* at the generic level.

The bone referred to the pubis of *Machimosaurus* in Hua *et al.* (1993); Hua (1999); Young *et al.* (2014b) is not included in our description. Indeed, the bone displays all the characteristics of a derived teleosauroid humerus: shortening of humeral shaft; posterior deflection of the articular proximal head; distal torsion of the condyles in relation to the coronal plane; continuous surface between the deltopectoral crest and the proximal articular head.

Ilium

The ilium of *Machimosaurus* (Fig. 61) corresponds to the posterior half of a left ilium. The posterior extension of the postacetabular process only reaches about half of the total dorsoventral height of the bone resulting in a relatively short posteacetabular process, which is similar to chat is observed in *Sericodon jugleri*. *Neosteneosaurus edwardsi* (i.e. NHMUK PV R 3701, NHMUK PV R 2076, NHMUK PV R 3898) also displays a relatively short postacetabular process compared to *Lemmysuchus obtusidens*, but it is not as short as *Machimosaurus*. Similar to *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*, the postacetabular process of *Machimosaurus* takes the overall shape of a Lancet arch whose apex points dorsoposteriorly. Indeed, the dorsal and ventral margins of the postacetabular process are both convex, with the dorsal

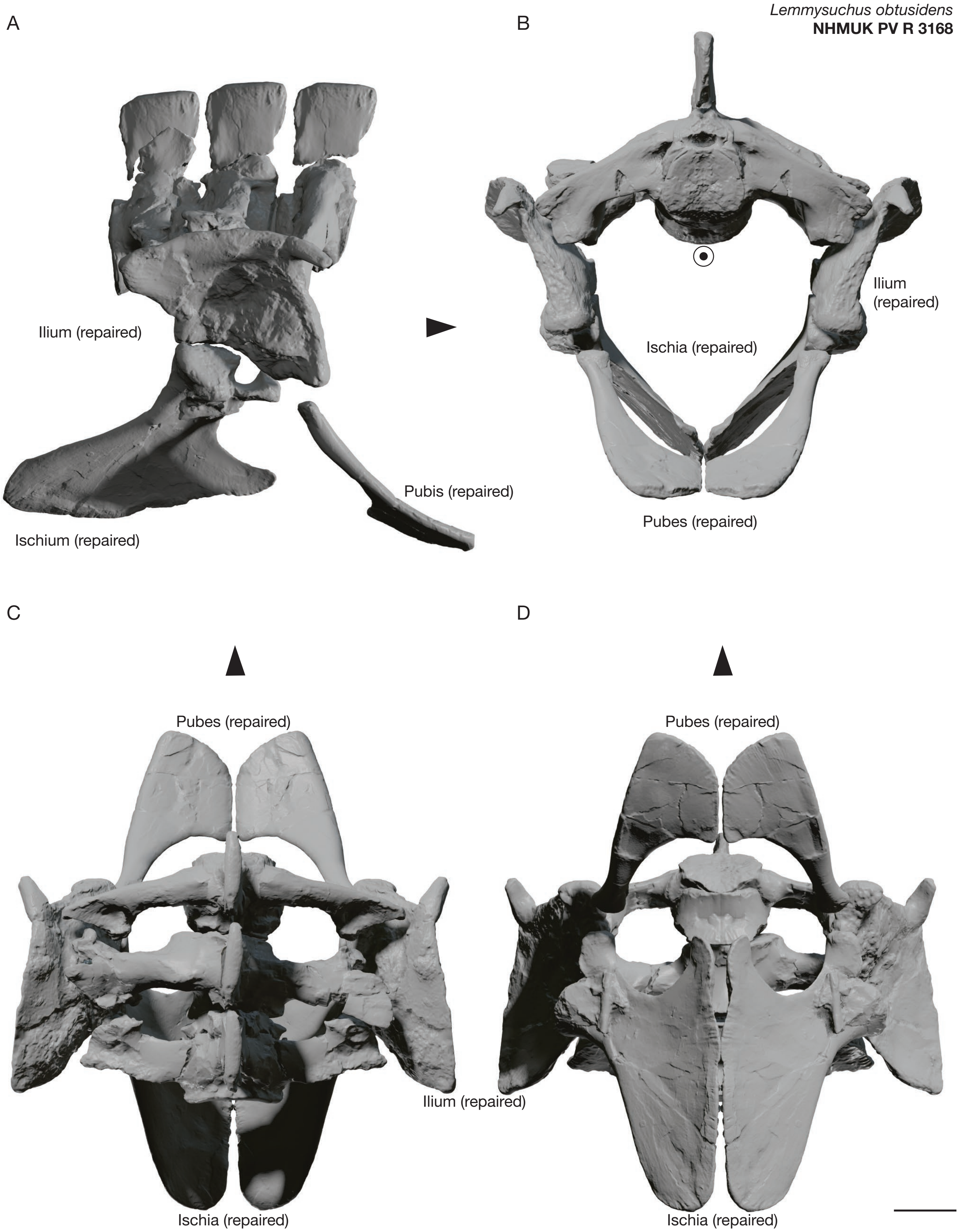


FIG. 60. — Pelvic reconstruction of *Lemmysuchus obtusidens* (Andrews, 1909), NHMUK PV R 3168 (holotype): **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. Arrow points anteriorly. Target indicates anterior. The left ischium and right ilium and pubis are mirrored. Scale bar: 5 cm.

one – the iliac crest – displaying a stronger curvature (which differs from *Sericodon jugleri*). The entirety of the lateral surface bordering the margins of the postacetabular process up to the base of the preacetabular process is strongly rugged: it shows a series of densely packed shallow ridges and sulci indicating the presence of a cartilage cap *in vivo*. Anteriorly, the transition from the postacetabular to the preacetabular process is marked by a dorsoventrally shallow but anteroposteriorly elongated notch as in *Charitomenosuchus leedsi*, but contracts with *Lemmysuchus obtusidens* and also *Neosteneosaurus edwardsi* (i.e. NHMUK PV R 3701, NHMUK PV R 2076, NHMUK PV R 3898). Around its mid-length, the ventral margin of the postacetabular process inverts its concavity and becomes concave. This point corresponds to the transition between the postacetabular process and the posterior margin of the ilium, which culminates ventrally to form the posterior corner of the ischial peduncle. Unfortunately, it is not certain if a small crest or tubercle was present around the concavity inversion as in *Neosteneosaurus edwardsi* (preserved in NHMUK PV R 2076).

The ischial peduncle of *Machimosaurus* forms a shallow crescent as in *Lemmysuchus obtusidens*, *Neosteneosaurus edwardsi* (i.e. NHMUK PV R 3701, NHMUK PV R 2076, NHMUK PV R 3898), and also *Charitomenosuchus leedsi*. Indeed, its dorsal and ventral margins are both strongly arched without forming an angled peak. It is possible that the pubic peduncle towered the ischial peduncle as in *Neosteneosaurus edwardsi*, but it is not preserved. The bony acetabulum was presumably anteroposteriorly wide as seen in other teleosauroids (e.g. *Charitomenosuchus leedsi*; *Neosteneosaurus edwardsi* PETMG R178, NHMUK PV R 3701, NHMUK PV R 2076, and NHMUK PV R 3898; *Lemmysuchus obtusidens*; etc.).

The posterior half of the supraacetabular crest stops around the apex of the bony acetabulum as in other teleosauroids, and its surface appears to have be similarly pitted.

Ischium

The posterior half of the ischium of *Machimosaurus* (Fig. 61) is preserved, which shows the presence of a dorsoventrally thick posterior process. Indeed, the posterior margin of the ischium forms a strong sinusoidal shape: it is markedly concave dorsally and convex ventrally, with the inflection point located around the mid-length of the margin. The surface of the posterior margin surrounding the inflection point is almost parallel to the ventral margin of the ischium (corresponding to the ischial blade). This is mainly due to the strong concavity of the dorsal portion of the posterior margin which forms a marked bent. Similarly, the strong convexity of the ventral portion of the posterior margin almost forms an obtuse corner. As a result, the posterior process of the ischium appears relatively tubular whereas being dorsoventrally thick throughout its length as in *Sericodon jugleri*. *Lemmysuchus obtusidens* also possesses a dorsoventrally thick posterior process although not tubular, and the overall shape of its posterior margin is smoother without any marked bent like *Machimosaurus*. *Proexochokefalos* cf. *bouchardi* also shows a relatively tubular posterior process, but relatively more slender than *Machimosaurus*. The extremity of the posterior process of *Machimosaurus* appears to form a ventroposteriorly oriented peak, rather than a flat to slightly convex surface as in *Charitomenosuchus leedsi*, *Proexochokefalos* cf. *bouchardi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*.

Pubis

The pubis of *Machimosaurus* (Figs 62; 63) displays an overall slender shape due to a long shaft and narrow pubic apron similar to that of *Suchodus durobrivensis*. Other crocodyliforms like *Hyposaurus natator* or *Thalattosuchus superciliosus* NHMUK PV R 2054 display relatively slender pubis, but those are slightly less similar to that of *Machimosaurus* (Fig. 62). Hence, the pubis of *Machimosaurus* contrasts with those of rhacheosaurines (i.e. *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Cricosaurus bambergensis*) and geosaurines (i.e. *Geosaurus giganteus*) which possess reduced pubic symphysis and wide pubic apron.

In *Machimosaurus*, the medial margin forms a marked bent around the level of the pubic symphysis (like in *Teleosaurus* sp.) which creates an external obtuse angle of approximately 135°. As a result, the area surrounding the pubic symphysis strongly protrudes from the main body of the pubic apron. Such an abrupt transition is seen in few other thalattosuchians, namely *Cricosaurus albersdoerferi* and *Lemmysuchus obtusidens*. The pubic symphysis of *Machimosaurus* corresponds to about 35% of the total length of the bone (reconstructed based on both pubes; Fig. 62), which is slightly longer than in other teleosauroids (i.e. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*) except *Macrospondylus bollensis* for which the pubic symphysis of *Machimosaurus* is greatly larger. The length of the shaft of *Machimosaurus* is slightly shorter than that of the pubic symphysis as it reaches about 30% of the the total reconstructed length of the bone. Comparatively, in *Suchodus durobrivensis*, the pubic shaft and pubic symphysis display similar lengths, and those reach around 36% of the total length of the bone. In *Thalattosuchus superciliosus* NHMUK PV R 2054 and *Hyposaurus natator*, however, the pubic symphysis is shorter than the shaft, and reaches between 18 – 24% of the total length of the pubis. Another similarity between *Suchodus durobrivensis* and *Machimosaurus* (Fig. 62), which is also shared with *Lemmysuchus obtusidens*, is the acute angle formed between the pubic symphysis and the median of the shaft: about 22° for *Machimosaurus*, and 28° for *Suchodus durobrivensis* and *Charitomenosuchus leedsi*, and 30° for *Lemmysuchus obtusidens* and *Neosteneosaurus edwardsi*. Nevertheless, the other teleosauroids appear dissimilar to *Machimosaurus* due to a larger pubic plate laterally to the median of the shaft. Indeed, in *Machimosaurus*, the distal margin of the bone connecting the pubic symphysis with the lateral margin of the pubis is relatively short (less than the length of the pubic symphysis unlike in *Lemmysuchus obtusidens*). Also, the junction between the pubic symphysis and the distal blade of *Machimosaurus* forms a relatively small angle of approximately 127° which contributes to the shortness of the distal blade, as in *Neosteneosaurus edwardsi* compared with *Lemmysuchus obtusidens* or *Charitomenosuchus leedsi*. The exact shape of the

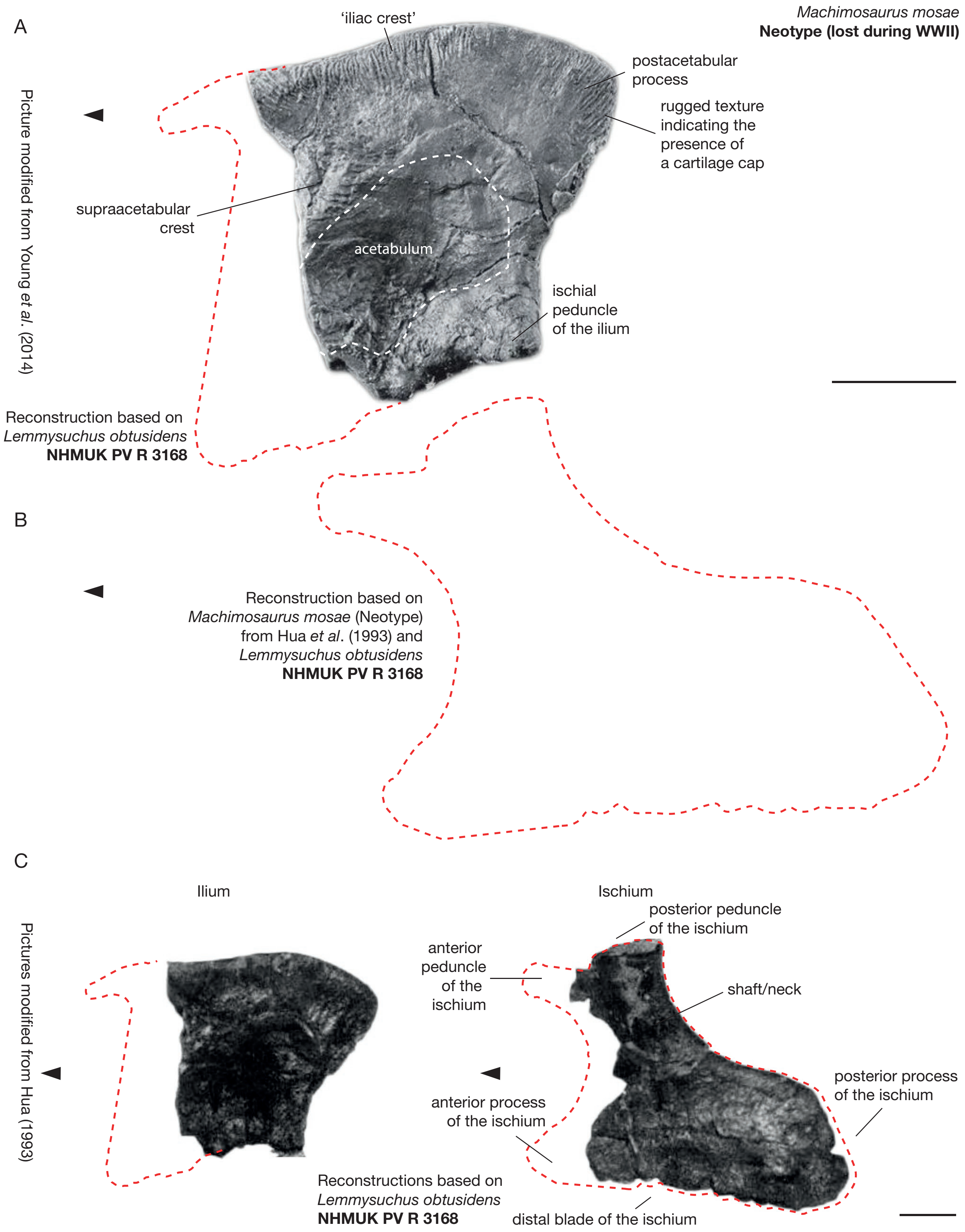


FIG. 61. — Left ilium and ischium of the lost neotype of *Machimosaurus mosae* Sauvage & Liénard, 1879: **A**, left ilium in lateral view; **B**, hypothetical reconstruction of left ischium in lateral view; **C**, pelvic girdle in lateral view as it appears in Hua *et al.* (1993). Arrow point anteriorly. Picture in **A** modified from Young *et al.* (2014). Pictures in **C** modified from Hua *et al.* (1993). Scale bars: 5 cm.

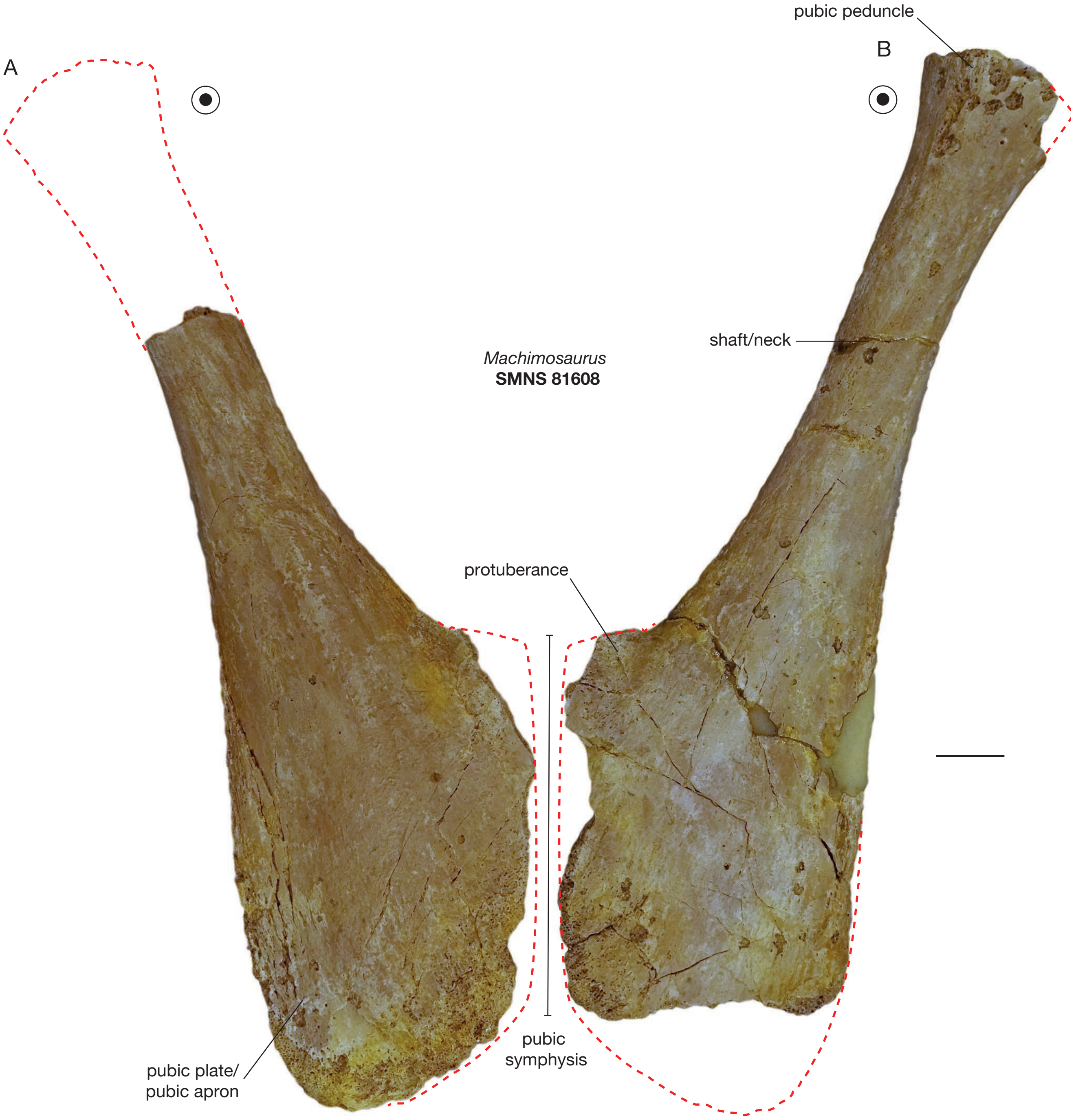


Fig. 62. — Right and left pubes of *Machimosaurus* sp., SMNS 81608: **A**, right pubis in anterior view; **B**, left pubis in anterior view. Target indicates anterior. Scale bar: 1 cm.

distal margin of *Machimosaurus* (Figs 62; 63) is uncertain, but was presumably slightly arched as in other thalattosuchians (i.e. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*).

In *Machimosaurus*, the junction between the distal and the lateral margins is achieved through a blunt right-angle corner which does not appear to protrude laterally, as in *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, and *Lemmysuchus obtusidens*, *contra*(*Mycterosuchus nasutus* or '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 to a lesser extent. The lateral margin of the pubis of *Machimosaurus* forms a tenuous sinusoid, with the portion bordering the pubic apron being convex and gradually switching to concave as it climbs back up towards the peduncle. The undulation of the lateral margin of the pubis is even less perceptible in *Suchodus durobrivensis*, but is more clear in *Lemmysuchus obtusidens*. Comparatively, the medial margin of the pubis of *Machimosaurus* appears almost straight with a slight undu-

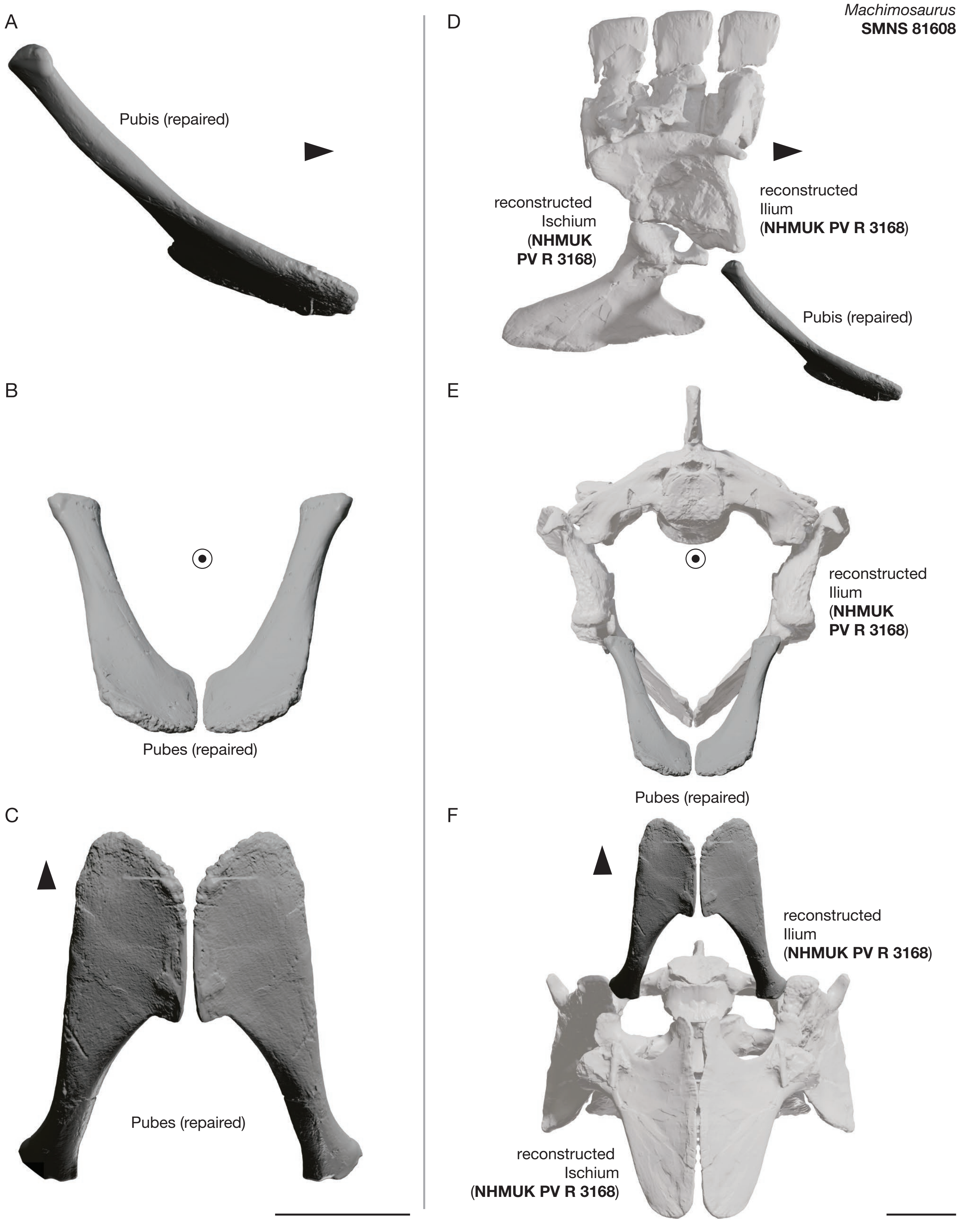


Fig. 63. — Reconstruction of the pelvic girdle of *Machimosaurus* sp. (SMNS 81608, **A**-**F**) and *Lemmysuchus obtusidens* (Andrews, 1909) (NHMUK PV R 3168, **D**-**F**): **A**, right lateral view; **B**, anterior view; **C**, ventral view; **D**, right lateral views; **E**, anterior views; **F**, ventral views. Target indicates anterior. Arrow points anteriorly. The right pubis of SMNS 81608 is mirrored, the left pubis is rapaired. 3D models of SMNS 81608 courtesy of Roland Sookias. Reconstructed bones only serve as a qualitative representation of the pelvic girdle of *Machimosaurus* sp. Scale bars: 5 cm.

lation around the junction between the shaft and the distal blade. This shape is not present in other thalattosuchians (i.e. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus albersdoerferi*, *Geosaurus giganteus*, *Lemmysuchus obtusidens*). The pubic peduncle of *Machimosaurus* flares out from the shaft but is only slightly larger mediolaterally than the thinnest portion of the shaft similar to *Dakosaurus maximus*, but unlike in *Suchodus durobrivensis*, *Thalattosuchus superciliosus* NHMUK PV R 2054, *Cricosaurus suevicus*, *Cricosaurus bambergensis*, *Geosaurus giganteus*.

THE PELVIC GIRDLE SKELETON OF DYROSAURIDS

Anthracosuchus balrogus Hastings, Bloch & Jaramillo, 2014

For measurements, see Tables 7-9.

Pubis

The pelvic girdle of *Anthracosuchus balrogus* (Fig. 64) is only known from two fragmentary pubes (*contra* Hastings *et al.* (2014)). Given the subtle difference in size between the two pubes, slight anatomical variations could presumably explain this effect. It is also possible that both bones belonged to two distinct individuals, since three different specimens have been described from the same strata (Hastings *et al.* 2014).

The pubis of *Anthracosuchus balrogus* (Fig. 64) displays a shape closer to that of *Cerrejonisuchus improcerus* than those of *Hyposaurus natator* and *Dyrosaurus maghribensis*. Indeed, the pubic plate of *Anthracosuchus balrogus* is slightly laterally deflected in the way of *Cerrejonisuchus improcerus* but to a lesser extent. This lateral flexure of the pubic apron is presumably caused by the length and orientation of the pubic symphysis and distal margin of the bone. In *Anthracosuchus balrogus*, the pubic symphysis forms an angle of approximately 136° with the medial margin of the pubis (leading to the shaft), and is relatively long (see Table 9) pushing the distal margin of the pubic plate further away distally. The latter is convex, but is also involved in the lateral deflection of the pubic apron: the overall obtuse angle it forms with the pubic symphysis expands the size of the pubic apron laterodistally, especially compared to *Hyposaurus natator* and *Dyrosaurus maghribensis* where the angle between the distal margin and the pubic symphysis is closer to 90°. In *Anthracosuchus balrogus*, the junction between the distal and lateral margins forms a blunt corner in the shape of a Lancet arch, in line with both margins (i.e. not significantly protruding). This shape contrasts with the squared and intensely protruding lateral lump of *Cerrejonisuchus improcerus*, and with the more discreet but still marked lateral protuberance of both *Hyposaurus natator* and *Dyrosaurus maghribensis*.

The lateral margin of the pubis of *Anthracosuchus balrogus* is slightly concave and appears almost straight, not totally unlike those of *Hyposaurus natator* and *Dyrosaurus maghribensis*. Conversely, in *Cerrejonisuchus improcerus*, the concavity of both lateral and medial margins is more accentuated. In parallel, the medial margin of the pubis of *Anthracosuchus balrogus* is slightly convex in the proximity of the junction with the pubic symphysis, but the concavity is inverted more proximally. This inversion of concavity coincides with a modification in the thickness of the pubic apron, with the central part of the bone being thicker. Hence, the posterior surface of the pubic apron appears to be slightly undulating. Along the distal margin of the pubic apron, starting from the symphysis and encompassing the lateral corner of the pubic plate, is a rugged area marking the presence of a cartilage *in vivo*.

Cerrejonisuchus improcerus Hastings, Bloch, Cadena & Jaramillo, 2010

For measurements, see Tables 7-9.

Pubis

The pubis of *Cerrejonisuchus improcerus* (Fig. 65) displays a unique shape among Dyrosauridae: its slender proximal extremity coupled with its oblong distal blade bear resemblance to a hockey stick. This shape is made possible through the size and shape of its pubic symphysis, its relation with the other margins of the bone, as well as the shape of the lateral protuberance. Like other dyrosaurids, the pubis of *Cerrejonisuchus improcerus* remains relatively narrow mediolaterally (e.g. *Hyposaurus natator*, *Dyrosaurus maghribensis*, and *Anthracosuchus balrogus*) whereas elongated proximodistally. Still, the pubis of *Cerrejonisuchus improcerus* contrasts with that of other dyrosaurids in possessing a large pubic apron (induced by a long pubic symphysis, like *Anthracosuchus balrogus*) coupled with a squared lateral protuberance at the extremity of its distal blade.

The pubic peduncle of *Cerrejonisuchus improcerus* is slightly wider than the pubic shaft mediolaterally, as in *Dyrosaurus maghribensis* but as opposed to *Hyposaurus natator*. Distally, the pubic peduncle subtly slims down to form the pubic shaft (or neck). The latter ensures the junction between the pubic peduncle and the distal blade, and is identifiable through to the mediolateral widening distally which marks the start of the pubic apron. As in other dyrosaurids (i.e. *Hyposaurus natator*, *Dyrosaurus maghribensis*), the lateral and medial margins of the shaft are weakly concave, so that they appear almost straight. These concave margins do not stop with the shaft, but rather carry on to form portions of the pubic apron's margins. The medial concave margin of the pubis is shorter than the lateral one, and ends where the pubic symphysis starts. The concave medial margin is also slightly deeper than the lateral concave margin of the pubis. The later, however, presents a large extension and almost forms the entirety of the lateral margin of the pubis similar to *Hyposaurus natator* and *Dyrosaurus maghribensis*, but *contra Anthracosuchus balrogus*. Distally, the lateral concave margin ends with a small lateral protuberance like those of *Hyposaurus natator* and *Dyrosaurus maghribensis*. The protuberance displays a weakly convex border laterally, whereas its dorsal and ventral margins appear relatively straight (notably due to their shortness). The lateral

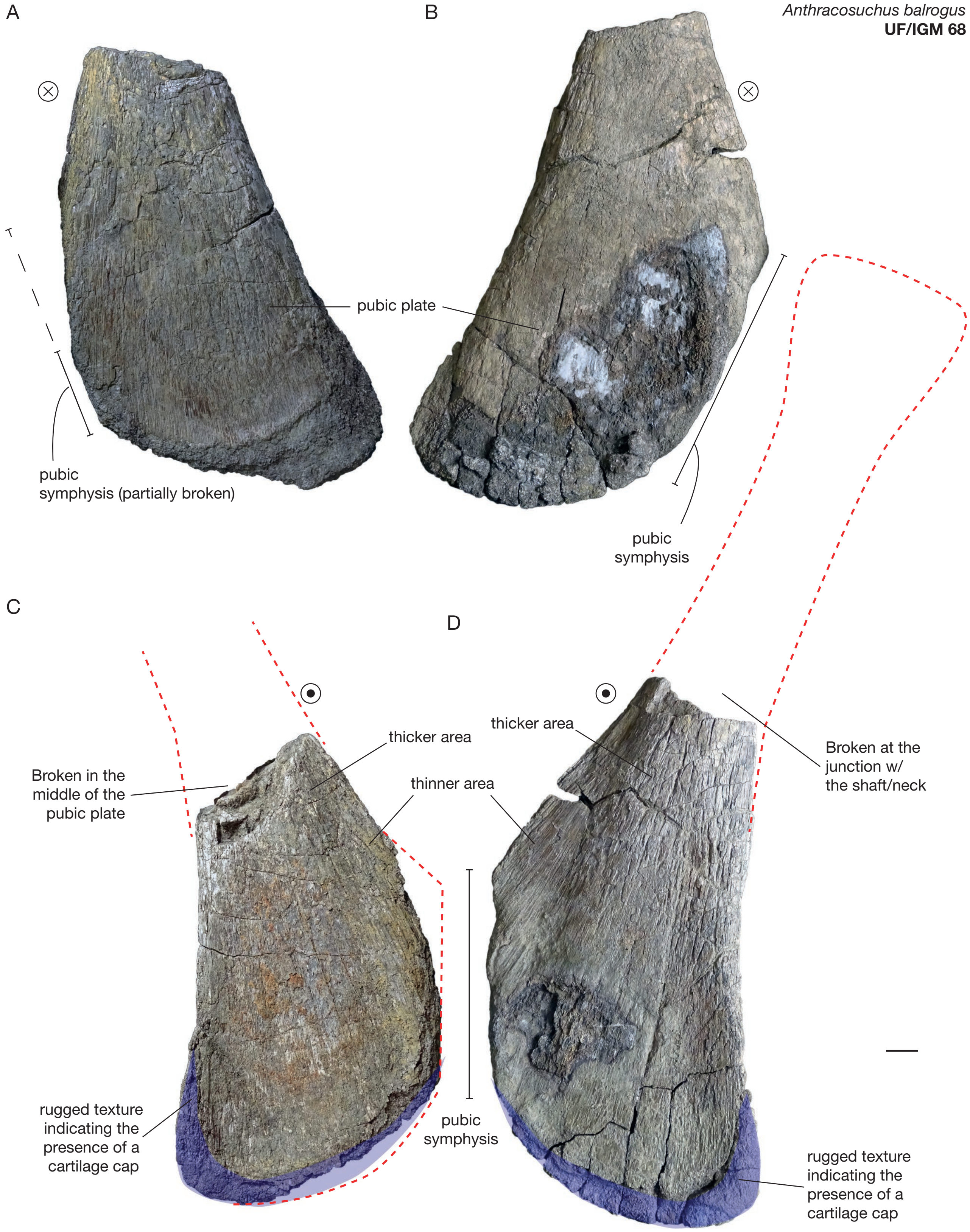


FIG. 64. — Right and left pelvic girdle elements of *Anthracosuchus balrogus* Hastings, Bloch & Jaramillo, 2014, UF/IGM 68: **A**, right pubis in posterior view; **B**, left pubis in posterior view; **C**, right pubis in anterior view; **D**, left pubis in anterior view. **Dotted lines** used to recreate the putative shape of the pubis; the actual length of the shaft is unknown. **Blue translucent area** highlights the distal rugged portion of the pubis. **Target** indicates anterior. **Cross** indicates posterior. Scale bar: 1 cm.

protuberance forms the distal corner of the pubic plate, and thus connect the strictly lateral margin of the pubis with the ventral border of the bone. The ventral margin of the pubic apron is quite straight and reaches about half of the length of the pubic symphysis, with which it forms an obtuse angle of approximately 125°. A similar value can be found in *Hyposaurus natator*, whereas *Dyrosaurus maghribensis* displays more of a right angle between its pubic symphysis and its ventral margin. The pubic symphysis of *Cerrejonisuchus improcerus* (Fig. 65; Table 9) is proportionally larger than in any other dyrosaurids (i.e. *Hyposaurus natator*, *Dyrosaurus maghribensis*, and *Anthracosuchus balrogus*), and presumably play a role in the size of the pubic apron. The pubic symphysis of *Cerrejonisuchus improcerus* appears almost parallel to the shaft (angle of approximately 20° between them), which was the case for *Dyrosaurus maghribensis contra Hyposaurus natator* which displayed a greater angle (about 30°). The dorsal corner of the pubic symphysis forms a right angle with the concave medial margin of the pubis, as opposed to the obtuse angle displayed by other dyrosaurids (i.e. *Hyposaurus natator*, *Dyrosaurus maghribensis*, and *Anthracosuchus balrogus*). Considering the potential existence of a respiration involving pubic movements, such an enlarged pubic apron presumably enabled to displace consequent visceral masses (Scavezzoni & Fischer 2021). In parallel, the overall size of the pubic apron, and subsequent pubic symphysis, presumably impacted the angle of pubic rotation compared to extant crocodylians (Claessens 2004).

Hyposaurus natator (Troxell, 1925)

For measurements, see Tables 7-9.

Ilium

Similar to that of *Congosaurus bequaerti* (MRAC 1806, Fig. 72), the ilium of *Hyposaurus natator* (YPM VP.000753, holotype [Fig. 66]; NJSM 23368 [Fig. 67]) stands out from those of thalattosuchians in possessing a well-developed preacetabular process and acetabular perforation, a mediolaterally deep acetabulum, laterally prominent supraacetabular crest, distinct and laterally prominent peduncles, and a large postacetabular process proportionally to its size.

The ilium of *Hyposaurus natator* displays a series of intraspecific morphological variations across its two specimens YPM VP.000753 (Fig. 66) and NJSM 23368 (Figs 67; 68). Starting with the overall outline of the bone, YPM VP.000753 displays a more pronounced preacetabular process in being anteroposteriorly longer than that of NJSM 23368. The preacetabular crest of YPM VP.000753 also stands out due to the almost right angle its ventral margin forms with the anterior edge of the ilium. The postacetabular process is also quite different between both specimens as it is dorsoventrally taller for NJSM 23368 compared to YPM VP.000753. This variation in size is accompanied by differing dorsal and ventral margins for the postacetabular process, which may presumably explain the difference. Indeed, the dorsal and ventral margins of NJSM 23368 are relatively more convex than those of YPM VP.000753, and their junction with the rest of the ilium is marked by shallow recesses only. In YPM VP.000753, the convex ventral and dorsal margins of the postacetabular process appear shorter due to extended concave recesses bordering them. Other great differing features between YPM VP.000753 and NJSM 23368 include a more prominent supraacetabular crest and a wider acetabular perforation for YPM VP.000753, whereas NJSM 23368 bears relatively larger peduncles with more embossed articular facets.

The anterior margin of the ilium underneath the preacetabular process is relatively straight with the anterior border of the pubic peduncle only dimly protruding, which contrasts with the more prominent one of *Congosaurus bequaerti*. The preacetabular process of *Hyposaurus natator* is well developed (it is larger in YPM VP.000753 than in NJSM 23368) and displays a clear anterodorsal orientation, which differs from the more anteriorly aligned process of *Congosaurus bequaerti* and *Acherontisuchus guajiraensis*. There is a difference in size of the preacetabular process between YPM VP.000753 and NJSM 23368 that can be partly explained through weathering. The dissimilarity could also possibly reflect intraspecific variations like sexual dimorphism. In extant crocodylians, the preacetabular process is the attachment site for the *ilio-costatis* and *ilio-tibialis 1* muscles (Romer 1923). In both *Hyposaurus natator* specimens, the preacetabular process resembles a beak or a hook (Figs 66; 67) with the dorsal rim of the process being globally convex whereas its ventral margin is concave. The shape of the dorsal margin of the preacetabular process is dominated by the bend located at about ⅓ of its extension anteriorly; one could argue that the portion posterior to the peak of the bend is actually slightly concave (as impacted by the dorsal recess, see below) whereas the anterior portion is more convex. There is a parallelepiped area laterally emanating from the preacetabular process which culminates ventrally in forming the supraacetabular crest. Whereas this area is smooth and convex for *Hyposaurus natator* YPM VP.000753, it is less hollow and slightly pitted in *Congosaurus bequaerti*. In *Hyposaurus natator* NJSM 23368 this area is also slightly pitted rather than smooth. Yet, this difference in depth between *Congosaurus bequaerti* and *Hyposaurus natator* betrays the greater mediolateral thickness of the preacetabular process of *Congosaurus bequaerti*. There is also a difference in the size of the supraacetabular crest between both *Hyposaurus natator*: YPM VP.000753 displays a more pronounced crest than NJSM 23368.

In *Hyposaurus natator*, the junction between the preacetabular process and the iliac crest is achieved through a marked depression, much clearer than in *Congosaurus bequaerti*, *Acherontisuchus guajiraensis* and *Dyrosaurus maghribensis*, which gives a cosine wave appearance to the dorsal margin of the ilium.

There is a subtle difference between NJSM 23368 and YPM VP.000753: the first one actually displays a shallower hollow which could potentially be linked to the smaller size of the preacetabular process. Unlike *Congosaurus bequaerti*, the iliac crest of *Hyposaurus natator* is relatively thin lateromedially and is also globally smoother: the medial and lateral surfaces bordering the crest bear a subtle repousse aspect,′ as if it were gently hammered from the inside. The postacetabular process as a whole is longer (anteroposteriorly) than

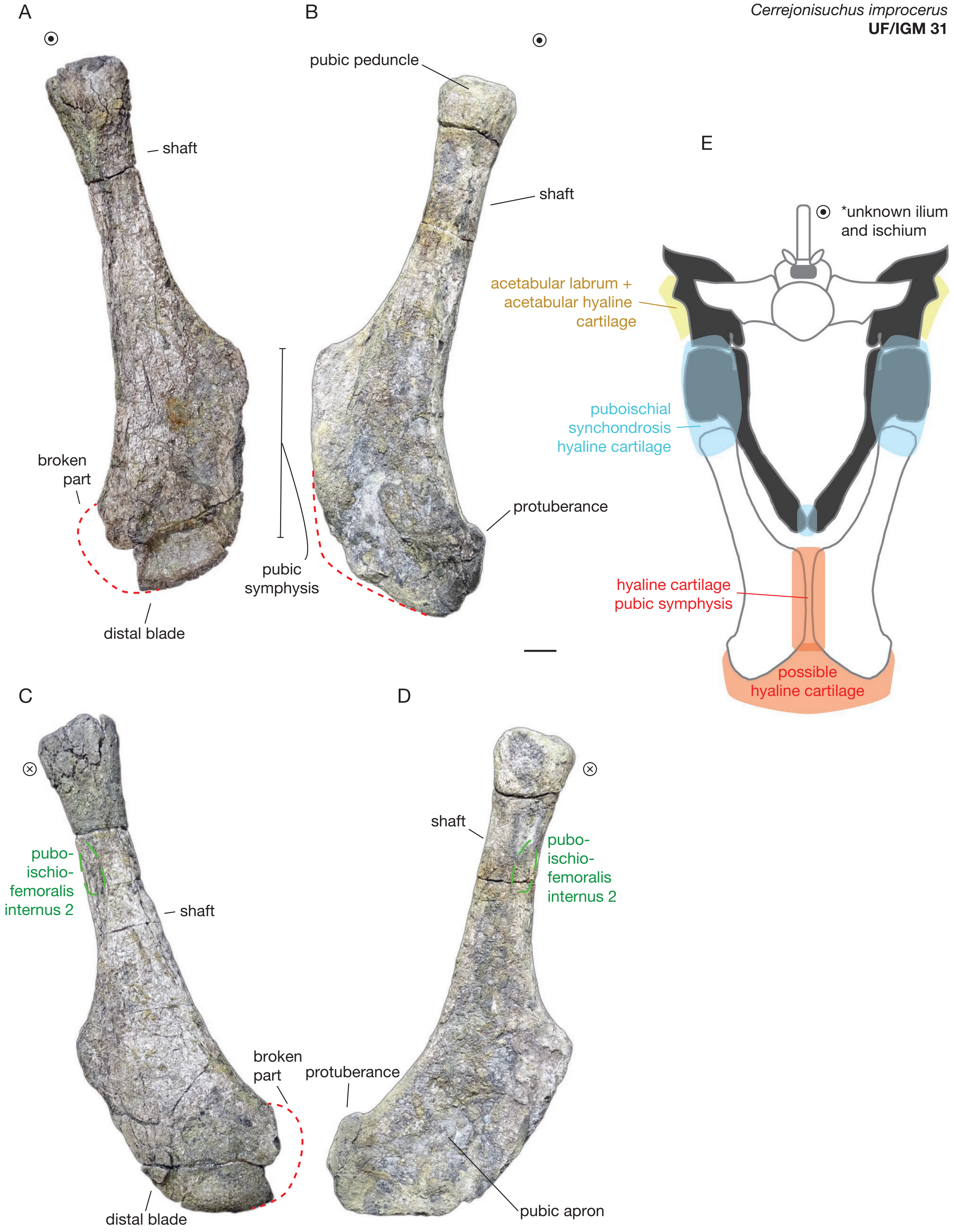


Fig. 65. — Right and left pubes of *Cerrejonisuchus improcerus* Hastings, Bloch, Cadena & Jaramillo, 2010, UF/IGM 31: **A**, right pubis in anterior view; **B**, left pubis in anterior view; **C**, right pubis in posterior view; **D**, left pubis in posterior view; **E**, reconstruction of the pelvic girdle of *Cerrejonisuchus improcerus* in anterior view. **Translucent areas** represent cartilaginous structures *in vivo*; their reconstruction is based on the works of Tsai & Holliday (2015) and Tsai *et al.* (2019). **Target** indicates anterior. **Cross** indicates posterior. Modified from Scavezzoni & Fischer (2021). Scale bar: 1 cm.

TABLE 10. — List of the angle between the ventral margins of the pubic and ischial peduncles of the ilium in degree. Abbreviations: **PP**, pubic peduncle; **IP**, ischial peduncle.

Species	Inventory number	Lateral view angle between PP and IP	Medial view angle between PP and IP
Caiman crocodilus	NHMW 30900	124.34	133.40
Mecistops cataphractus	RBINS 18374	144.08	145.8
Congosaurus bequaerti	MRAC 1806	122.24	109.62
Hyposaurus natator	YPM VP.000985	148.92	114.33
	YPM VP.000753	169.64	141.10
	NJSM 23368	165.56	108.21
Dyrosaurus maghribensis	OCP DEK-GE 252	158.71	–
	OCP DEK-GE 255	–	137.18
Acherontisuchus guajiraensis	UF/IGM 38	123.92	126.11

it is high (dorsoventrally), and takes the shape of an acute Lancet arch topped with a pointed peak at its (posterior-most) extremity. Its narrow appearance, which is a feature not present in *Congosaurus bequaerti*, is namely provoked by the concave recess at the junction between the ischial peduncle and the postacetabular process. The global orientation of the postacetabular process, based on its median, appears strictly anteroposterior, unlike that of *Congosaurus bequaerti* and *Acherontisuchus guajiraensis* which possessed a non negligible dorsal component. The postacetabular process of *Hyposaurus natator* NJSM 23368 appears almost symmetrical dorsally and ventrally like *Dyrosaurus maghribensis*, but for *Hyposaurus natator* YPM VP.000753 the dorsal margin seems more inflated. This difference is probably caused by the relative extension of the ventral recess between the ischial peduncle and the postacetabular process, which is once more limited in the case of *Hyposaurus natator* NJSM 23368 (i.e. like the dorsal hollow posteriorly to the preacetabular process). In *Hyposaurus natator* and *Acherontisuchus guajiraensis*, almost the entire lateral surface of the postacetabular process is concave, whereas for *Congosaurus bequaerti* and *Dyrosaurus maghribensis* this area is more restricted. Conversely, in *Hyposaurus natator* the medial surface of the postacetabular process is nearly entirely convex, whereas in *Congosaurus bequaerti* the medial surface is not evenly inflated and is rather irregular.

The peduncles appears slightly different between the *Hyposaurus natator* specimens, with *Hyposaurus natator* NJSM 23368 displaying more embossed articular facets than *Hyposaurus natator* YPM VP.000753, hence giving a stouter appearance to its peduncles. Both peduncles border the acetabulum ventrally and are separated by a wide gap corresponding to the acetabular perforation (Fig. 68). The perforation in *Hyposaurus natator* NJSM 23368 and YPM VP.000753 is large (see Table 11) both anteroposteriorly and dorsoventrally (almost as high as it is wide) which greatly contrasts with *Congosaurus bequaerti* and *Dyrosaurus maghribensis*. Yet, the size of the acetabular perforation is not even between *Hyposaurus natator* specimens; indeed, the acetabular perforation of YPM VP.000753 is proportionally larger than than that of NJSM 23368 but the difference is subtle. In both cases, the iliac acetabular perforation appears almost as vast as its counterpart on the ischium.

In both NJSM 23368 and YPM VP.000753, the ischial and pubic peduncles have their ventral margins quite parallel (see Table 10), which greatly contrasts with *Congosaurus bequaerti* and *Acherontisuchus guajiraensis*. This phenomenon could be caused by more ventrally extended pubic and ischial peduncles for *Hyposaurus natator* (Figs 66; 67) compared to *Congosaurus bequaerti*. This greater extension also presumably played a role in the more developed height of the acetabular perforation. This hypothesis could also explain what is observed in *Acherontisuchus guajiraensis*.

In ventral view, both peduncles are distinct, well developed, and equivalent in size. Their outline is wedge-shaped with their concavity oriented towards each other and thereby the acetabulum, similar to *Congosaurus bequaerti* (Fig. 74). The ischial peduncle resembles that of other dyrosaurids (i.e. *Congosaurus bequaerti*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*): in lateral view it displays a globally triangular outline with its ventral margin being slightly concave at its midpoint. The ischial peduncle protrudes laterally from the acetabulum and potentially acted as a barrier which prevented the femur from gliding posteriorly. Hence, the ischial peduncle presumably formed the foundation of the posterior wall of the articular capsule *in vivo*, which corresponds to the function of the antitrochanter of extant crocodylians (Tsai & Holliday 2015). On the lateral surface of the bone, the facet of the pubic peduncle draws two adjoined triangles similar to *Congosaurus bequaerti*, *Dyrosaurus maghribensis* and *Acherontisuchus guajiraensis*. Indeed, the posterior-most portion of the pubic peduncle of *Hyposaurus natator* takes the shape of an isosceles triangle (Figs 66; 67). Moving anteriorly, the pubic peduncle then displays another triangular shape whose apex is located on the anterior margin of the ilium and in doing so forms the anterior margin of the peduncle. The junction between those shapes is angular and could be seen as an inverted triangle as in other dyrosaurids (i.e. *Congosaurus bequaerti*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*). The maximal height of the lateral facet of the pubic peduncle of *Hyposaurus natator* does not exceeds that of the ischial peduncle dorsally as it is the case in many other crocodyliforms (e.g. *Mecistops cataphractus*, *Caiman crocodilus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Charitomenosuchus leedsi*, *Congosaurus bequaerti*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*). There is however a slight difference in height between the pubic peduncles of the two specimens of *Hyposaurus natator*, with YPM VP.000753 displaying a dorsally shorter anterior-most facet compared to NJSM 23368.

As for other dyrosaurids, the acetabulum of *Hyposaurus natator* is well-developed: it is mediolaterally deep (thanks notably to the orientation of the peduncles, Fig. 74), and covers a large area both anteroposteriorly (about half the total length) and dorsoventrally (more than half the height of the bone from the ventral margin of the peduncles). Its deepest point seems relatively centred as in *Dyrosaurus maghribensis*, whereas for

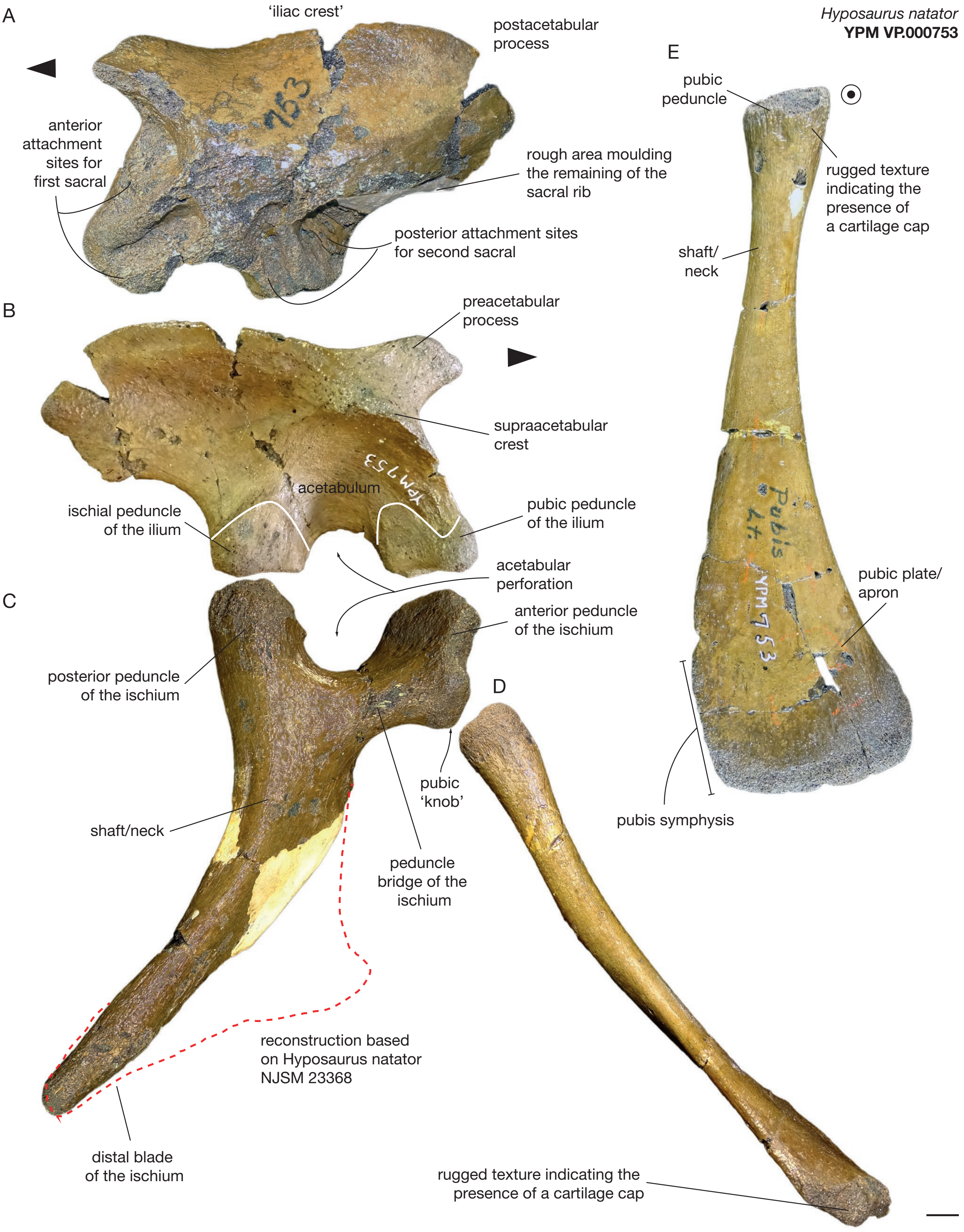


FIG. 66. — Right pelvic girdle elements of *Hyposaurus natator* (Troxell, 1925), YPM VP.000753, holotype: **A**, right ilium in medial view; **B**, right ilium in lateral view; **C**, right ischium in lateral view; **D**, right pubis in lateral view; **E**, left pubis in posteroventral view. **Target** indicates anterior. **Arrow** points anteriorly. Scale bar: 1 cm.

Table 11. — List of the height and width of both the acetabulum and acetabular perforation of dyrosaurids in mm. Abbreviations: **ACE**, acetabulum; **GAP**, acetabular perforation. **ACE** height is taken between top of supraacetabular crest and top of **GAP**. **ACE** width is taken at mid **ACE** height.

Species	Inventory number	ACE. h	ACE. w	GAP. w	GAP. h
Congosaurus bequaerti	MRAC 1806	72.28	63.41	24.01	5.60
Hyposaurus natator	YPM VP.000985	37.25	37.48	15.63	7.50
	YPM VP.000753	40.25	54.60	29.51	13.59
	NJSM 23368	42.38	34.66	18.20	10.10
Acherontisuchus guajiraensis	UF/IGM 38	82.36	61.32	29.3	20.38
Dyrosaurus maghribensis	OCP DEK-GE 252	89.25	108.79	36.92	9.91
Dyrosaurus maghribensis	OCP DEK-GE 255	–	–	42.09	11.49

Congosaurus bequaerti and *Acherontisuchus guajiraensis* it was located near the summit of the ischial peduncle. The supraacetabular crest borders the acetabulum dorsally, but appears to be limited to the anterior half of it. The supraacetabular crest of *Hyposaurus natator* appears to start more ventrally on the anterior margin of the ilium as in *Acherontisuchus guajiraensis* and *Dyrosaurus maghribensis*, making it greater than that of *Congosaurus bequaerti*. Thereby, the posterior side of the acetabulum, between the supraacetabular crest and the ischial peduncle, is open and directly leads to the concave central part of the postacetabular process by means of a slight bump as it was observed for *Congosaurus bequaerti* and *Dyrosaurus maghribensis*. Mediolaterally, the supraacetabular crest represents the thickest portion of the ilium, and was the attachment site for a soft tissue structure probably similar to the acetabular labrum of extant crocodylians.

Medially, the surface of the ilium forms a convex parabola with its vertex (or peak) being located directly dorsally to the sacral rib attachment sites for the sacral ribs, just above the acetabular perforation. *Hyposaurus natator* displays two main attachment sites, one for each sacral. The anterior attachment site is slightly larger than the posterior one but both are overall equal in size, unlike in *Dyrosaurus maghribensis* and *Congosaurus bequaerti*. Each attachment site is located directly medially to a peduncle: the first attachment site is placed medially to the pubic peduncle, whereas the second one is located medially to the ischial peduncle. Within each attachment site, a thin ridge emanating from the dorsal margin of the imprint partially subdivides it into two subareas, giving the impression of four distinct parabolic imprints. Yet, the ridge slowly fades away ventrally, so that each sub-areas are united along the ventral margin of the ilium. There is a difference in the sacral rib attachment sites from NJSM 23368 and YPM VP.000753: in the latter, the subdividing ridge is well developed and creates four distinct indentations with four vertexes (or peaks), whereas in NJSM 23368 the separation between the posterior-most imprints is more tenuous (i.e. less protruding), thus giving the impression of only three imprints. Furthermore, NJSM 23368 shows a large rugged area posteriorly to the second attachment site, whereas this area is much more restricted in YPM VP.000753. This area is shallower than the actual attachment sites, probably because it was merely guiding the posterior extension of the second sacral rib. Indeed, its shallowness presumably prevents it from being used as an anchor point for the sacral rib, so that it probably rather served as an additional stabilizing or locking feature. There is a similar area observed on the ilium of other dyrosaurids that presumably filled the same purpose.

Ischium

The ischium of *Hyposaurus natator* (YPM VP.000753, holotype [Fig. 66]; NJSM 23368 [Fig. 67]) differs from those of thalattosuchians (e.g. *Lemmysuchus obtusidens*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Torvoneustes carpenteri*, etc.) in possessing: an enlarged anterior peduncle that exceeds the posterior peduncle in size; a profound acetabular perforation; a twisted distal blade compared to the orientation of the peduncles; a more anteroposteriorly restricted distal blade; a limited anterior process, and a narrow posterior process.

Overall, the ischium of *Hyposaurus natator* is similar to that of other dyrosaurids (i.e. *Dyrosaurus maghribensis* and *Acherontisuchus guajiraensis*) and extant crocodylians (i.e. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) in displaying well-developed peduncles and a rotated distal blade which does not extend posteriorly more than half of the total anteroposterior proximal length (i.e. of both peduncles) of the ischium. In this way, the distal blade of those crocodyliforms resembles the blade of a hatchet or a small axe.

Proximally, the ischium of *Hyposaurus natator* bears two peduncles separated by a substantial gap. Each articular surface is identifiable thanks to its pitted texture. The anterior peduncle is large and exceeds the size of the posterior peduncle, similar to *Acherontisuchus guajiraensis* but unlike *Dyrosaurus maghribensis*, extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus*) and thalattosuchians (e.g. *Torvoneustes carpenteri*, *Aeolodon priscus*, *Neosteneosaurus edwardsi*, etc.) where the opposite relation is usually observed. In *Hyposaurus natator* and other dyrosaurids (i.e. *Dyrosaurus maghribensis* and *Acherontisuchus guajiraensis*), the articular surface of the anterior peduncle is rounded and extends both dorsally and anteriorly, wrapping all the available surface of this extremity of this process. The presence of a rounded and extensive articular surface for the anterior peduncle presumably conveys the existence of a relatively mobile articulation between the pubis and the ischium. Such an articulation could have been made possible through the presence of a thick but flexible cartilaginous coat *in vivo*, wrapping both the anterior peduncle of the ischium and the peduncle of the pubis, similar to extant crocodylians (Farmer & Carrier 2000a; Gans & Clark 1976; Munns *et al.* 2012; Tsai & Holliday 2015; Tsai *et al.* 2019).

The articular surface of the anterior peduncle is actually divided into two subsurfaces – anterior and dorsal – of differing function. The dorsal share of the articular surface is wedge-shaped, with the concavity facing dorsally. This dorsal

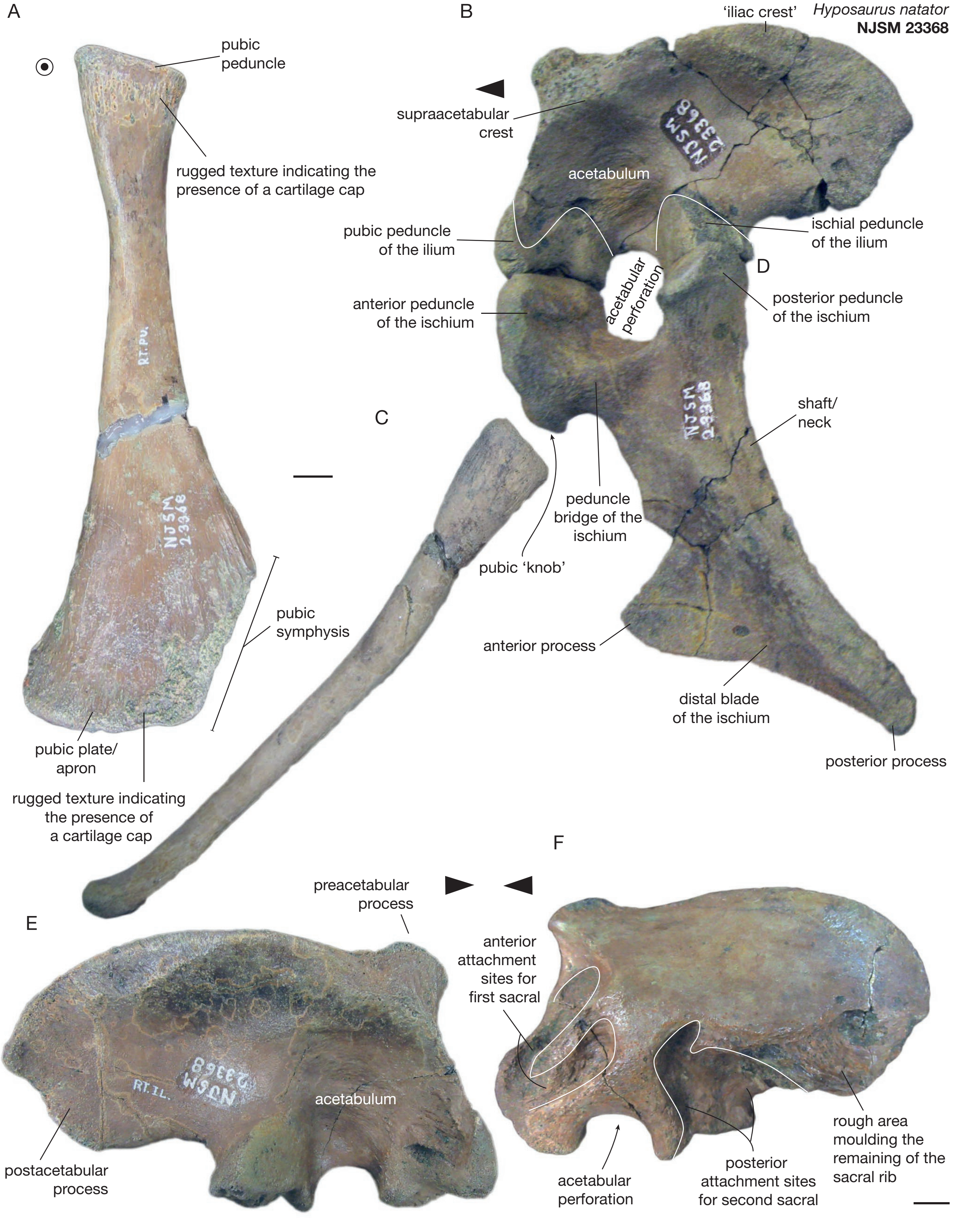


FIG. 67. — Right and left pelvic girdle elements of *Hyposaurus natator* (Troxell, 1925), NJSM 23368: **A**, right pubis in anterior view; **B**, left ilium in lateral view; **C**, left pubis in lateral view; **D**, left ischium in lateral view; **E**, right ilium in lateral view; **F**, right ilium in medial view. **Target** indicates anterior. **Arrow** points anteriorly. Pictures courtesy of Wayne Callahan. Scale bars: 1 cm.

portion forms the counterpart of the pubic peduncle of the ilium (Figs 66; 67). The bony facets of the anterior peduncle of the ischium and pubic peduncle of the ilium were not in direct contact throughout their whole length, unlike the interlocking ischial peduncle of the ilium and posterior peduncle of the ischium. On the reconstruction of both NJSM 23368 and YPM VP.00753 (Fig. 68) the anterior peduncle of the ischium and pubic peduncle of the ilium appear to have been in contact, but it is possible that some deformation prevents the peduncles of YPM VP.00753 to fully embrace one another. In addition, the entire area was presumably covered with cartilaginous structures ensuring the connection between both bones.

The anterior surface of the peduncle makes up the remaining, and almost the totality, of the articular surface of the anterior peduncle. This surface is larger in NJSM 23368 compared to YPM VP.000753, so that the anterior peduncle of NJSM 23368 appears dorsoventrally taller (Fig. 68). The anterior surface of the peduncle is also wedge-shaped but with the concavity oriented medially; the ventral portion appears like a distinct peduncle – the pubic 'knob' – (as in *Dyrosaurus maghribensis* (Jouve *et al.* 2006) and *Acherontisuchus guajiraensis*), which corresponds to the area where the peduncle of the pubis theoretically connected to the ischium. The peduncle bridge of the ischium constitutes the thinnest part of the anterior peduncle; it connects the articular extremity of the peduncle with the shaft of the ischium. The peduncle bridge is concave in all orientations, giving a flared appearance to the anterior peduncle of the ischium. The dorsal surface of the peduncle bridge constitutes the ventral border of the acetabular perforation. There is a difference in the length of the peduncle bridge between *Hyposaurus natator*, with that of NJSM 23368 being slightly shorter that that of YPM VP.000753 (Figs 66C; 67D). The same dissimilarity can be found among the *Dyrosaurus maghribensis* specimens.

The posterior peduncle is smaller than the anterior peduncle. In dorsal view, the overall outline of the posterior peduncle appears like a thicker version of the wedge-shaped anterior peduncle, with the concavity oriented anteriorly in this case. The articular surface of the posterior peduncle is slightly truncated leading to a strictly dorsal area and a more anterolateral one. The strictly dorsal area was connected to the ventral surface of the ischial peduncle of the ilium (both where interlocked), whereas the anterolateral one follows on from the shape of the ischial peduncle of the ilium. The neck of the posterior peduncle is concave laterally, medially, and anteriorly where it forms the posterior wall of the acetabular perforation. The ischial acetabular perforation is almost as large as its counterpart on the ilium (Fig. 68). The acetabular perforation of dyrosaurids (e.g. *Hyposaurus natator* [Figs 66; 67], *Dyrosaurus maghribensis* and *Acherontisuchus guajiraensis*) is ventrally delimited by the peduncle bridge of the ischium, whereas that of thalattosuchians is laterally deflected and forms a tilted incision on the peduncle bridge (e.g. *Lemmysuchus obtusidens* [Fig. 59], '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804, *Torvoneustes carpenteri*, etc.). Posteriorly, the neck of the posterior peduncle is rather convex, but the concavity is inverted for the remaining of the posterior margin of the ischium (i.e. including the shaft and distal blade). Indeed, the overall anterior and posterior margins of the ischium underneath the peduncles are concave. Ventrally to the peduncles, two consecutive areas can be observed: first is a bottleneck portion corresponding to the shaft or neck of the ischium; and second is a flared out area called the distal blade. The transition between the two parts is set at the start of the distal enlargement and torsion of the neck. Indeed, the distal blade of the ischium gradually shifts from the orientation of the shaft to display a more medial orientation distally, similar to extant crocodylians (i.e. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]). This shift in orientation is intended for both ischia to meet medially along their distal blade.

In *Hyposaurus natator* and other dyrosaurids, the anteroposterior flaring of the distal blade is relatively contained, unlike thalattosuchians for which the distal blade protrudes both anteriorly and posteriorly. Still, the shaft and posterior process of *Hyposaurus natator* are more slender than on the ischium of *Dyrosaurus maghribensis*, which displays a relatively thick shaft along with a short posterior process. As a consequence, the anterior and posterior extremity of the distal blade of *Dyrosaurus maghribensis* appear almost on the same level ventrally, whereas in *Hyposaurus natator* the posterior extremity is located further ventrally than the anterior one.

Similar to many other crocodyliforms (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* , '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Torvoneustes carpenteri*, etc.), the anterior process of the distal blade of *Hyposaurus natator* is situated more dorsally than the posterior process (Fig. 68). The curved margin (anterior) leading to the anterior process is thereby shorter, but in return shows a greater concavity than the (posterior) margin leading to the posterior process. The anterior process is pointing anteriorly, whereas the posterior process points strictly ventrally unlike thalattosuchians (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi* , '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Torvoneustes carpenteri*, etc.), extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*), and *Acherontisuchus guajiraensis*. Each peak (anterior and posterior) of the distal blade is only partially angular as each is composed of a relatively straight margin on one side and a concave one on the other. The ventral border of the distal blade uniting both processes is subtlety concave and its surface is strongly pitted throughout its length. *In vivo*, both distal blades were ventrally connected, not unlike thalattosuchians (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Thalattosuchus superciliosus*, *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, etc.).

Pubis

The pubis of *Hyposaurus natator* (YPM VP.000753, holotype [Fig. 66]; NJSM 23368 [Fig. 67]) differs from those of thalattosuchians (e.g. *Lemmysuchus obtusidens*, '*Metriorhynchus*'

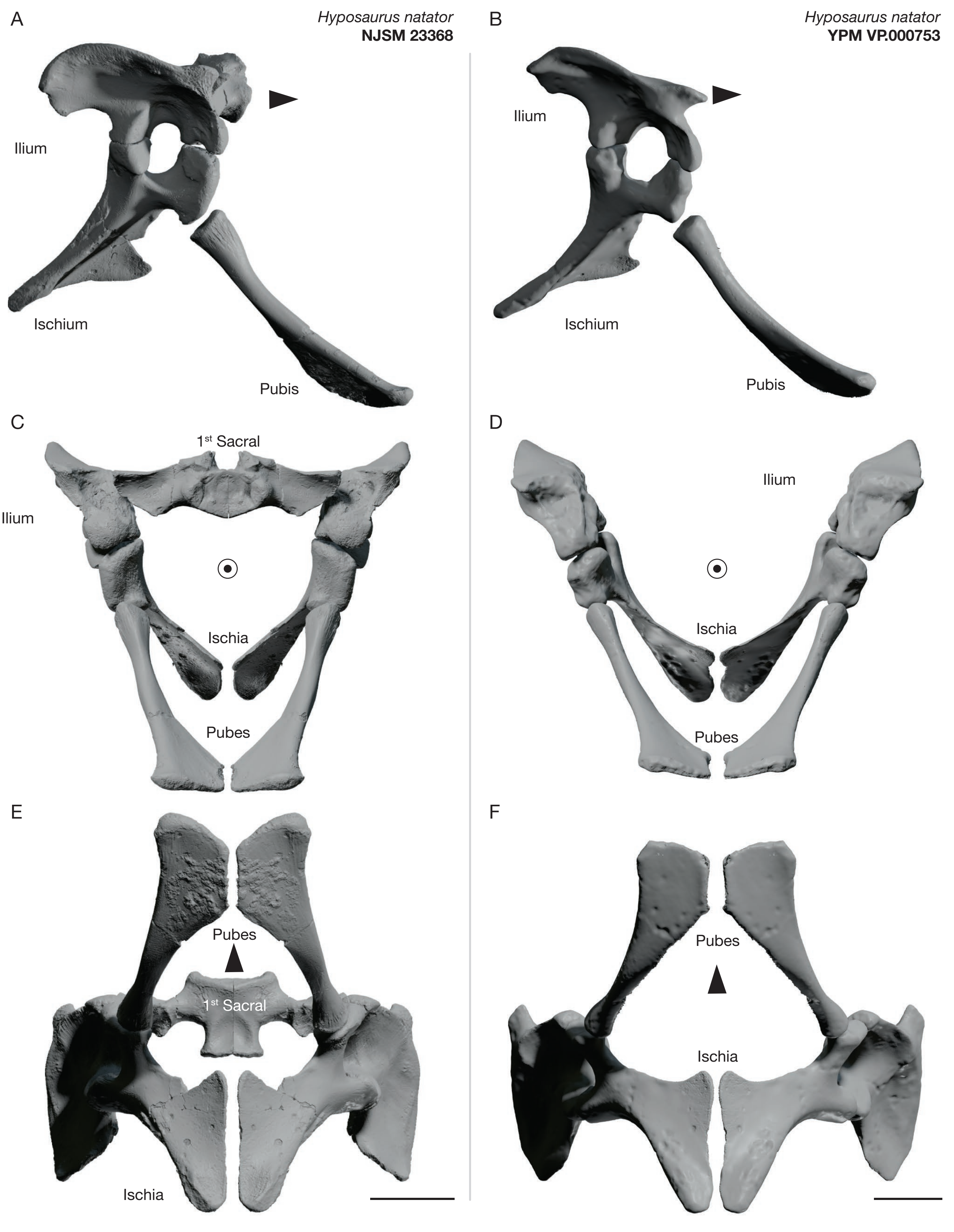


FIG. 68. — Reconstruction of the pelvic girdle of *Hyposaurus natator* (Troxell, 1925), YPM VP.000753 (**B**, **D**, **F**) and NJSM 23368 (**A**, **C**, **E**): **A**, **B**, right lateral views; **C**, **D**, anterior views; **E**, **F**, ventral views. **Target** indicates anterior. **Arrow** points anteriorly. The left ilium, ischium and pubis of YPM VP.000753 are mirrored. The ischium of YPM VP.000753 has been partially reconstructed. The left pubis and right ilium and ischium of NJSM 23368 are mirrored. 3D models of NJSM 23368 courtesy of Candice Stefanic. Scale bars: 5 cm.

brachyrhynchus NHMUK PV R 3804, *Suchodus durobrivensis*, etc.) and extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) in being relatively longer and slender due to an elongated pubic plate (shaft reaches about 36-37% of total length). Similar to thalattosuchians, the pubis of *Hyposaurus natator* further differs from that of extant crocodylians in possessing a large pubic symphysis.

The global shape of the pubis of *Hyposaurus natator* (YPM VP.000753, holotype [Fig. 66]; NJSM 23368 [Fig. 67]) is similar to that of other dyrosaurids (i.e. *Dyrosaurus maghribensis*, *Cerrejonisuchus improcerus*, *Anthracosuchus balrogus*) in being both elongated proximodistally and narrow mediolaterally. Proximally, the pubis of *Hyposaurus natator* displays a relatively short neck (about 36-37% of total length, see Table 9) and an even shorter shaft (about 26% of total length, see Table 9) whose sections are elliptic throughout. The shaft and the neck both correspond to transition portions between the peduncle and the pubic apron (Fig. 4). The shaft itself stretches from the peduncle proximally up until the distal widening, which marks the beginning of the pubic apron. The shaft is topped with a slightly concave articular facet called the pubic peduncle. The pubic peduncle displays a sloping articular surface in anteroposterior view, which may actually reflect the curved or wedged anterior surface of the anterior peduncle of the ischium. A similar feature is observed among extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]). The area surrounding the pubic peduncle is scarred for about 1-2cm, which indicates the presence of a cartilage cap *in vivo*. The junction between the shaft and the pubic plate is identifiable thanks to both the anteroposterior flattening and dorsal bending of the bone (visible in lateral and medial views). There, the pubis starts to gradually widen lateromedially in the distal direction. At the junction between the shaft and the pubic plate, the lateral and medial margins of the shaft are locally parallel then rapidly flare out proximally and distally, creating concave lateral and medial margins. Conversely, the anterodorsal and posteroventral surfaces of the pubis (in lateral view starting from the junction) only dimly flare out proximally, and even become slightly finer distally. The distal portion of the pubis – the pubic plate or apron – comprises five distinct margins: the two lateral ones, the two medial ones, and finally the distal one. The concave medial margin is shorter than the lateral one as it abruptly transitions (through an obtuse bend) into the straight margin constituting the pubic symphysis. In YPM VP.000753 (Fig. 66), the concavity of the medial margin is lesser than that of NJSM 23368 (Fig. 67) and bears almost a straight look. The pubic symphysis was covered by cartilage *in vivo* as the pitted texture reveals, and served as the connection point with the other pubis. The length of the pubic symphysis is significantly greater in *Hyposaurus natator* (about 22% of total pubis length for NJSM 23368, whereas it reaches about 18.4% in YPM VP.000753, see Table 9) than what is observed in extant crocodylians (e.g. about 7.3% for *Caiman crocodilus* NHMW 30900 and about 12.9% for *Mecistops cataphractus* RBINS 18374). Opposite to the pubic symphysis is a short margin relatively straight or subtlety convex which connects the large and concave lateral margin with the distal margin. This short lateral margin is not as protruding as in *Cerrejonisuchus*, so it cannot be called a protuberance. The distal margin, which connects the lateral and medial margins of the pubis, appears relatively straight but is slightly convex anterodorsally. Indeed, the pubic apron is slightly bulged dorsally starting from the proximal extremity of the pubic symphysis.

The presence of a large pubic symphysis, coupled with rounded respective peduncles on the pubis and ischium (Fig. 68), conveys the relative mobility of the pubes and also presumably the existence of a pelvic aspiration (Brocklehurst *et al.* 2020).

DYROSAURUS MAGHRIBENSIS (JOUVE, IAROCHÈNE, BOUYA & AMAGHZAZ, 2006)

For measurements, see Tables 7-9.

Ilium

The ilium of *Dyrosaurus maghribensis* (OCP DEK-GE 252 and OCP DEK-GE 255; Fig. 69) is similar to that of other dyrosaurids in possessing a well-developed postacetabular process, large peduncles, a wide acetabular perforation, and a relatively short preacetabular process. In this way *Dyrosaurus maghribensis* differs from Thalattosuchia and Crocodylia.

Dyrosaurus maghribensis specifically differs from *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis* in displaying a wide acetabulum and a long supraacetabular crest bordering it dorsally. Moreover, the sacral rib attachment sites for the sacrals are proportionally larger in *Dyrosaurus maghribensis* than in *Congosaurus bequaerti* or *Hyposaurus natator*. *Dyrosaurus maghribensis* also stands out from other dyrosaurids in having a large and 'blunt' preacetabular process and a relatively flat dorsal margin, that is slightly bulged in the way of *Congosaurus bequaerti* and opposed to *Acherontisuchus guajiraensis*.

The preacetabular process of the ilium of *Dyrosaurus maghribensis* (OCP DEK-GE 252 and 255; Fig. 69) takes the shape of a right angle whose sides and peak are rounded, thus giving a blunt appearance to the preacetabular hook. The orientation of the preacetabular process of OCP DEK-GE 252 and 255 is not entirely clear due to its preservation state, but it appears to be mainly anterior. Comparatively, the preacetabular process of *Dyrosaurus maghribensis* OCP DEK-GE 254 (Jouve *et al.* 2006) seems sharper and oriented anterodorsally. Also, the anterior margin of the preacetabular process of OCP DEK-GE 254 is greater than those of OCP DEK-GE 252 and 255, resulting in a shorter distance between the preacetabular hook and the pubic peduncle for OCP DEK-GE 254.

Laterally emerging from the preacetabular process is an oblong area culminating in the supraacetabular crest. Directly underneath the preacetabular process is a straight surface corresponding to the anterior margin of the ilium; this margin is relatively long in the case of OCP DEK-GE 252 and OCP DEK-GE 255, whereas it is shorter for OCP DEK-GE 254

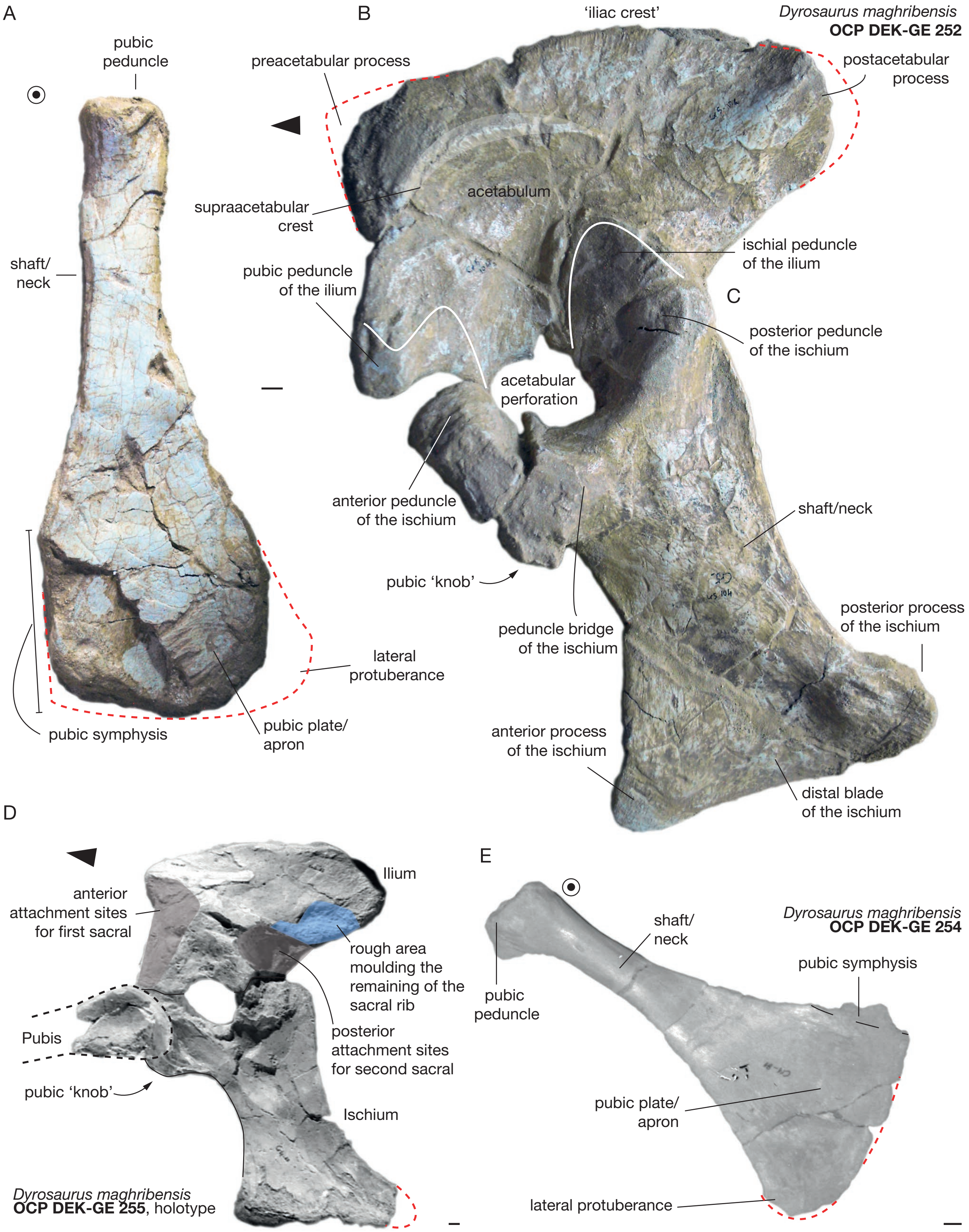


FIG. 69. — Pelvic girdle elements of *Dyrosaurus maghribensis* Jouve, Iarochène, Bouya & Amaghzaz, 2006: **A**-**C**, OCP DEK-GE 252; **A**, left pubis in anterior view; **B**, left ilium in lateral view; **C**, left ischium in lateral view; **D**, right pelvic girdle in medial view of the holotype (OCP DEK-GE 255); **E**, right pubis in anterior view (OCP DEK-GE 254). **Target** indicates anterior. **Arrow** points anteriorly. Scale bars: 1 cm.

(Jouve *et al.* 2006). This surface forms the junction between the preacetabular process and the pubic peduncle. In *Dyrosaurus maghribensis* OCP DEK-GE 252 and 255, the articular facet of the pubic peduncle does not significantly protrude anteriorly and remains within the extension of the anterior margin of the ilium, as in *Hyposaurus natator* YPM VP.000753. In contrast, *Dyrosaurus maghribensis* OCP DEK-GE 254 displays a more embossed articular facet for the pubic peduncle which make it protrude slightly anteriorly, similar to *Congosaurus bequaerti*, *Hyposaurus natator* NJSM 23368, and *Acherontisuchus guajiraensis*. Yet the pubic peduncle of *Congosaurus bequaerti* is longer anteroposteriorly than that of *Dyrosaurus maghribensis* (Figs 69; 72). Like many other crocodyliforms, the pubic peduncle of *Dyrosaurus maghribensis* is less elevated dorsoventrally than the ischial peduncle is (e.g. *Mecistops cataphractus*, '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804; *Thalattosuchus superciliosus*, *Congosaurus bequaerti*, etc.). Both peduncles are taller than the acetabular perforation, as in other dyrosaurids (e.g. *Congosaurus bequaerti*, *Acherontisuchus guajiraensis*). Similar to other dyrosaurids and extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*), the pubic peduncle of *Dyrosaurus maghribensis* is composed of two small adjoined triangles: the first one forming the anterior rim of the pubic peduncle, and the second one constituting the lateral surface of the peduncle. The latter resembles a flattened isosceles triangle oriented towards the acetabulum (i.e. posteriorly), whereas the first one appears more like a right angled triangle facing partly laterally and anteriorly, similar to other dyrosaurids and extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Congosaurus bequaerti*, *Hyposaurus natator*, and *Acherontisuchus guajiraensis*).

The pubic peduncle of the ilium of *Dyrosaurus maghribensis* (Fig. 69) is entirely separated from the ischial peduncle by the acetabular perforation, like other dyrosaurids and extant crocodylians.

The acetabular perforation of *Dyrosaurus maghribensis* is longer anteroposteriorly than it is deep dorsally; similar proportions are found for *Congosaurus bequaerti* (for which it is less high dorsoventrally than *Dyrosaurus*, and *Hyposaurus natator*). However, *Acherontisuchus guajiraensis* strongly differs from *Dyrosaurus maghribensis* with its anteroposteriorly short and dorsally deep acetabular perforation. The acetabular perforation of *Dyrosaurus maghribensis* is relatively well developed in all specimens as it reaches more than half the length of either peduncle of the ilium. In this way, the acetabular perforation of *Dyrosaurus maghribensis* is closer to that of *Hyposaurus natator* than *Congosaurus bequaerti*, for which the acetabular perforation is less deep dorsoventrally. Yet, the acetabular perforation of *Dyrosaurus maghribensis* is still distinct from that of *Hyposaurus natator* in being shallower dorsally. The ischial peduncle succeeds the acetabular perforation posteriorly, and forms the posterior border of the acetabulum. Contrary to the pubis peduncle, the ischial peduncle is strongly oblique so that its posterior part protrudes from the overall plane formed by the postacetabular process. In this way, the post acetabular process forms a bony barrier posteriorly, hence it was presumably the attachment site of a structure similar to the antitrochanter of extant crocodylians (Tsai & Holliday 2015). As in Crocodylia, Thalattosuchia and other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*), the lateral articular surface of the ischial peduncle of *Dyrosaurus maghribensis* resembles a tilted isosceles triangle pointing globally dorsally. This triangular lateral surface is also oriented anteriorly towards the centre of the acetabulum, mirroring the inclination of the pubic peduncle. This effect is actually emphasized by the posterior protrusion of the ischial peduncle. The ventral portion of the ischial peduncle meets with the dorsal part of the posterior peduncle of the ischium, and is slightly truncated so that the medial extremity of the ischial peduncle is more ventrally situated that the lateral one. Consequently, the lateral surface of the ischial peduncle appears like a titled triangle.

The postacetabular process of *Dyrosaurus maghribensis* (Fig. 69) is relatively small compared to other dyrosaurids as it accounts for less than half of the total length of the ilium. The ventral margin of the postacetabular process directly stems from the posterior corner of the ischial peduncle. The junction between the two appears smooth similar to that of extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus*). However, it differs from that of *Congosaurus bequaerti*, and *Hyposaurus natator* which display a small concave indentation between the ischial peduncle and the postacetabular process, and further differs from that of *Acherontisuchus guajiraensis* which possesses a large but shallow concave recess. Overall, the postacetabular process of all specimens of *Dyrosaurus maghribensis* is asymmetrical and appears like a beak: its ventral margin is almost exclusively concave whereas its dorsal margin is convex, thus giving a global hooked look. This effect is actually accentuated by the relative height of the postacetabular process, with those bearing a smaller process also show a more emphasized beak appearance (e.g. OCP DEK-GE 252; Fig. 69B). Hence, the ventral margin of the postacetabular process of *Dyrosaurus maghribensis* is distinct from that of *Congosaurus bequaerti*, and *Hyposaurus natator* for which the ventral margin shows an overall greater convexity, and also differs from *Acherontisuchus guajiraensis* for which the convex margin extends up to half the length of the postacetabular process. The extremity of the postacetabular process (Fig. 69D) looks like a Lancet arch as in other dyrosaurids; indeed, the posterior-most portion of the ventral margin changes concavity to become convex in this area. The dorsal rim of the postacetabular process, known as the 'iliac crest, is entirely convex from its junction with the preacetabular process up to its posterior peak. On its lateral surface, the whole area is scarred perpendicularly to its margin which conveys the existence of a cartilaginous cap *in vivo*. The convexity of the dorsal margin of the postacetabular process is subtle as in *Congosaurus bequaerti*. Moreover, the junction between the postacetabular process and the preacetabular process is also marked by a shallow recess for OCP DEK-GE 252 and 255 like *Congosaurus bequaerti* and *Acherontisuchus guajiraensis*, and like the extant crocodylians *Mecistops cata-*

phractus (Fig. 8) and *Caiman crocodilus* (Fig. 9), adding to the smooth overall profile of the iliac crest. In OCP DEK-GE 254, the junction between the postacetabular process and the preacetabular process displays a greater concavity, not unlike that of *Hyposaurus natator*.

The preacetabular process of *Dyrosaurus maghribensis* is not well preserved (Fig. 69), but seems large and bulky, unlike those of extant crocodylians (e.g. *Mecistops cataphractus* and *Caiman crocodilus*) and other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*). Indeed, the preacetabular process of *Dyrosaurus maghribensis* OCP DEK-GE 252 and 255 does not sharpen anteriorly, but rather forms a rounded right angle due to its slightly convex margins. In the case of OCP DEK-GE 254, the preacetabular process appears to have been more angular than those of OCP DEK-GE 252 and 255. The area encased between the margins of the preacetabular process and the supraacetabular crest is inclined and culminates at its junction with the supraacetaular crest. The latter forms the dorsal margin of the acetabulum, and appears like a prominent arch (like that of *Acherontisuchus guajiraensis*) which extends as far posteriorly as the acetabulum. In *Congosaurus bequaerti*, and *Hyposaurus natator*, the supraacetabular crest is not so well defined and does not extend as far back posteriorly. The supraacetabular crest of *Dyrosaurus maghribensis* however differs from that of *Acherontisuchus guajiraensis* in displaying a wider concavity.

The acetabulum of *Dyrosaurus maghribensis* (Fig. 69; see Table 11) is proportionally large compared to the ilium as a whole. Also, the acetabulum of *Dyrosaurus maghribensis* is almost as high as it is wide, giving it a semi-spherical appearance unlike the rather elliptical appearance of other dyrosaurids. Its deepest portion seems to be located directly above the acetabular perforation, in between the pubic and ischial peduncles. In other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*), the deepest point of the acetabulum appears to be located more dorsally, closer to the suparaacetabular crest.

Medially, the ilium of *Dyrosaurus maghribensis* bears two distinct scars for the attachment of the sacral ribs. In OCP DEK-GE 255 (Fig. 69D) and OCP DEK-GE 254 (see Jouve *et al.* 2006) the anterior attachment site is the largest, and covers the area extending from the pubic peduncle up until the peak of the preacetabular process. In OCP DEK-GE 255, however, the outline of the anterior attachment site differs from that of OCP DEK-GE 254 in resembling an asymmetrical parabola whose vertex points dorsoposteriorly. The shape of the anterior attachment site in OCP DEK-GE 254 appears more semicircular. The posterior attachment site of *Dyrosaurus maghribensis* is deeper than the anterior one but also more limited spatially. The overall shape of the posterior attachment site approximates that of two joined parabolas, with the upper one being the smallest. The actual anchoring site for the sacral rib was limited to the lower parabola. In OCP DEK-GE 255, the lower parabola covers half of the ischial peduncle and a similar area over the postacetabular process, whereas in OCP DEK-GE 254 the lower parabola extends over the entire ischial peduncle. The upper parabola constitutes a shallower depression dorsally to the posterior attachment site which presumably bore the ’winglet’ posterior extension of the second sacral rib similar to extant crocodylians (e.g. see *Alligator mississippiensis* (Daudin, 1801) on Fig. 74C).

Ischium

The ischium of *Dyrosaurus maghribensis* (Fig. 69) resembles that of other dyrosaurids in displaying: a thick shaft; limited anterior and posterior processes (which do not protrude much beyond the peduncles); a well-developed anterior peduncle; and a twisted distal blade in relation to the shaft.

Consequently, the ischium of *Dyrosaurus maghribensis* (Fig. 69) differs from that of other thalattosuchians in lacking: a posterior process extending beyond more than half the proximal anteroposterior length (defined by the peduncles); a reduced anterior peduncle (smaller in size than the posterior peduncle); a short shaft; a large and flat distal blade.

Overall, the ischium of *Dyrosaurus maghribensis* (Fig. 69) is similar to that of extent crocodylians and other dyrosaurids as it displays relatively large peduncles separated by a wide acetabular perforation (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*). The latter is as long as its twin borne on the ilium but is slightly deeper. The total length of the proximal extremity encompassing both peduncles almost reaches the length of the distal blade of the ischium, unlike *Hyposaurus natator* for which the distal blade exceeds the proximal extremity in size. Mediolaterally, the anterior peduncle of the ischium of *Dyrosaurus maghribensis* is as wide as the ventral surface of the pubic peduncle of the ilium as both peduncles were connected *in vivo* (Fig. 69D). The anterior peduncle is separated from the shaft by a narrow bridge, ventral to the acetabular perforation. More anteriorly, the anterior peduncle of the ischium expands dorsally to contact the pubic peduncle of the ilium, and ventrally to form the distinct ‘button’ or ‘knob’ (see OCP DEK-GE 254 in Jouve *et al.* (2006), or Fig. 69D) for the articulation with the pubis (Jouve *et al.* 2006). Indeed, similar to other dyrosaurids and extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Acherontisuchus guajiraensis*), the anterior peduncle of *Dyrosaurus maghribensis* (Fig. 69) is well developed: its dorsoventral height accounts for more than twice its anteroposterior width (see Table 8), hence offering a large articular surface for the pubis as mentioned above. The presence of an extra articular area for the pubis being almost similar to a peduncle on the ventral side of the articular surface of the anterior peduncle of the ischium is a characteristic of Dyrosauridae, and is not found in either Crocodylia (e.g. *Palaeosuchus palpebrosus* RVC-JRH-PP1 [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9] or Thalattosuchia (e.g. ‘*Metriorhynchus*’ *brachyrhynchus* NHMUK PV R 4763 [Fig. 22] or *Lemmysuchus obtusidens* [Fig. 59]). Hence, the articular surface of the anterior peduncle of *Dyrosaurus maghribensis* significantly flares out, in the way of other dyrosaurids (i.e. *Hyposaurus natator*, *Acherontisuchus guajiraensis*), and is thus quite different from what is observed in extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*).

In extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]), the relative dorsal expansion of the anterior peduncle compared to the posterior peduncle can be attributed to the difference in inclination between both iliac peduncles (i.e. when their ventral margins are not parallel). Conversely, the anterior peduncle of the ischium of *Dyrosaurus maghribensis* and other dyrosaurids (i.e. *Hyposaurus natator*, *Acherontisuchus guajiraensis*) and thalattosuchians (e.g. *Torvoneustes carpenteri* or *Neosteneosaurus edwardsi*) never extends dorsally over the dorsal margin of the posterior peduncle of the ischium. Still, the anterior peduncle of the ischium of *Dyrosaurus maghribensis* and dyrosaurids appears to be more expanded dorsally compared to that of thalattosuchians due to a deeper acetabular perforation, especially on the lateral side of the ischium.

The peduncle bridge of the ischium of *Dyrosaurus maghribensis* OCP DEK-GE 252 and 254 are shorter and thicker than that of OCP DEK-GE 255 and other dyrosaurids (i.e. *Hyposaurus natator*, *Acherontisuchus guajiraensis*) and extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*) on top of their short extension, which does not help in the matter, the dorsal and ventral margins of the peduncle bridge are merely concave resulting in a thick appearance. Such a short peduncle bridge in OCP DEK-GE 252 and 254 gives the impression that the anterior peduncle directly emerges from the shaft. Conversely, the holotype OCP DEK-GE 255 displays a consequently longer peduncle bridge (Fig. 69D), similar to what is observed in other dyrosaurids (i.e. *Hyposaurus natator*, *Acherontisuchus guajiraensis*).

The posterior peduncle of *Dyrosaurus maghribensis* is large with its mediolateral length being equivalent to the dorsoventral height of the anterior peduncle, and robust. Also, its articular surface is truncated resulting in an additional triangular portion facing towards the acetabulum, in line with the lateral surface of the ischial peduncle of the ilium. The main articular facet of the posterior peduncle, its dorsal surface, is connected to the ilium through the ischial peduncle. Similar to other dyrosaurids (i.e. *Hyposaurus natator*, *Acherontisuchus guajiraensis*), the posterior peduncle appears short and bulky due to a thick neck connecting it to the main shaft. This effect is created by the shape of the anterior and posterior margins of the neck of the posterior peduncle of *Dyrosaurus maghribensis*, which are respectively concave and convex. Unlike extant crocodylians (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*), the posterior peduncle of dyrosaurids is slightly elevated, giving them a deeper acetabular perforation.

The shaft of the ischium of *Dyrosaurus maghribensis* (Fig. 69) is thick, and does not significantly slim down from the bases of the peduncles, unlike *Hyposaurus natator* and *Acherontisuchus guajiraensis*. This effect is imputable to the feeble concavity and shortness of the ventral margin of the peduncle bridge of the ischium. In OCP DEK-GE 252, this effect is even more emphasized by the important convexity of the posterior margin of the neck of the posterior peduncle. Consequently, in OCP DEK-GE 252 the posterior margin of the ilium appears convex on the first half, and only becomes concave on the second half of its total dorsoventral height. In OCP DEK-GE 254 and 255, the posterior margin of the shaft is more subtlety convex (Fig. 69D and Jouve *et al.* 2006), similar to *Hyposaurus natator*. In parallel, the anterior margin of the ischium underneath the anterior peduncle is entirely concave in all specimens. The relative thickness of the shaft of the ilium added to shortness of the distal blade (anteroposteriorly) convey a less intense impression of flaring out of the ischium compared to *Hyposaurus natator*. As in extant crocodylians and other dyrosaurids (i.e. *Hyposaurus natator* and *Acherontisuchus guajiraensis*), the posterior portion of the ischium directly underneath the posterior peduncle is thicker mediolaterally than its anterior counterpart. Moreover, the section joining, in a direct line, the peduncle bridge of the ischium and the posterior process of the distal blade corresponds to the thickest part of the ischium, similar to extant crocodylians and other dyrosaurids. Hence, there is an abrupt change in thickness anteriorly to and posteriorly to this line, which emphasises it. This line also corresponds to the axis along which the rotation of the distal blade (in relation to the peduncles) occurs, so that the anterior corner of the distal blade is actually set more medially than its posterior corner (as in extant crocodylians).

The distal blade of the ischium only subtly protrudes posteriorly from the posterior peduncle (i.e. it does not extend over more than half of the total proximal length of the ischium) unlike thalattosuchians (e.g. *Thalattosuchus superciliosus* or *Charitomenosuchus leedsi*). The anterior process of the distal blade is located slightly more dorsally than the posterior corner (unlike *Hyposaurus natator* where this is more emphasised), and the margin connecting both is concave. As in other dyrosaurids but unlike thalattosuchians, the distal processes of the ischium of *Dyrosaurus maghribensis* (Fig. 69) are relatively blunt, and the posterior process does not exceed more than twice the size of the anterior process. Similar to *Hyposaurus natator*, the peak of the anterior process is oriented anteriorly whereas that of the posterior process faces another direction. However, in *Dyrosaurus maghribensis* the peak of the posterior process appears to be oriented more posteriorly than ventrally unlike *Hyposaurus natator*. There is a difference in the shape of the processes between the specimens, with OCP DEK-GE 255 displaying a thicker anterior process and a thinner (and slightly longer) posterior one compared to those of OCP DEK-GE 252.

Pubis

The pubic peduncle of *Dyrosaurus maghribensis* (Fig. 69) is narrow, and its mediolateral width almost equals that of the shaft underneath it. This contrasts with that of *Hyposaurus natator* for which the shaft widens greatly to form the pubic peduncle proximally. In *Cerrejonisuchus improcerus* (Fig. 65), the proximal enlargement is more subtle than in *Hyposaurus natator* and is hence more similar to *Dyrosaurus maghribensis*. For this reason, the shaft of the pubis of *Dyrosaurus maghribensis* appears to display essentially straight margins laterally and medially. The shaft itself stretches from the peduncle proximally up until the distal widening, which marks the beginning of the pubic apron.

Overall, the pubis of *Dyrosaurus maghribensis* (Fig. 69) appears relatively slender as its pubic apron does not flare out drastically. Indeed the lateral and medial margins of the pubis (up to the inflection point, which corresponds to the pubic symphysis medially) display a low concavity, with the medial margin being the lowest. Yet, the pubic apron of *Dyrosaurus maghribensis* is proportionally larger than that of *Hyposaurus natator* (see Table 9), but is more limited than that of *Cerrejonisuchus improcerus*. Geometrically, the pubic apron of *Dyrosaurus maghribensis* is quite symmetrical with the lateral margin of the bone almost mirroring the medial one. This effect is mainly due to the size and orientation of the pubic symphysis, which is relatively short and parallel to the pubic shaft. Indeed, depending on the inclination and length of the pubic symphysis, the pubic apron is subject to deflect more or less laterally as in *Hyposaurus natator* or *Cerrejonisuchus improcerus*. In the case of *Dyrosaurus maghribensis*, the pubis was positioned slightly more upright than for *Hyposaurus natator*, similar to *Cerrejonisuchus improcerus*.

Distally, the pubic apron is bordered by a convex margin, joining the pubic symphysis with the lateral margin of the bone. The junction between the lateral margin of the bone and the distal one forms a small lateral protuberance in the way of *Hyposaurus natator* (Figs 66; 67) or *Cerrejonisuchus improcerus*.

Acherontisuchus guajiraensis
Hastings, Bloch & Jaramillo, 2011
For measurements, see Tables 7-9.

Ilium

Overall, the ilium of *Acherontisuchus guajiraensis* (Figs 70; 71) is similar to those of other dyrosaurids in possessing large peduncles and a well-developed postacetabular process greater or equal to the anteroposterior length of the acetabulum (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, and *Dyrosaurus maghribensis*).

The preacetabular process of the ilium of *Acherontisuchus guajiraensis* is longer anteroposteriorly than it is high dorsoventrally. Its dorsal margin is slightly concave whereas its ventral one is subtlety convex, leading to a pointed and drooping hook shape unlike any dyrosaurids. Hence, the orientation of the preacetabular process is anterodorsally, which contrasts with *Hyposaurus natator* and *Dyrosaurus maghribensis*. Even though the overall shape is different, the preacetabular process of *Congosaurus bequaerti* was similarly oriented.

The area enclosed within the margins of the preacetabular process and the supraacetabular crest is strongly pitted, and is also more elevated laterally along the side of the supraacetabular crest than near the preacetabular process. Like in other dyrosaurids (especially visible in *Congosaurus bequaerti* and *Hyposaurus natator*), the supraacetabular crest of *Acherontisuchus guajiraensis* is formed of a wide anterior portion (laterally prominent) and a less marked posterior rim. Overall, the supraacetabular crest is both strongly apparent and greatly arched with its vertex located at the posterior-most point of the bordering pitted area. Hence, the dorsal and posterior margins of the acetabulum are well defined. Similar to other dyrosaurids, the acetabulum of *Acherontisuchus guajiraensis* forms a relatively deep hollow medially (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, and *Dyrosaurus maghribensis*). However, the acetabulum of *Acherontisuchus guajiraensis* appears squeezed anteroposteriorly, posteriorly tilted (i.e. the concavity opens anteriorly and ventrally), and restricted to the anterior-most portion of the ilium. This effect is emphasized by the strong convexity of the supraacetabular crest, along with the posterior component in the orientation of its main axis. In other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*, and *Dyrosaurus maghribensis*), the supraacetabular crest is less convex, and the acetabulum is more open and proportionally wider.

The junction between the iliac crest and the preacetabular process is achieved through a slightly concave hollow (Fig. 70), similar to *Dyrosaurus maghribensis* but contrasting with *Congosaurus bequaerti* and *Hyposaurus natator*. The iliac crest, which forms the dorsal border of the postacetabular process, shows an important convexity with its apex located at about ⅔ of its total length posteriorly. However, the convexity on both sides of the apex is of different intensity, with the anterior portion being the weakest. Such a marked convexity for the iliac crest is not found in other dyrosaurids, and thus gives a unique appearance to the ilium of *Acherontisuchus guajiraensis*. The entire lateral surface of the iliac crest is scarred with perpendicular ridges, marking the presence of a cartilage cap *in vivo*. Posteriorly, the postacetabular process culminates in the shape of a Lancet arch whose apex is located at about the mid-height of the postacetabular process, similar to other dyrosaurids. The ventral margin of the postacetabular process is also markedly convex, which resembles the ilia of other derived dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator*), but differs from the more subtlety arched postacetabular processes of *Dyrosaurus maghribensis*. However, in *Acherontisuchus guajiraensis*, the convex portion of the ventral margin of the postacetabular process stops at about its mid distance with the ischial peduncle. From there, the ventral margin of the postacetabular process becomes moderately concave, forming the posterior border of the ischial peduncle at this anterior extremity. *Hyposaurus natator* is the only dyrosaurid bearing a similar configuration (more specifically YPM VP.000753, but NJSM 23368 does not depart too much).

The lateral surface of the postacetabular process of *Acherontisuchus guajiraensis* is evenly concave over almost its entire surface, like *Hyposaurus natator* but unlike *Congosaurus bequaerti* or *Dyrosaurus maghribensis* for which only a localized portion appears concave.

In *Acherontisuchus guajiraensis* (Figs 70; 71), the ischial and pubic peduncles bear consequent differences in their respective size and orientation of their ventral surface. In contrast, in other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator* and *Dyrosaurus maghribensis*), the difference is more subtle. The ischial peduncle is dorsoventrally higher than it is anteroposteriorly long. Similar to other many other crocodyliforms (e.g. *Palaeosuchus palpebrosus*, *Mecistops cataphractus*, *Caiman crocodilus*, *Suchodus durobrivensis*, *Thalattosuchus superciliosus*, *Congosaurus bequaerti*, *Hyposaurus natator*, *Dyrosaurus maghribensis*, etc.), the ischial peduncle takes the global shape of a triangle. Similar to *Congosaurus bequaerti* and *Hyposaurus natator* NJSM 23368, the ischial peduncle greatly protrudes from the ilium with two noticeable facets: one is triangular and borders the acetabulum posteriorly, and the other one is more wedge-shaped. The former was presumably the anchoring site for a structure similar to the antitrochanter of extant crocodylians (Tsai & Holliday 2015), whereas the latter assured the connection to the posterior peduncle of the ischium. Unlike any other dyrosaurids, the pubic peduncle of the ilium of *Acherontisuchus guajiraensis* is large and its ventral margin forms a bent at about ⅓ of its length posteriorly; presumably, only the posterior-most portion of the peduncle met with that of the ischium. Also, none of the two tilted portions of the ventral surface of the pubic peduncle are parallel to that of the ischial peduncle. Comparatively, *Congosaurus bequaerti* is the only other dyrosaurid displaying pubic and ischial peduncles with differing orientations of their ventral surfaces. The lateral surface of the pubic peduncle is poorly preserved (Hastings *et al.* 2011), so the exact shape of its articular facets is not identifiable.

The important size of the pubic peduncle could be a consequence of the position, orientation and dimensions of the bony acetabulum, especially since most of the bony acetabulum is borne on the pubic peduncle. Looking on the medial side of the ilium, it also appears that most of the area belonging to the pubic peduncle is scarred with attachment sites for the first sacral. Hence the important size of the sacral ribs could have had an influence on the relative size of the pubic peduncle. The anterior margin of the ilium connecting the preacetabular process to the pubic peduncle is short and relatively straight. The important size of the pubic peduncle also brings it closer to the preacetabular process.

Both peduncles are separated by a gap – the acetabular perforation – similar to other dyrosaurids and extant crocodylians (thalattosuchians bear a significantly smaller perforation). The acetabular perforation of *Acherontisuchus guajiraensis* (Fig. 70; Table 11) is taller dorsoventrally than it is long anteroposteriorly, which differs from all other dyrosaurids (i.e. *Congosaurus bequaerti*, *Hyposaurus natator* and *Dyrosaurus maghribensis*) for which the acetabular perforation is usually longer than it is tall. In *Acherontisuchus guajiraensis*, the acetabular perforation is relatively smaller than in other dyrosaurids as its base length anteroposteriorly only reaches a fraction of that of the pubic peduncle. To that regard, the acetabular perforation of *Acherontisuchus guajiraensis* is closer to that of *Congosaurus bequaerti* than other dyrosaurids. The narrow appearance of the acetabular perforation of *Acherontisuchus guajiraensis* mirrors that of the bony acetabulum. The latter is provoked by notably a different inclination of the ischial peduncle whose largest width is oriented more lateromedially as in *Congosaurus bequaerti* than anteroposteriorly as in *Hyposaurus natator* and *Dyrosaurus maghribensis*. This placement of the ischial peduncle reduces the overall anteroposterior length of the bony acetabulum. In *Acherontisuchus guajiraensis* the small size of the acetabular perforation on the ilium is presumably counterbalanced by the relatively larger size of the acetabular perforation on the ischium.

Medially, the ilium of *Acherontisuchus guajiraensis* stands out by possessing wide and deep attachment sites for both sacrals. Comparatively, for *Congosaurus bequaerti*, *Hyposaurus natator* YPM VP.000753, and for the *Dyrosaurus maghribensis* specimens (Jouve *et al.* 2006) the anterior attachment site is the largest, whereas for *Hyposaurus natator* NJSM 23368 (Fig. 67) the posterior one is the largest. In *Acherontisuchus guajiraensis*, the anterior attachment site is composed of two distinct triangular indentations separated by a prominent ridge. Hence, the anterior-most portion is the widest whereas the posterior-most one is the tallest. The anterior attachment site as a whole stretches from the preacetabular process (at its mid-height) dorsally, up to the acetabular perforation posteriorly (almost encompassing the entire area of the pubic peduncle). Comparatively, the posterior attachment site is also well-developed, occupying a similar area in size than the anterior attachment site. A distinctive feature of *Acherontisuchus guajiraensis* in relation to other dyrosaurids is the close proximity of both attachment sites which, along with their large sizes, entails a sound support of the pelvic girdle and a potentially better allocation of load. Overall, the posterior attachment site takes the shape of a blunt and dorsally oriented hook (Fig. 70). It spreads posteriorly from the point along the ventral margin of the postacetabular process where the concavity inverts, up until the anterior attachment site anteriorly. Also, it extends as high dorsally as the posterior-most portion of the anterior attachment site. Dorsally to the posterior attachment site is a rough area along which the posterior winglet of the second sacral presumably pressed (Fig. 70). It runs from the apex of the postacetabular process to near the top of the posterior attachment site.

Ischium

The ischium of *Acherontisuchus guajiraensis* (Fig. 70) is in poor preservation state. Notably, the distal blade is broken anteriorly, the anterior peduncle is missing its dorsal portion, and the posterior peduncle is almost entirely hollowed out. Still, the ischium of *Acherontisuchus guajiraensis* appears to stand out from those of *Hyposaurus natator* and *Dyrosaurus maghribensis* in possessing the combination of a short peduncle bridge and a large pubic knob on its anterior peduncle (Figs 70; 71).

The anterior peduncle of *Acherontisuchus guajiraensis* appears to be missing portions medially and dorsally (Fig. 70B, E). Presumably, most of the anterior and anteroventral (i.e. the pubic ’knob’) articular facets are present whereas the dorsal portion of the articular surface is absent (Fig. 70E). Hence, the medial portion of the anterior peduncle of *Acherontisuchus guajiraensis* has been tentatively reconstructed (Fig. 70E) based on those of *Hyposaurus natator* (YPM VP.000753, YPM VP.000985, and NJSM 23368). Overall, the articular surface of the anterior peduncle of *Acherontisuchus guajiraensis* displays a mediolaterally wide pubic ‘knob’ in relation to the mediolateral width of the peduncle bridge compared to other dyrosaurids

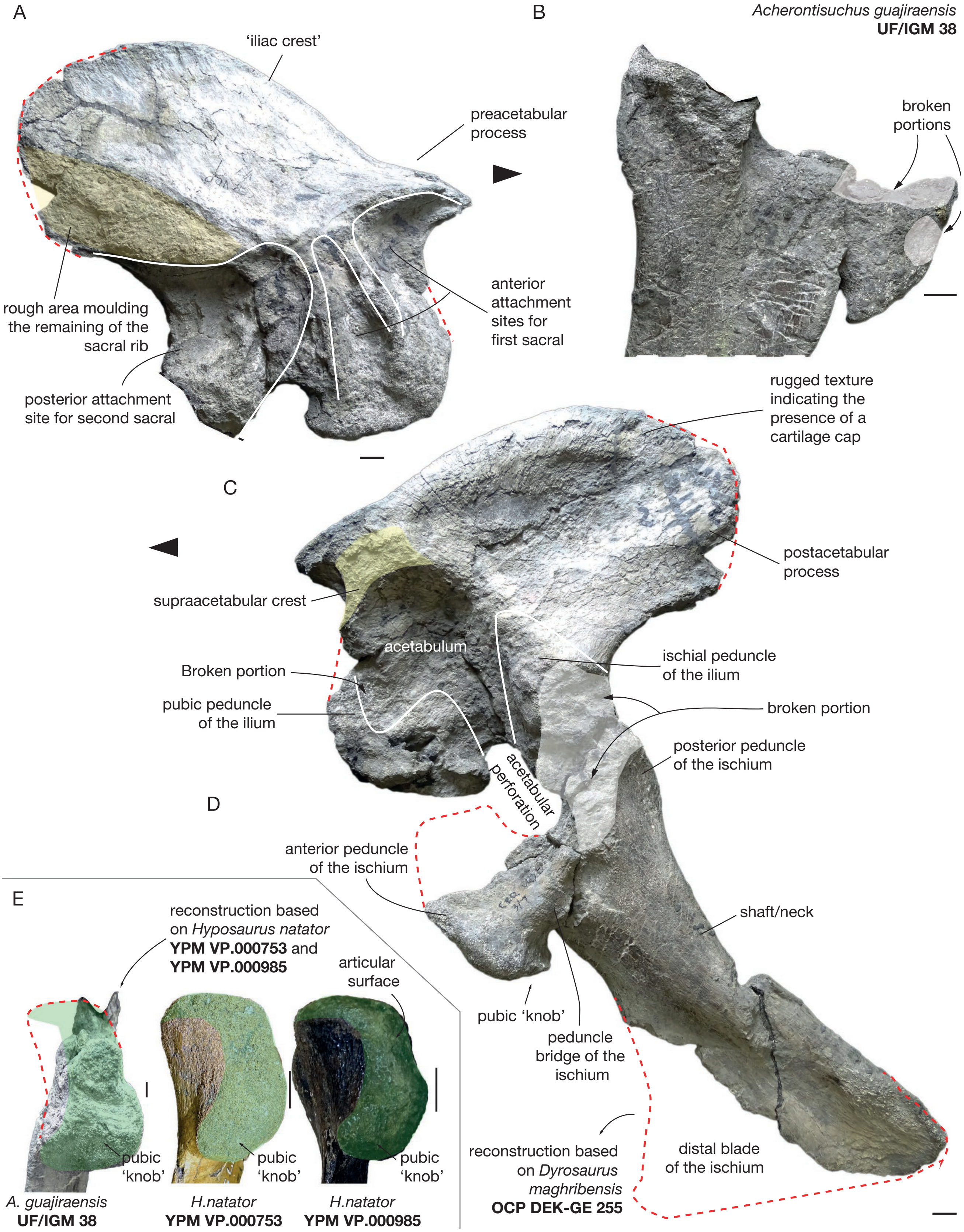


FIG. 70. — Left pelvic girdle elements of *Acherontisuchus guajiraensis* Hastings, Bloch & Jaramillo, 2011, UF/IGM 38: **A**, left ilium in medial view; **B**, detail of left ischium in medial view; **C**, left ilium in lateral view; **D**, left ischium in lateral view; **E**, detail of dyrosaurid ischia in anterior view. **Arrow** points anteriorly. Scale bars: 1 cm.

(i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*). It is possible that the dorsal expansion of the articular surface of *Acherontisuchus guajiraensis* was larger than what is preserved.

The dorsal margin of the peduncle bridge is broken, so its actual shape remains unknown. Still, based on the relative position of the pubic peduncle of the ilium of *Acherontisuchus guajiraensis* and also other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*), it is possible that the missing portion of the peduncle bridge and anterior peduncle rapidly rose dorsally to meet the ilium (Fig. 70). As in other dyrosaurids, the mediolateral thickness of the peduncle bridge of *Acherontisuchus guajiraensis* drastically reduces from about its mid-height, which implies a relatively thin breadth for the broken portion of the dorsal margin (and presumably accounts for its preservation state). This hollow borne by the peduncle bridge and anterior peduncle forms the ventral portion of the acetabulum. There is a prominent rim separating the peduncle bridge in two asymmetrical halves, from which the thickness of the bone decreases dorsally. The rim stems from the anterior extremity of the posterior peduncle, and can be followed up until the dorsal extremity of the anterior peduncle. Overall, the rim takes the shape of a wide and concave parabola, and marks the ventral border of the bony acetabulum. In other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*), the rim on the peduncle bridge underlining the ventral border of the acetabulum is less prominent than in *Acherontisuchus guajiraensis*, and is also located more dorsally. Indeed, in *Hyposaurus natator* (YPM VP.000753, YPM VP.000985, and NJSM 23368) and *Dyrosaurus maghribensis*, the rim is almost on the same level as the dorsomedial corner of the peduncle bridge (medial side of the acetabular perforation of the ischium) and thus appears like a dorsolateral corner. For this reason, the peduncle bridge of *Hyposaurus natator* and *Dyrosaurus maghribensis* has the appearance of a strictly dorsal area, whereas *Acherontisuchus guajiraensis* seems to possess a lateral component in the orientation of the surface positioned dorsally to the rim. It is possible that some deformations have provoked this orientation in the hollow dorsal surface of the ischium of *Acherontisuchus guajiraensis*. The combination of the extension of the hollow surface, added to the relative height of the bony acetabulum on the ilium conveys the existence of an enlarged acetabulum for *Acherontisuchus guajiraensis* compared to other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*). The large and oval shape of the entire acetabulum (i.e. ilium plus ischium) of *Acherontisuchus guajiraensis* presumably reflect the unique shape its femur (i.e. strong sigmoid shape due to prominent anterior deflection of femoral head and likewise posterior deflection of distal condyles), and the subsequent articular capsule.

The anterior peduncle of *Acherontisuchus guajiraensis* presumably extended as far dorsally as the posterior peduncle (Figs 70; 71), similar to all other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*). The overall outline of the articular facet of the posterior peduncle is preserved, revealing its relatively triangular outline which appears almost as long dorsoventrally (or mediolaterally) than it is anteroposteriorly. In parallel, the preservation state of the posterior peduncle allow us to take a peek at its junction with the ilium and the orientation of the articular facets involved: thus, the articular facet of the posterior peduncle seems tilted towards the ilium rather than dorsally oriented as in other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*). This orientation of the posterior articular facet in *Acherontisuchus guajiraensis* plays a role in its greater dorsal extension (along with the ventral deflection of the anterior peduncle). The neck of the posterior peduncle is composed of a concave anterior margin and a strongly convex posterior one, resembling that of *Dyrosaurus maghribensis* OCP DEK-GE 252 but more accentuated. Lateromedially, the convex posterior portion of the neck is also the thinnest portion, which gradually thickens anteriorly.

Underneath both peduncles, the anterior and posterior margins of the ischium display each a concave shape of differing intensity. In their convergent area, they form the shaft or neck of the ischium, then they diverge to create the distal blade. At its thinnest point, the shaft of *Acherontisuchus guajiraensis* (Fig. 70) displays the smallest anteroposterior length among dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*) (Hastings *et al.* 2011). Also, when looking at the ischial length starting from the base of the peduncles up until the tip of the distal blade, the thinnest portion of the shaft of *Acherontisuchus guajiraensis* is located more proximally than in other dyrosaurids. The posterior margin of the ischium of *Acherontisuchus guajiraensis* is weakly concave and thus appears almost straight, like *Hyposaurus natator* NJSM 23368 and *Dyrosaurus maghribensis* OCP DEK-GE 254 (Jouve *et al.* 2006), as opposed to *Hyposaurus natator* YPM VP.000753 and *Dyrosaurus maghribensis* OCP DEK-GE 252. Potentially, the shape of the posterior margin of the ischium of *Acherontisuchus guajiraensis* could also be subjected to intraspecific variations. The anterior margin of the ischium of *Acherontisuchus guajiraensis* has not been recovered. Since the anterior margin of the ischium seems less subject to variations among Dyrosauridae (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*), the ischium of *Acherontisuchus guajiraensis* and has been reconstructed based on that of *Dyrosaurus maghribensis* OCP DEK-GE 255. Yet, the distal margin of the position of the anterior process of the ilium, and its shape, remain unknown.

Lateromedially, the surface of the ischium underneath the peduncles varies in thickness, with the thicker portion of the bone forming a beam connecting the base of the anterior peduncle and the distal corner of the ischial blade, similar to other dyrosaurids (i.e. *Hyposaurus natator* and *Dyrosaurus maghribensis*). The lateral surface of the ischium anterior to the beam is strongly concave in the region of the distal blade, but in the area of the shaft it is still slightly convex. The gradual transition between the two areas takes place underneath (i.e. ventrally to) the constriction of the shaft.

The distal corner of the ischial blade of *Acherontisuchus guajiraensis* is rounded and does not appear to form a protruding posterior process as in *Dyrosaurus maghribensis*. Also, the distal corner of *Acherontisuchus guajiraensis* appears to flatten

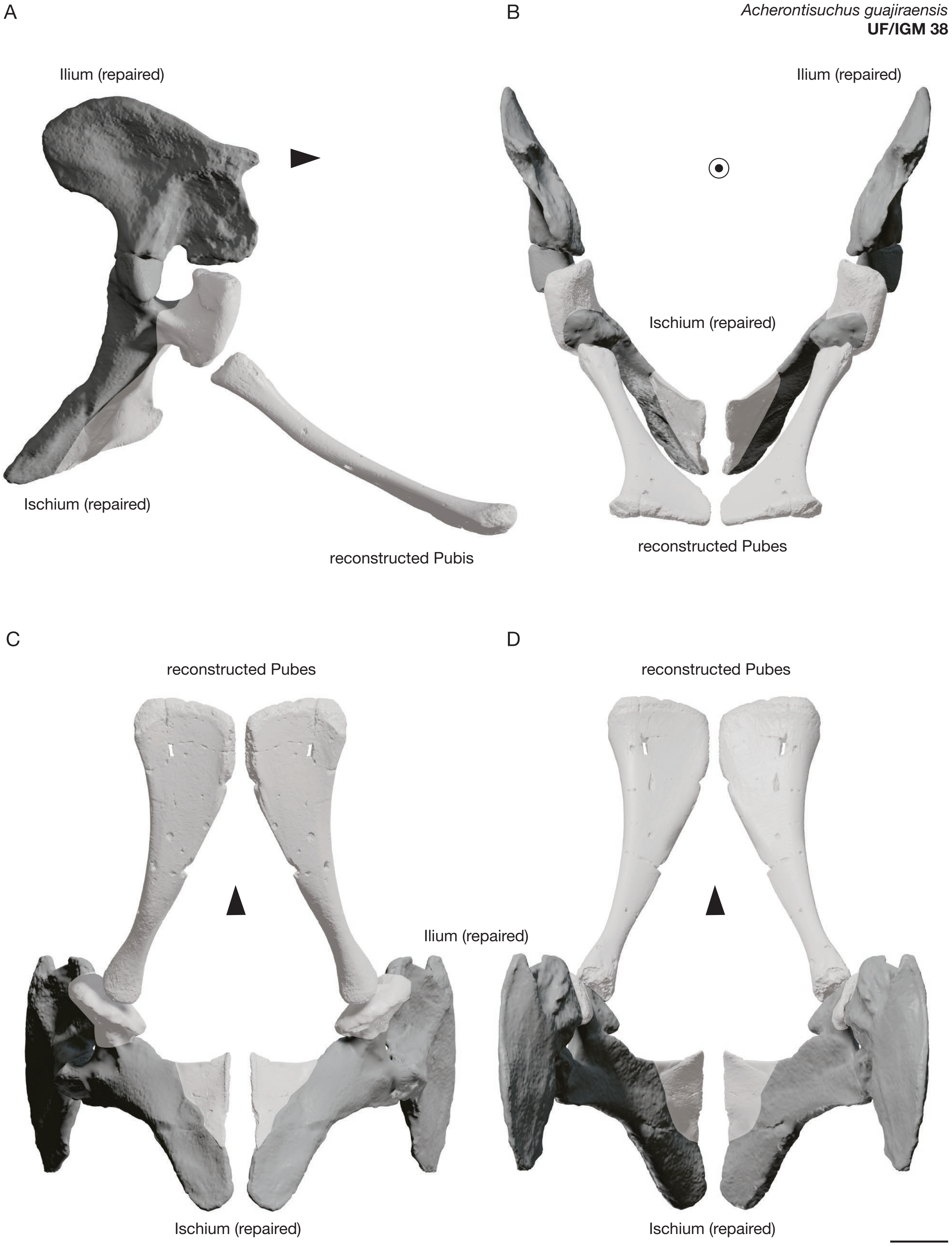


FIG. 71. — Pelvic reconstruction of *Acherontisuchus guajiraensis* Hastings, Bloch & Jaramillo, 2011, UF/IGM 38; ischium has been repaired based on *Hyposaurus natator* (Troxell, 1925), NJSM 23368; pubis have been recreated based on *Hyposaurus natator,* YPM VP.000753; **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. **Arrow** points anteriorly. **Target** indicates anterior. Original 3D models of YPM VP.000753 courtesy of Narimane Chatar; original 3D models of NJSM 23368 courtesy of Candice Stephanic. Reconstructed bones only serve as a qualitative representation of the pelvic girdle of *Acherontisuchus guajiraensis*. Scale bar: 5 cm.

lateromedially at the same time as the beam turns outward, unlike *Hyposaurus natator* which displays an anteriorly curled corner. From this point, the distal (or ventral) margin of *Acherontisuchus guajiraensis* bends medially to connect with the overall concavity of the ischial blade. The lateral surface of the distal corner is strongly pitted, indicating the presence of a cartilage cap *in vivo*.

CONGOSAURUS BEQUAERTI DOLLO, 1914
For measurements, see Tables 7-9.

The pelvic girdle of *Congosaurus bequaerti* MRAC 1806 (Fig. 72) is limited to the ilium, as the ischium and pubis have not been recovered for this taxon. The ilium of *Congosaurus bequaerti* sharply contrasts with that of other thalattosuchians in possessing a well-developed postacetabular process (which specifically differs from that of metriorhynchoids), along with a short (anteroposteriorly) but thick (lateromedially) preacetabular process, and deeply carved medial attachments sites for the sacral ribs. Yet, while teleosauroid thalattosuchians also display a postacetabular process, its relative size proportionally to the total anteroposterior length of the ilium is still inferior to what is observed in *Congosaurus bequaerti*, *Hyposaurus natator* or *Acherontisuchus guajiraensis*.

Compared to *Hyposaurus natator* and *Acherontisuchus guajiraensis*, the ilium of *Congosaurus bequaerti* shows a greatly reduced acetabular perforation and, in parallel, a taller bony acetabulum. The ilium of *Congosaurus bequaerti* also displays a shorter preacetabular process in relation to *Hyposaurus natator* and *Acherontisuchus guajiraensis*, but a more massive and higher postacetabular process compared to *Hyposaurus natator* (as that of *Hyposaurus natator* is concave ventrally, and that of *Congosaurus bequaerti* is not). However, the postacetabular process of *Acherontisuchus guajiraensis* is dorsoventrally taller than that of *Congosaurus bequaerti* due to a more convex iliac crest. Other great differences between *Hyposaurus natator* and *Congosaurus bequaerti* include the difference of inclination between the pubic and ischial peduncles, the number of attachments sites for the sacrals medially (in *Congosaurus bequaerti* the posterior-most imprints are almost fused), and the roughness of the iliac blade. The depth and number of attachments sites is a distinctive feature of dyrosaurids versus thalattosuchians and extant crocodylians.

The preacetabular process of *Congosaurus bequaerti* is short and thick: anteriorly, the preacetabular process does not protrude much from the main mass of the ilium similar to *Dyrosaurus maghribensis*, but unlike *Hyposaurus natator* and *Acherontisuchus guajiraensis*. In addition, the dorsoventral thickness of the preacetabular process of *Congosaurus bequaerti* reaches both its anteroposterior length and mediolateral width. The peak of the preacetabular process is truncated, and thus is not positioned midway but rather ventrally. Still, the preacetabular process points anteriorly, but with a small dorsal component. There is a rugged area covering the lateral side of the preacetabular process which stretches out both ventrally and posteriorly, but also laterally up until it meets with the supraacetabular crest. Posteriorly, this rugged area stops just under the start of the convex iliac blade dorsally. The region directly bordering the supraacetabular crest shows a subtle change in coarseness. The preacetabular process reaches its maximal mediolateral thickness at its junction with the supraacetabular crest. In *Congosaurus bequaerti* (Fig. 72), the supraacetabular crest appears to be made of two distinct portion: a relatively wide anterior rugged and laterally protruding part, and a more slender posterior rim (like in *Acherontisuchus guajiraensis* and *Hyposaurus natator*). This rim may actually not be part of the supraacetabular crest as it appears to be a simple byproduct of two adjacent convex areas, even if it is delimiting the acetabulum and the postacetabular process. Comparatively, *Dyrosaurus maghribensis* also displays an anterior portion laterally prominent but its posterior rim is wider than in *Congosaurus bequaerti*.

In *Mecistops cataphractus* the supraacetabular crest is identified thanks to its relief and rugged texture, but it is slightly more difficult in *Caiman crocodilus* as only the depth is present. For *Congosaurus bequaerti*, the supraacetabular crest will be limited to the coarse and prominent ridge, similar to extant crocodylians and thalattosuchians. *Acherontisuchus guajiraensis* and *Hyposaurus natator* possess a similar supraacetabular crest, but *Hyposaurus natator* YPM VP.000753 shows a smoother dorsal area overhanging the process. The supraacetabular crest borders the anterior half of the acetabulum dorsally, and was presumably the attachment site for a soft tissue structure equivalent to the acetabular labrum of extant crocodylians.

The dorsal margin of the ilium of *Congosaurus bequaerti* (Fig. 72) is almost exclusively convex, with a very localized shallow recess at the dorsal base of the preacetabular process. Throughout its length, the iliac blade is scarred perpendicularly to its extension; this coarseness indicates the presence of a cartilage cap *in vivo*. The extremity of the postacetabular process points posteriorly, with a small dorsal component. As both dorsal and ventral borders of the postacetabular process are convex, the peak takes the shape of a ribbed vault similar to other dyrosaurids (e.g. *Hyposaurus natator*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*). Yet, the postacetabular process of *Dyrosaurus maghribensis* appears relatively less convex. Comparatively, the postacetabular process in extant crocodylians strongly differs from dyrosaurids and teleosauroids in being slender (i.e. more elongated anteroposteriorly and thinner dorsoventrally) and in possessing an enlarged rugged area in the place of its peak. In *Congosaurus bequaerti*, there is seemingly no transition between the convex ventral margin of the postacetabular process and the ischial peduncle, whereas in *Hyposaurus natator* the transition is marked by an inversion of concavity. The absence of a recessed area posteriorly to the ischial peduncle in *Congosaurus bequaerti* accounts for the thickness its postacetabular process (Fig. 72).

Anteriorly, the pubic peduncle of the ilium forms a thick rounded area which breaks the straight monotony of the anterior margin of the ilium. The junction between the anterior and dorsal margins of the pubic peduncle is achieved through a re-entrant angle giving the impression of an inverted triangle. Laterally, the facet of the pubic peduncle bears two triangular shapes as it is the case in other dyrosaurids (i.e. *Hyposaurus natator*, *Dyrosaurus maghribensis*, *Acherontisuchus guajiraensis*):

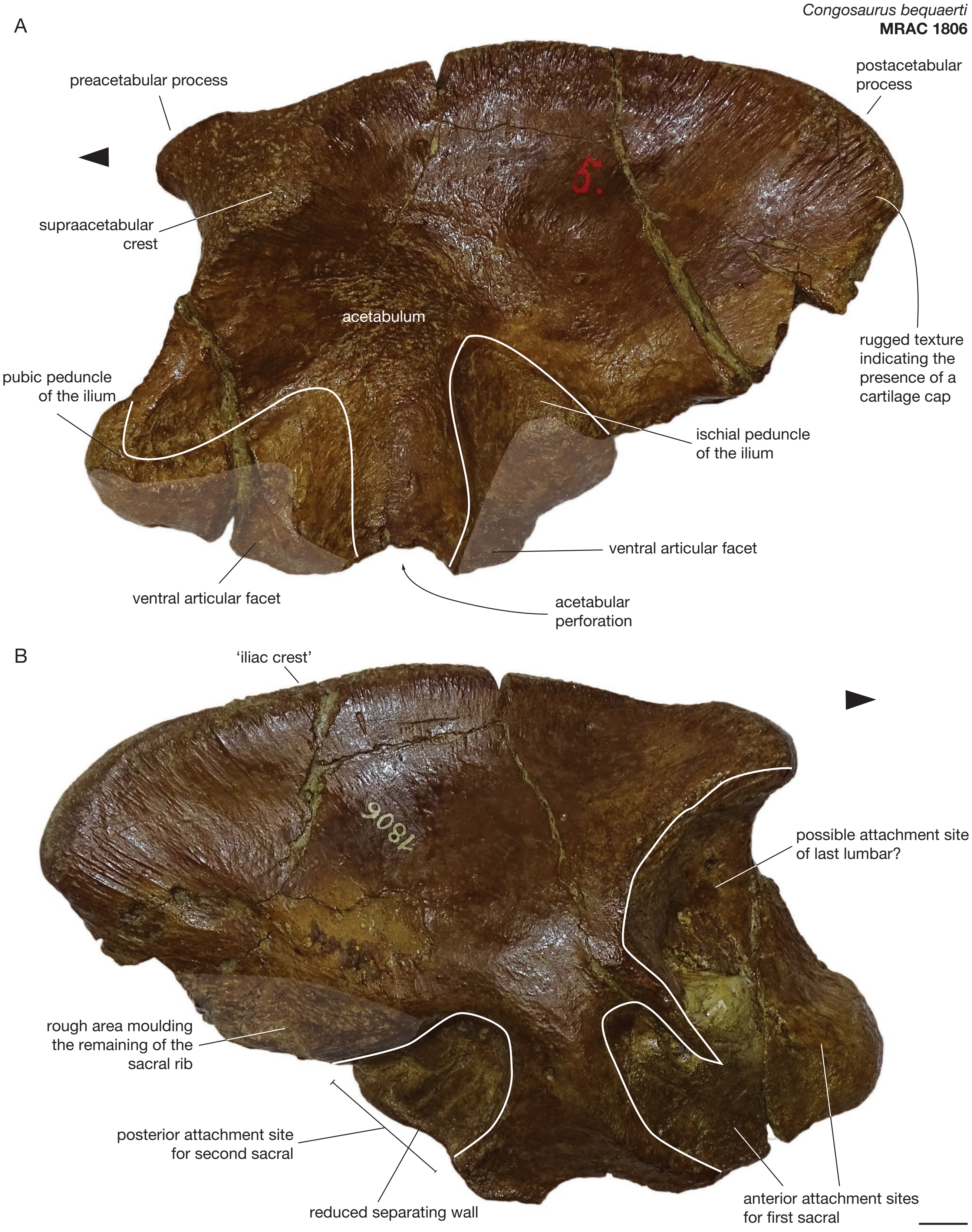


FIG. 72. — Left ilium of *Congosaurus bequaerti* Dollo, 1914, MRAC 1806 (holotype): **A**, lateral view; **B**, medial view. **Arrow** points anteriorly. Scale bar: 1 cm.

the apex of the anterior triangle meets with the anterior margin of the bone whereas the posterior shape appears like an isosceles triangle dorsally. The maximal dorsoventral height of the pubic peduncle appears to reach that of the ischial peduncle, as in *Hyposaurus natator* and *Acherontisuchus guajiraensis*.

In *Congosaurus bequaerti*, the ischial peduncle is a large process resembling an isosceles triangle whose vertex angle is dorsally facing. The ischial peduncle borders the acetabulum posteriorly as it markedly protrudes laterally. Hence, it was presumably the attachment site for a structure equivalent to the crocodylian antitrochanter in *vivo* (Tsai & Holliday 2015). At about ¼ of its height starting from its base (ventrally), the lateral surface of the ischial peduncle is truncated to form the articular facet it shares with the ischium. The ischial and pubic peduncles are clearly separated by a gap, the acetabular perforation (similar to teleosauroids but contrary to metriorhynchoids), whose anteroposterior length is greater than its dorsoventral height, similar to *Dyrosaurus maghribensis contra Hyposaurus natator* and *Acherontisuchus guajiraensis*. In this way, the acetabular perforation of *Congosaurus bequaerti* appears relatively reduced. It is possible that the ischium (not preserved) bore a greater acetabular perforation to counter this structure on the ilium. In parallel, the inclination of the pubic peduncle could also help increase the size of the acetabular perforation, notably by necessitating a longer peduncle bridge on the ischium (Fig. 73). The relative shortness of the acetabular perforation of *Congosaurus bequaerti* brings the ilium of teleosauroids like *Lemmysuchus obtusidens* to mind. Still, the acetabular perforation of *Congosaurus bequaerti* is more pronounced than in most teleosauroids (e.g. *Lemmysuchus obtusidens*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*).

The ventral margin of the ischial peduncle is parallel to the tangent to the ventral margin of the postacetabular process: as a consequence, the distal margin of the ischial peduncle points both ventrally and posteriorly (similar to what is observed in *Acherontisuchus guajiraensis*, *Mecistops cataphractus* or *Caiman crocodilus*) and forms an angle of approximately 120-125° with the ventral margin of the pubic peduncle (see Table 10). Conversely, in *Hyposaurus natator* and *Dyrosaurus maghribensis*, the ventral margins of the ischial and pubic peduncles appear almost parallel and are mostly ventrally oriented. The different orientation and shape of the peduncles between the ilia of *Congosaurus bequaerti* and *Hyposaurus natator* plus *Dyrosaurus maghribensis* would presumably imply dissimilarity in the way the ischium connects to the ilium as well.

The 'open' orientation of the iliac peduncles of *Congosaurus bequaerti* (Fig. 72) resembles the configuration of both *Acherontisuchus* and *Dyrosaurus maghribensis*, but also that of extant crocodylians (e.g. *Palaeosuchus palpebrosus* RVC-JRH-PP1 [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]) for which the anterior peduncle of the ischium and the pubic peduncle of the ilium do not contact each other, at least not entirely, and are covered (presumably for extinct taxa) with hyaline cartilage *in vivo*. It is possible that the configuration of *Congosaurus bequaerti* approximated that of extant crocodylians, in which the ischium either partly contacted the ilium anteriorly (see below), or was set further ventrally avoiding contact between the ischium and pubic peduncle of the ilium (Fig. 73). In the case of *Dyrosaurus maghribensis*, however, the pubic peduncle of the ilium appears to have been in contact in its entirety with the dorsal articular surface of the ischium.

The ventral margin of the pubic and ischial peduncles are not parallel which conveys the idea that the ischium of *Congosaurus bequaerti* presented an anterior peduncle similar to those of extant crocodylians (e.g. *Palaeosuchus palpebrosus* RVC-JRH-PP1 [Fig. 7], *Mecistops cataphractus* RBINS 18374 [Fig. 8], *Caiman crocodilus* NHMW 30900 [Fig. 9]). Hence, for *Congosaurus bequaerti*, it is possible that the anterior peduncle of the ischium presented a short anteroposterior articular surface with a long dorsoventral articular surface like *Mecistops cataphractus* (Fig. 8), with only a fraction of the anterior peduncle of the ischium meeting with the pubic peduncle of the ilium. Contrastively, it is also possible that there was a gap between the pubic peduncle of the ilium and the anterior peduncle of the ischium similar to *Hyposaurus natator*. The vertex angle of the pubic peduncle points dorsally, and the peduncle borders the acetabulum ventrally. The short dorsal extension of the pubic peduncle was presumably intended to leave more room to the acetabulum. Anteriorly, the margin ilium of *Congosaurus bequaerti* is concave, and is bordered ventrally by the pubic peduncle, and dorsally by the preacetabular process.

The bony acetabulum of *Congosaurus bequaerti*, which can be viewed as a 3D parabola, is mediolaterally deep (i.e. along the coronal plane), similar to *Hyposaurus natator*. The deepest point of the bony acetabulum of *Congosaurus bequaerti* is located near the dorsal peak of the ischial peduncle. In contrast, the bony acetabulum of extant crocodylians appears greatly shallower (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Alligator mississippiensis* [Fig. 74], *Crocodylus niloticus*, *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]). This difference in depth, which is better observed in ventral view (Fig. 74), is not given by the distance between the anterior-most peak of the pubic peduncle and the posterior-most peak of the ischial peduncle, but rather by their relative inclination: in extant crocodylians, both peduncles are mainly oriented laterally, and in *Congosaurus bequaerti* and *Hyposaurus natator* the peduncles appear to be predominantly facing each other. This difference gives extant crocodylian a relatively more open but shallow bony acetabulum, whereas the acetabulum of *Congosaurus bequaerti*, *Hyposaurus natator* and *Acherontisuchus guajiraensis* appears more narrow and deep. This fact is reinforced by the presence of an even more pronounced supraacetabular crest in *Congosaurus bequaerti* and *Hyposaurus natator* than in extant crocodylians (Fig. 74). The significant mediolateral depth and relative anteroposterior narrow appearance of the bony acetabulum in *Congosaurus bequaerti*, *Hyposaurus natator* and *Acherontisuchus guajiraensis* presumably conveys a better bony congruence between the femoral head and the ilium than what is observed in extant crocodylians (Tsai & Holliday 2015; Tsai *et al.* 2019). Similarly, the more prominent attachment sites for the capsular soft tissues on the ilium of *Congosaurus bequaerti* and other dyrosaurids (namely the supraaacetabu-

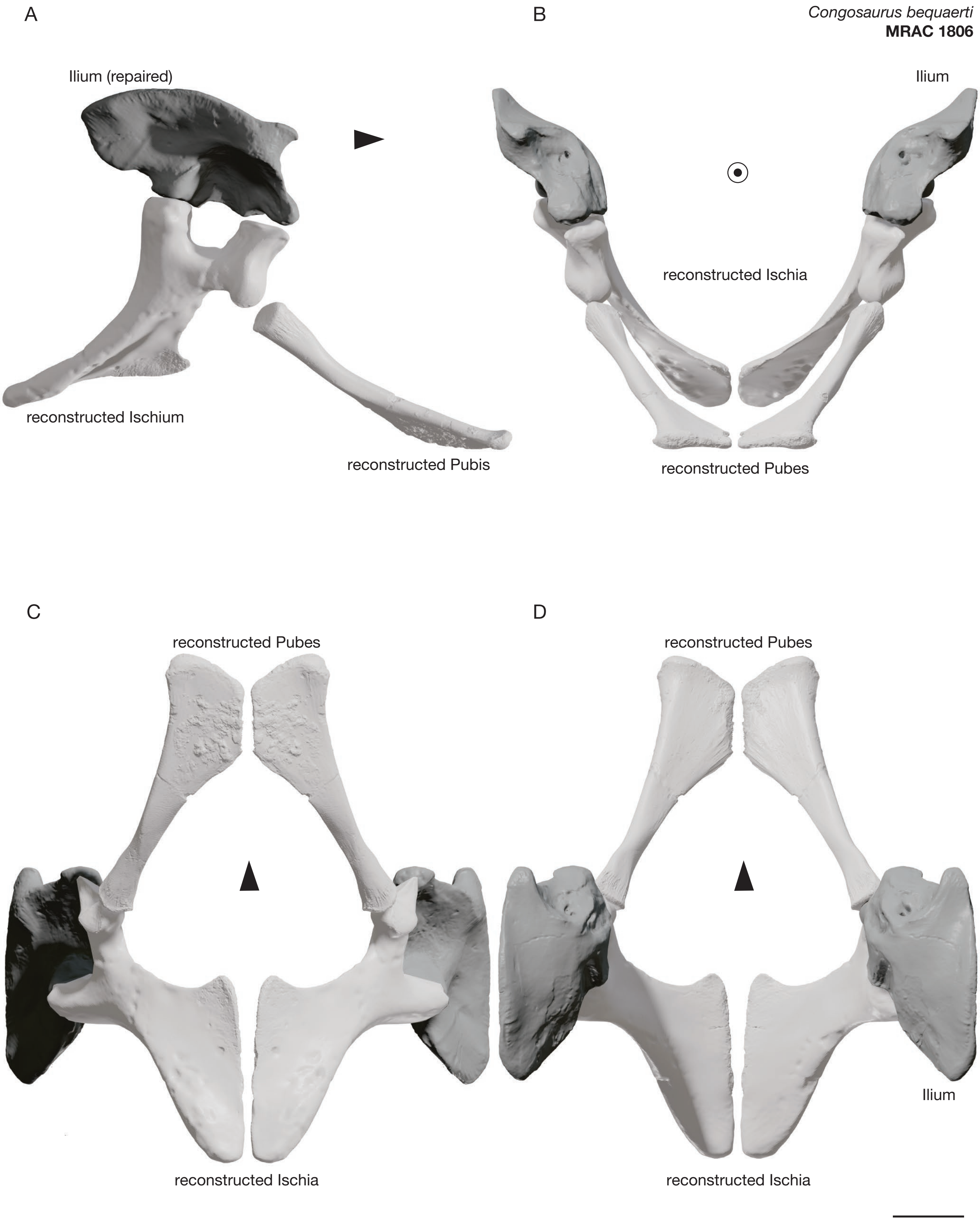


FIG. 73. — Pelvic reconstruction of *Congosaurus bequaerti* Dollo, 1914, MRAC 1806 (holotype); ischium and pubis have been recreated based on those of *Hyposaurus natator* (Troxell, 1925), NJSM 23368; **A**, lateral view; **B**, anterior view; **C**, ventral view; **D**, dorsal view. **Arrow** points anteriorly. **Target** indicates anterior. Original 3D models of NJSM 23368 courtesy of Candice Stefanic. Reconstructed bones only serve as a qualitative representation of the pelvic girdle of *Congosaurus bequaerti*. Scale bar: 5 cm.

lar crest and ischial peduncle) hypothetically helped better border the femoral head (again better bony congruence), so that the articular capsule in *Congosaurus bequaerti* and other dyrosaurids was presumably formed by slightly more calcified elements than what is observed in extant crocodylians. Still, the majority of the caspular articulation was seemingly composed of soft tissues, as the dyrosaurid ilium does not display an actual ball and socket articulation in the way of extant birds (Kuznetsov & Sennikov 2000; Tsai & Holliday 2015) and appears close to extant crocodylians. In parallel, the shape of the crocodylian and *Congosaurus bequaerti* and *Hyposaurus natator* femoral head is slightly different, with the femur of *Congosaurus bequaerti* and *Hyposaurus natator* displaying a rounder outline in dorsal view and a globally thicker head in the dorsoventral direction (visible in anteroposterior views). This larger femoral head could potentially account for the deeper bony acetabulum on the ilium. Besides the depth, the acetabulum of *Congosaurus bequaerti* also covers an extensive area both dorsoventrally and anteroposteriorly (i.e. within the sagittal plane), like the acetabulum of *Hyposaurus natator* and *Lemmysuchus obtusidens*. Comparatively, the acetabulum of *Dyrosaurus maghribensis* appears proportionally larger both dorsoventrally and anteroposteriorly. In comparison, metriorhynchoids differ from *Congosaurus bequaerti* and other dyrosaurids as they display a more limited acetabulum along both the sagittal and coronal planes (e.g. *Tyrannoneustes lythrodectikos*, *Thalattosuchus superciliosus*, *Suchodus durobrivensis*, etc.).

The relative extension (especially the dorsoventral height) of the bony acetabulum and acetabular perforation (see Table 11) differs between *Congosaurus bequaerti* and other dyrosaurids (Fig. 72). Proportionally, the acetabular perforation of *Congosaurus bequaerti* appears limited facing the large bony acetabulum (which reaches about 13 times the height of the acetabular perforation), whereas *Hyposaurus natator* and *Dyrosaurus maghribensis* possesses a more developed acetabular perforation for a shorter bony acetabulum (about 4 times the height of the acetabular perforation). Comparatively, *Acherontisuchus guajiraensis* also displays a short acetabular perforation anteroposteriorly, but the latter forms a greater dorsal indentation than in *Congosaurus bequaerti*. The small size of the acetabular perforation in *Congosaurus bequaerti* could possibly be linked to the relative inclination of the pubic and ischial peduncles (Figs 72; 73), as a similar relation is observed in extant crocodylians (e.g. *Mecistops cataphractus*, *Caiman crocodilus*). Since the hip joint capsule presumably extended as far ventrally as the ischium as in extant crocodylians (Tsai & Holliday 2015; Tsai *et al.* 2019), the relative dorsoventral height of the bony acetabulum and acetabular perforation probably did not impact the size of the hip joint capsule *in vivo* individually. Nevertheless, the dimensions of the acetabular perforation has a direct influence over the potential excursion of the femur, and its sole presence informs on the existence of intrinsic capsular ligaments (Tsai & Holliday 2015). In extant crocodylians, the soft inner wall covering the acetabular perforation acts like a buffer during the femoral excursion, preventing the articular capsule to be sucked in (Kuznetsov & Sennikov 2000). A smaller acetabular perforation could presumably mean that the need for a buffer is lower during a hypothetical high walk posture. It could also potentially imply that the femoral excursion and/or its constraints are somehow less significant than what is observed in extant crocodylians (Kuznetsov & Sennikov 2000; Tsai *et al.* 2019). Yet, the actual acetabular perforation of *Congosaurus bequaerti* was probably greater than what is observed on the ilium solely. Indeed, the ischium of *Congosaurus bequaerti* has not been recovered and presumably largely contributed to the acetabular perforation. In extant crocodylians, the acetabular perforation is concurrently composed by the ilium and the ischium, but only the portion formed by the ilium bears one of the insertion of the *ligamentum capitis femoris* along its margin (Kuznetsov & Sennikov 2000; Tsai & Holliday 2015; Tsai *et al.* 2019). Hence, a difference in height of the acetabular perforation may presumably change the location of the *ligamentum capitis femoris* insertion. This could have an influence on either the length of the ligament, or its insertion on the femoral head, or the relative position of the femur within the joint cavity. In extant crocodylians, this ligament holds the femur during its excursion provoked by the high walk posture (and the initial lack of congruence between the femur and the acetabulum) (Kuznetsov & Sennikov 2000; Tsai *et al.* 2019). It is relatively safe to infer that *Congosaurus bequaerti* and other dyrosaurids possessed intrinsic ligaments as well, which accommodated the movements of the femur during elevated postures. The femoral excursion is an ability inherent to the shape of the femoral head and the shallowness of the bony acetabulum (Kuznetsov & Sennikov 2000; Tsai & Holliday 2015); consistent shapes betraying a lack of congruence between the femur and acetabulum are encountered in the pelvic girdles of *Congosaurus bequaerti* and other dyrosaurids.

Medially, the ilium of *Congosaurus bequaerti* (Fig. 72) bears three distinct indentations indicating the sacral rib attachment sites for the sacral ribs, as in *Acherontisuchus guajiraensis*. These markings are borne directly medially to the pubic and ischial peduncles, and are thus separated by the acetabular perforation. The anterior attachments sites, corresponding to the first sacral, are composed of two elliptic imprints which are fused ventrally. The anterior-most imprint of the first sacral is wide, and extends from the tip of the preacetabular process to the mid-length of the ventral margin of the pubic peduncle. Its concavity is strictly anteriorly oriented so that its peak points posteriorly. The second indentation of the first sacral is directly annexed to the anterior-most imprint, with which it only shares a thin separating wall dorsally. Its elliptic shape is more squeezed, its peak points dorsoposteriorly, and its base is entirely comprised within the remaining half of the ventral margin of the pubic peduncle as it is bordered by the acetabular perforation posteriorly. Posterodorsally to the second attachment site is an oval rugged portion, which presumably molded the shape of the receding posterior part of the second sacral rib (which presumably ensures extra support) like similar shapes in extant crocodylians (e.g. see *Alligator*

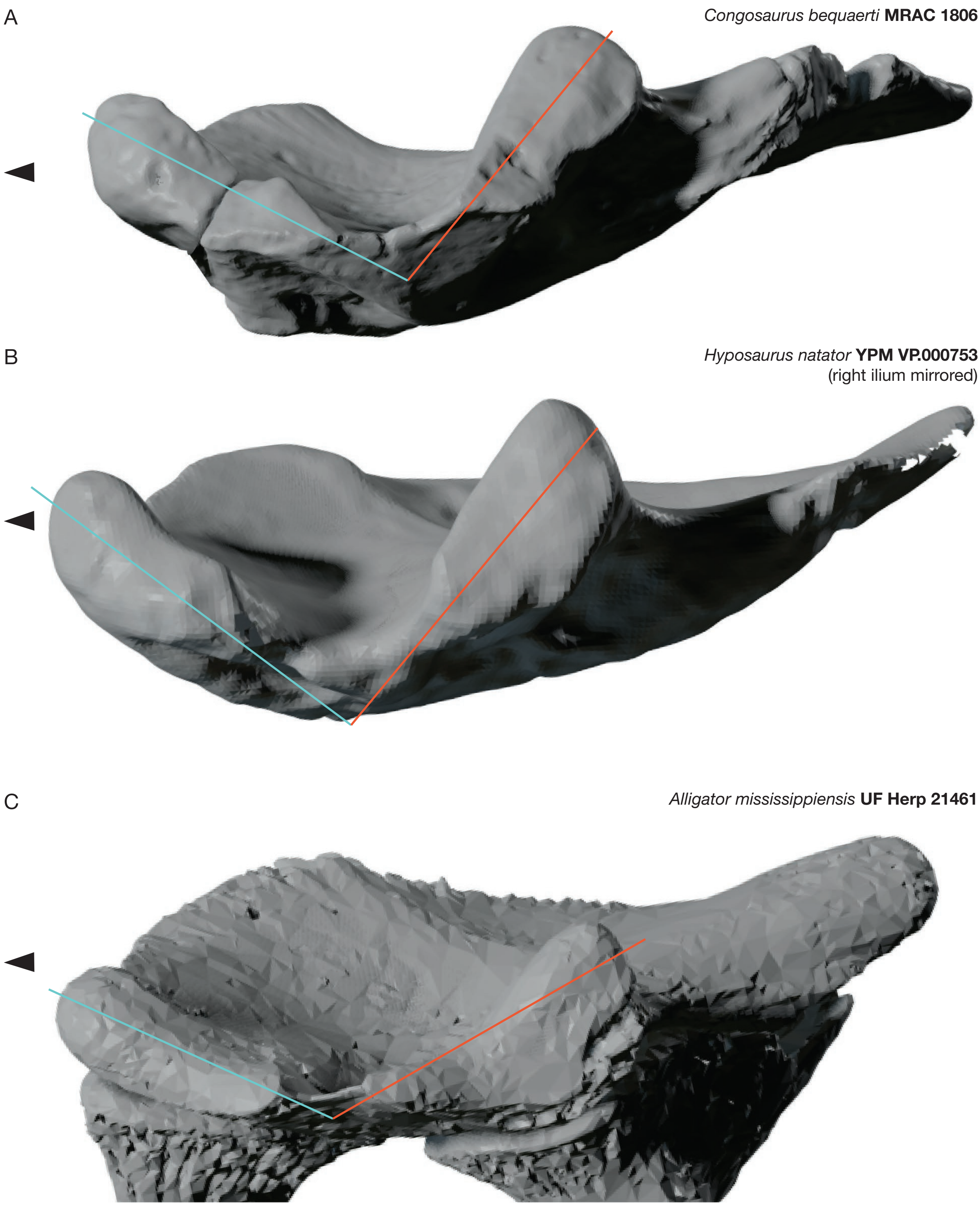


FIG. 74. — Crocodyliformes ilia in ventral view: **A**, left ilium of *Congosaurus bequaerti Dollo, 1914,* MRAC 1806 (holotype); **B**, right ilium of *Hyposaurus natator* (Troxell, 1925), YPM VP.000753 (holotype, mirrored); **C**, right ilium of *Alligator mississippiensis* (Daudin, 1801), UF Herp 21461. **Blue line** corresponds to median of each pubic peduncle; **red line** corresponds to median of each ischial peduncle. The **arrow** points anteriorly. The pubic peduncle of *Congosaurus bequaerti* has been restored. Not to scale.

mississippiensis UF Herp 21461 on Fig. 74). As this part is convex, it probably did not serve as an anchor point. The attachment site for the second sacral appears like the mirrored version of the posterior-most indentation of the first sacral, yet slightly wider. Indeed, the greater axis of both ellipse seems to share about the same length, as well as a similar inclination angle with a 90° difference, so that the peak of the elliptic attachment site belonging to the second sacral points dorsoanteriorly rather than dorsoposteriorly. Ventrally, the attachment site for the second sacral extends from the posterior-most margin of the ischial peduncle to about the ⅔ of its length anteriorly. Around the center of the surface corresponding to the attachment site for the second sacral, there is a shallow isolated ridge, which is not connected to either the ventral margin of the ilium nor the dorsal margin of the attachment site. Looking at this area from a ventral view of the ilium reveals that the ridge actually defines the junction between two slightly different portions of the second attachment site: indeed, the posterior half is slightly more medially driven (i.e. deeper) than the anterior half making them appearance like a pair of steps. This difference in depths within the posterior attachment site reflects the existence of a minor subdivision in the ending of the second sacral rib. Nevertheless, the ridge does not define partially nor completely distinct elliptic indentations as only one summit is present for this attachment site, which contrasts with *Hyposaurus natator* and *Dyrosaurus maghribensis*. Despite this, the depth of the sacral rib attachment sites is relatively similar throughout the ilium. Undoubtedly, the depth of the sacral rib attachment sites forms one of the typical dyrosaurid features; in this way, dyrosaurid ilia differ from those of extant crocodylians and thalattosuchians.

In *Congosaurus bequaerti*, the relatively small size of the posterior attachment site compared to the anterior one implies that the contribution of the first sacral in holding the pelvic girdle exceeded that of the second one (Fig. 72), similar to what is observed in *Dyrosaurus maghribensis* Jouve *et al.* (2006). Conversely, the contribution of each sacral rib appears to have been slightly more balanced for *Hyposaurus natator* and *Acherontisuchus guajiraensis*. In extant crocodylians the relation is inverted as the posterior attachment site (for the second sacral) is greater than the anterior one (e.g. *Mecistops cataphractus* [Fig. 8] and *Caiman crocodilus* [Fig. 9]). This dissimilarity between both *Congosaurus bequaerti* and *Hyposaurus natator* could be explained by the distinct orientation of their peduncles: the inclination angle between the peduncles of *Congosaurus bequaerti* possibly conveys a slightly different orientation of the whole ilium compared to that of *Hyposaurus natator*. A different adjustment of the ilium potentially impacted the transmission of load from the limbs, and thereby required differing anchor sites. The dissimilarity could also be caused by the general position of the ilium relatively to the axial skeleton: in *Alligator mississippiensis* (Fig. 74) the ilium is shifted posteriorly compared to the centre of the sacral region, so that it is the second sacral that supports most of the ilium; in *Palaeosuchus palpebrosus* (Fig. 7) the ilium is shifted anteriorly and thereby the opposite relation is observed where the first sacral bears most of the weight. In *Palaeosuchus palpebrosus* (Fig. 7), two conditions are observed with the left ilium being supported by three processes (the two sacrals plus the first caudal), whereas in the right ilium the sacral ribs cover almost the entirety of the sacral rib attachment sites, leaving very little to no room for the lateral process of the first caudal.

DISCUSSION

Organization of the pelvic area and locomotive implications

The pelvic girdle of thalattosuchians (Figs 75-79) is located further ventrally than in crocodylians (Fraas 1902) or dyrosaurids (Figs 81; 82), which gives thalattosuchians a more rounded cross-section at the pelvic area (Figs 84; 85). This effect is even more pronounced in metriorhynchoids compared to teleosauroids (Fig. 84) due to their difference in sacral rib length (Figs 87-89). Yet, the inclination of the sacral ribs in relation to the coronal plane appears relatively constant (average angle between 40° and 55° with the coronal plane) within Thalattosuchia (e.g. *Lemmysuchus obtusidens* and *Suchodus durobrivensis*, Fig. 84). The relative inclination of the sacral rib is measured through the angle formed between the coronal plane and a line running along the middle of the sacral rib. Due to the deformation in several specimens, the values presented are averaged and only bear a qualitative sense as they help represent the relative positioning of the pelvic girdle.

In Thalattosuchia, the relative lengthening of the sacral ribs increases the space available in the abdominal cavity by placing the pelvic girdle more ventrally (especially in metriorhynchoids). The latter is composed of completely interlocking ischia along their distal blade, turning it into a stiff ventral shield resembling the pelvic girdle of plesiosaurians (Fraas 1902; Williston 1908; Andrews 1913; Krahl 2021). For this reason, increasing the abdominal area can only be achieved through the deflection of the entire pelvic girdle ventrally, or with an enlargement of the pelvic elements. The long sacral ribs in Thalattosuchia gives them a relatively wide but also circular cross section at the pelvic area (especially in metriorhynchoids). For those taxa displaying large sacral ribs, the constriction of the body marking the junction between the trunk and the pelvic area was presumably less abrupt than what is observed in extant crocodylians (Grigg & Kirshner 2015). Moreover, in extreme pelagic forms (e.g. *Rhacheosaurus gracilis* [Fig. 83], *Cricosaurus suevicus* [Fig. 19)], *Cricosaurus albersdoerferi* [Fig. 20]) the relative size and shape of the thoracic and sacral ribs turns the entire trunk into a compact cylinder. The interspecific variability in the sacral rib dimensions within Thalattosuchia does not excessively alter the shape of the ilium and ischium within each superfamily (i.e. Metriorhynchoidea and Teleosauroidea; Fig. 86). However, the overall shape of the pubis fluctuates more clearly within Thalattosuchia, and could be linked to the sacral rib expansion. Naturally, there are several ways to connect both pubes medially, and each influence the overall shape of the pubic apron through the length and orientation of the pubic symphysis. The latter is notably shaped by the length of the pubic shaft and the spacing between each ischium (given by the sacral rib dimensions), thus operating as constraints as well. Hence, the entire shape of the pubis of extinct crocodyliforms (Figs 85; 87; 88) gives an insight into the overall architecture of their pelvic girdle such as its sectional width and the available space in the abdomen. The relative size of the pubic symphysis to the length of the bone is a strong anatomical constraint, regardless of the potential mobility of the bone.

Some teleosauroids show shorter and stouter sacral ribs (e.g. *Lemmysuchus obtusidens, Macrospondylus bollensis* [Fig. 84]) that somewhat resemble those of dyrosaurids and crocodylians; as a result, the teleosauroid ilium is placed more laterally, as opposed to a more ventral placement in metriorhynchoids. Also, the teleosauroid sacral ribs convey the relative inclination of the ilium laterally, not unlike what is observed in dyrosaurids. Such differences between Metriorhynchoidea and Teleosauroidea reflects their ability to support and carry their own weight on land.

Dyrosauridae instead exhibits sacral rib lengths and inclinations similar to Crocodylia, so that their ilium is also borne on the same level as the vertebral centra (i.e. horizontal). In comparison, the terrestrial mesoeucrocodylians *Araripesuchus tsangatsangana* Turner 2006, and *Yacarerani boliviensis* Novas, Pais, Pol, Carvalho, Scanferla, Mones & Suarez Riglos, 2009 display relatively short and horizontal sacral ribs (Turner 2006; Leardi *et al.* 2015), similar to what is observed in Crocodylia and Dyrosauridae. However the sacral ribs of *Simosuchus clarki* Buckley, Brochu, Krause & Pol, 2000, another terrestrial mesoeucrocodylian, appear relatively long compared to the size of their centrum (Sertich & Groenke 2010). In the potentially cursorial baurusuchids *Stratiotosuchus maxhechti* Campos, Suarez, Riff & Kellner, 2001 and *Baurusuchus albertoi* Nascimento & Zaher, 2010, the ilium is positioned dorsally to the sacral vertebra centra, and is anchored by three ribs (Nascimento & Zaher 2010; Riff & Kellner 2011).

In Thalattosuchia, the sacral rib attachment sites are adjacent and share a margin mesially, whereas the sacral rib attachment sites of extant crocodylians and dyrosaurids are fully separated and placed near the anterior and posterior margins of the bone. We hypothesise that the second configuration provides more stability to the girdle for terrestrial locomotion. Indeed, this type of configuration is also found in several terrestrial mesoeucrocodylians (e.g. *Araripesuchus tsangatsangana* (Turner 2006), *Simosuchus clarki* [Sertich & Groenke 2010], *Pissarrachampsa sera* Montefeltro, Larsson & Langer, 2011 [Godoy *et al.* 2016], *Sebecus icaeorhinus* Simpson, 1937 [Pol *et al.* 2012]). The latter, however, is peculiar in displaying a postacetabular process free of any anchoring site for the sacral ribs (Pol *et al.* 2012).

Within Thalattosuchia, metriorhynchoids (Figs 13; 14; 17; 24; 28; 32) bear the sacral rib attachment sites of their ilium near the dorsal border of the bone as opposed to the more centred ones of teleosauroids (Figs 48; 54; 59), extant crocodylians (Fig. 8), and dyrosaurids (Figs 64; 67; 69; 72). Yet, the exact position and orientation of these sacral rib attachment sites vary across metriorhynchoids (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 [Fig. 24], *Suchodus durobrivensis* [Fig. 28], *Thalattosuchus superciliosus* [Figs 13; 14], *Dakosaurus maximus* [Fig. 32]) which results in differing orientation of the ilium (and the whole pelvic girdle) among metriorhynchoids *contra* extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7]; *Mecistops cataphractus* [Fig. 8]; *Caiman crocodilus* [Fig. 9]).

Presumably, the relative position of the sacral rib attachment sites on the ilium varied according to the relative length of the sacral ribs, so that the taxa bearing the greatest sacral ribs also displayed the most titled ilia in relation to the coronal plane (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763 [Fig. 22], *Thalattosuchus superciliosus* [Figs 13; 14], *Cricosaurus suevicus* [Fig. 19], *Dakosaurus maximus* [Fig. 32]). Accordingly, the different inclination of their ilium compared to other metriorhynchoids (e.g. *Suchodus durobrivensis* [Fig. 28]) potentially impacted the length and action of certain muscles which could have lead to slightly different capacities for their hindlimbs. In turn, the metriorhynchoid orientation of the pelvic girdle may have influenced the hindlimb soft tissue anatomy, or at least the function of each muscle in a presumably constant muscular architecture throughout the clade. Extant crocodylians all possess a similar musculoskeletal anatomy, yet many differences arise in the exact position, constitution or function of each muscle, with some even unrepresented across clades (Otero *et al.* 2010).

Thalattosuchians display an overall reduced acetabular perforation on their pelvic girdle (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 3804 [Fig. 24], *Thalattosuchus superciliosus* [Fig. 13], *Cricosaurus araucanensis* [Fig. 17], *Lemmysuchus obtusidens* [Fig. 59], *Neosteneosaurus edwardsi* [Fig. 53], etc.) compared to extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8]) and dyrosaurids (e.g. *Hyposaurus natator* [Figs 66; 67], *Acherontisuchus guajiraensis* [Fig. 70]). In thalattosuchians, the acetabular perforation is almost exclusively borne by the ischium whereas the ilium possesses a greater share in the acetabular perforation in extant crocodylians and dyrosaurids. In Metriorhynchoidea, derived members appear to have an overall modified shape of their peduncle bridge, creating larger acetabular perforation (with the exception of *Thalattosuchus superciliosus* [Fig. 13]). Still, the acetabular perforation of metriorhynchoids remains smaller than that of teleosauroids. In comparison, the ilium of the mesoeucrocodylians *Mahajangasuchus insignis* Buckley & Brochu, 1999, *Araripesuchus tsangatsangana* and *Sebecus icaeorhinus* also shows a shallow acetabular perforation similar to most teleosauroids (and also *Congosaurus bequaerti*) (Buckley & Brochu 1999; Turner 2006; Pol *et al.* 2012), whereas the eusuchian *Allodaposuchus palustris* Blanco, Puértolas-Pascual, Marmi, Vila & Sellés, 2014 displays a relatively larger one, closer to modern crocodylians (Blanco *et al.* 2014). However, the overall size of the acetabular perforation in the semi-aquatic mesoeucrocodylian *Mahajangasuchus insignis* and the terrestrial mesoeucrocodylians *Araripesuchus tsangatsangana*, *Sebecus icaeorhinus*, *Yacarerani boliviensis* Novas, Pais, Pol, Carvalho, Scanferla, Mones & Suárez Riglos, 2009, *Pissarrachampsa sera* Montefeltro, Larsson & Langer, 2011, *Stratiotosuchus maxhechti* Campos, Suárez, Riff & Kellner, 2001 is markedly larger than what is observed in metriorhynchoids and most teleosauroids (Buckley & Brochu 1999; Turner 2006; Riff & Kellner 2011; Pol *et al.* 2012; Leardi *et al.* 2015; Godoy *et al.* 2016). This is due to the large and hemispherical acetabular perforation borne by their ischia, which resembles what is observed in *Hyposaurus natator* and *Dyrosaurus maghribensis*.

The existence of an acetabular perforation has been hypothesized as a correlate for a vertically positioned femur (Nesbitt

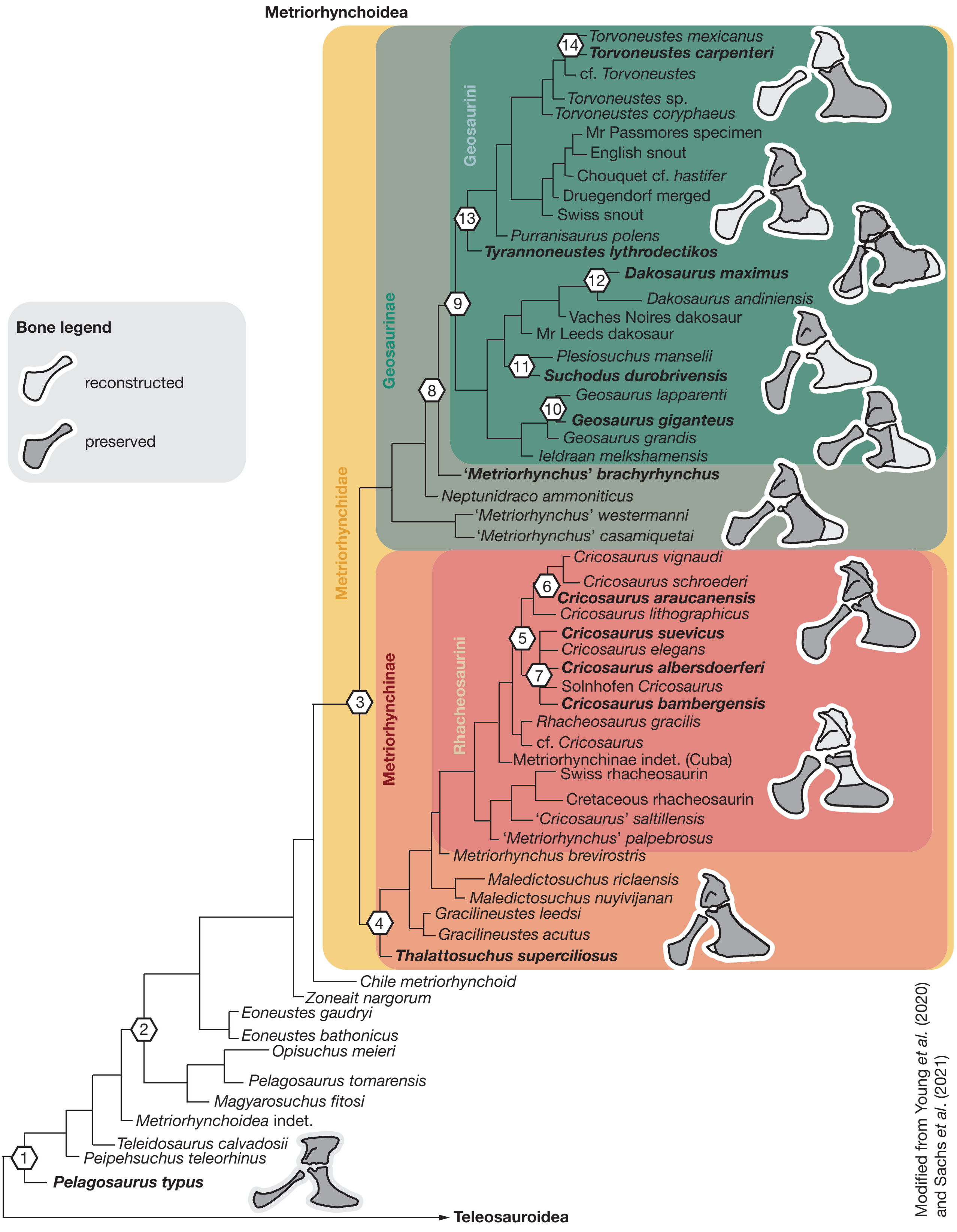
2011), but this perforation is present in extant crocodylians (Tsai & Holliday 2015). According to Tsai & Holliday (2015), the existence of an acetabular perforation is rather osteological evidence for the presence of intrinsic ligaments (i.e. ligaments fused to the articular capsule of the hip and found within the synovial cavity, like the anterior and posterior *ligamentum capitis*). In Thalattosuchia, the presence of a reduced acetabular perforation presumably reflects their terrestrial ancestry, and suggests that thalattosuchians possessed joint ligaments and presumably a hip joint architecture similar to extant crocodylians. These ligaments are known to reduce bone excursion, like the range of movements of the femur (*ligamentum capitis*), to prevent structural damage and are also closely linked to the environment and lifestyle of the animal (Tsai & Holliday 2015). Still, the hip of Crocodylia is known to display high flexibility (Reilly & Elias 1998; Grigg & Kirshner 2015; Tsai & Holliday 2015), notably achieved through an intricate array of ligaments and cartilaginous structures (Tsai & Holliday 2015). This complexity is thought to come from the acquisition of sprawling posture from erect ancestors (Tsai & Holliday 2015). Following this, Thalattosuchia presumably showed an important range of motion at the hip joint as well (due to its mostly cartilaginous articulation). In Metriorhynchidea (excluding basal members), the reduction of the ilium happened at the expense of the acetabular perforation and postacetabular process seemingly in order to retain the parts involved in the hip articulation. This presumably reflects the need to preserve a certain mobility for the hindlimbs in highly aquatic members of Metriorhynchoidea, either for active aquatic locomotion (e.g. for paraxial swimming, like rowing or underwater flight (Gutarra & Rahman 2022)), or even simply for steering.

The reduced acetabular perforation of Thalattosuchia may have potentially impacted their locomotion; the small size of the acetabular perforation leaves room for a small membrane covering it which, in turn, presumably offered limited accommodation of the femoral movements relative to Crocodylia (Tsai & Holliday 2015). It is possible that the femoral excursion was slightly different in Thalattosuchia compared to Crocodylia and thus did not provoke a modification of the shape of the articular capsule that would require to be compensated much with the membrane. The relative increase in size of the acetabular perforation in derived metriorhynchoids conveys the idea of a potentially increased range of movement of the femur (and hypothetical prevention of excursion). The larger acetabular perforation of teleosauroids within Thalattosuchia presumably reflects their relative terrestriality compared to metriorhynchoids (along with other traits such as the postacetabular process and shorter sacral ribs). Within Teleosauroidea, the aeolodontine *Sericodon jugleri* and the machimosaurids (e.g. *Macrospondylus bollensis* and *Charitomenosuchus leedsi*) appear to have developed a larger acetabular perforation, presumably to better accommodate the movements of the femur during locomotion (Figs 78; 79). In this regard, the large acetabular perforation of dyrosaurids presumably offered a great accommodation of the femoral movements similar to Crocodylia (Tsai & Holliday 2015).

MUSCULATURE AND HEPATIC PUMP

It is a general trend in fully aquatic tetrapods to reduce the size of their girdles dorsally due to the reduction of gravitational force on the body (Krahl 2021), especially if the main propulsive mode does not require the extensive use of limbs to carry their weight (Carroll 1997; Krahl 2021). Likewise, thalattosuchians, and more specifically metriorhynchoids, show a considerable reduction of their dorsal girdles (i.e. in the size of the ilium and scapula). The limbs alone are also severely affected in Thalattosuchia, with a global shortening of the whole forelimb and a relative lengthening of the hindlimb due to a proportionally long femur (Fraas 1902; Andrews 1913; Motani & Vermeij 2021; Johnson *et al.* 2023). Given that the pelvic girdle of fossil crocodyliforms is closer to extant crocodylians than birds or lizards (Tsai & Holliday 2015), it is possible that metriorhynchoids possessed a similar muscle and soft tissue architecture filling comparable functions to that of Crocodylia (Fig. 90). As mentioned above, the reduction of the pelvic girdle in metriorhynchoid thalattosuchians is mostly achieved through the downsizing of the ilium. With the constraint to preserve the parts involved in the hip articulation (i.e. the acetabulum and peduncles), the ilium essentially reduced the postacetabular process and the acetabular perforation. The consequences are a smaller and shallower acetabular perforation (which is mainly represented on the medial side of the ischium in most thalattosuchians), as well as a loss of anchoring surface for muscles. This presumably entails a relatively more cartilaginous hip capsule, a decline in the possible range of motion for the femur, and a reduction of potential articular movements through the weakening of muscle architecture. Indeed, in extant crocodylians, the postacetabular process bears laterally muscles connecting the ilium to the limbs and tail, including: *M. coccygeo-femoralis/caudofemoralis brevis, M. iliotibialis 3, M. iliofibularis, M. femorotibialis externus, M. ilio-ischio-caudalis, M. flexor tibialis internus 2* see Table 4 and fig. 90 (Romer 1923; Otero *et al.* 2010; Allen *et al.* 2014). Those muscles allow for abduction, adduction, flexion and extension movements of the hindlimbs (Romer 1923; Allen *et al.* 2014). On the medial side of the postacetabular process, dorsal muscles attach the ilium to dorsal vertebrae (Romer 1923). Hence, a reduction in the size of the postacetabular process in metriorhynchoids likely forces a decrease in the size and/or number of muscles attached on the ilium. As thalattosuchians still possess a relatively long femur, limb muscles potentially comprised long fascicles, even if the muscle density was lower throughout the pelvic girdle. Thereby, the decrease in size of the ilium presumably had a direct impact on limb movements, potentially reducing their strength and/or rapidity of execution compared to extant crocodylians (Allen *et al.* 2014). This mirrors the presumed inability for metriorhynchoids to carry their weight on solid ground (Herrera *et al.* 2017).

In comparison, the ilium of terrestrial and semi-aquatic mesoeucrocodylians invariably displays a long postacetabular process, whose shape and orientation fluctuates (e.g. *Mahajangasuchus insignis* (Buckley & Brochu 1999), *Notosuchus terrestris* (Fiorelli & Calvo 2008), *Sebecus icaeorhinus* (Pol *et al.* 2012),



Modified from Young *et al.* (2020) and Sachs *et al.* (2021)

Fig. 75. — Phylogeny of Metriorhynchoidea (Part 1). Figure modified from Young *et al.* (2020b) for the global phylogeny; relationships of *Cricosaurus suevicus* (Fraas, 1901), *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021) and *Cricosaurus bambergensis* (Sachs, Young, Abel & Mallison, 2019) modified from Sachs *et al.* (2021).

1 - [Ilium] Short and slender postacetabular process
- [Ilium] Long and slender preacetabular process
- [Ilium] Preacetabular process and iliac crest in line
- [Ilium] Large bony acetabulum
- [Ilium] Large acetabular perforation separating peduncles
- [Ilium] Large pubic peduncle and reduced ischial peduncle
- [Ilium] Two attachments sites centered on medial surface
- [Ischium] Large acetabular perforation oriented mediolaterally
- [Ischium] Long and slender distal blade
- [Ischium] Long and slender ischial shaft
- [Ischium] Reduced anterior peduncle
- [Ischium] Distal blades connect at angle >> 90°
- [Pubis] Long and slender pubis with short shaft
- [Pubis] Slightly concave pubic apron
- [Pubis] Short pubic symphysis (subsequent triangular pubic apron)

2 - [Ilium] Reduction of postacetabular process
- [Ischium] Anteriorposterior widening of shaft
- [Pubis] Overall shortening
- [Pubis] Widening of pubic apron
- [Pubis] Presumed increase of pubic symphysis

3 - [Ilium] Reduction of acetabular perforation
- [Ilium] Continous surface uniting both peduncles laterally
- [Ilium] Enlargment of ischial peduncle
- [Ilium] Loss of postacetabular process
- [Ilium] Inclination of preacetabular process
- [Ilium] Dorsal migration of attachment sites on medial surface
- [Ischium] Dorsoventral widening of distal blade
- [Ischium] Dorsoventral shortening and anteroposterior widening of shaft
- [Ischium] Reduction and medial inclination of acetabular perforation
- [Ischium] Distal blades connect at reduced angle ~90°
- [Pubis] Overall shortening of pubis
- [Pubis] Increase of pubic symphysis
- [Pubis] Angle between pubic symphysis and median of shaft ~40°
- [Pubis] Angle between pubic symphysis and distal blade ~120°

4 - [Ilium] Short, arched and strongly pitted supraacetabular crest
- [Ilium] Acetabular perforation forms a notch
- [Ilium] Attachments sites form deep prints
- [Ilium] Mediolaterally wide and dorsoventrally thin preacetabular process
- [Ilium] Dorsal and posterior margins form a protruding corner
- [Ischium] Anterior process (hook) is pointed and dorsally oriented

5 - [Ilium] Lengthening of preacetabular process (presumed)
- [Ilium] Widening of bony acetabulum (presumed)
- [Ilium] Posterior expansion of supraacetabular crest (presumed)
- [Ilium] Further reduction of dorsal margin of ilium (presumed)
- [Ilium] Dorsal migration of attachment sites (protrude over dorsal margin)
- [Ischium] Enlargement of anterior peduncle
- [Ischium] Anteroposterior thinning of shaft constriction
- [Ischium] Anterior and posterior processes in line with distal blade
- [Ischium] Further dorsoventral widening of distal blade
- [Pubis] Mediolateral widening of pubic apron
- [Pubis] Shortening of shaft proximodistally
- [Pubis] Widening of shaft and peduncle mediolaterally
- [Pubis] Increase of angle between pubic symphysis and distal blade ~140°

6 - [Ischium] Reduction of anterior process (hook)
- [Ischium] Further widening of distal blade (and posterior process)
- [Pubis] Further widening of pubic apron
- [Pubis] Further increase of pubic symphysis

7 - [Pubis] Reduction of pubic symphysis

Fig. 76. — Phylogeny of Metriorhynchoidea (Part 2). Figure modified from Young *et al.* (2020b) for the global phylogeny; relationships of *Cricosaurus suevicus* (Fraas, 1901), *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021) and *Cricosaurus bambergensis* (Sachs, Young, Abel & Mallison, 2019) modified from Sachs *et al.* (2021). Color alternating for readability.

8
- [Ilium] Lengthening of preacetabular process
- [Ilium] Attachment sites form bilobate protruding relief
- [Ilium] Shortening of dorsal margin of ilium
- [Ilium] Bony acetabulum is deeper with laterally hunched ilium
- [Ilium] Further reduction of acetabular perforation
- [Ischium] Anteroposterior thinning of shaft constriction
- [Ischium] Medial curvature of peduncle bridge
- [Ischium] Further reduction of anterior peduncle
- [Ischium] Lengthening of anterior and posterior processes
- [Ischium] Further reduction of acetabular perforation
- [Pubis] Increase of pubic symphysis (presumed)
- [Pubis] Shortening of shaft (presumed)

9
- [Ilium] Further reduction of acetabular perforation
- [Ilium] Reduction of preacetabular process
- [Ilium] Increase of dorsal margin of ilium
- [Ilium] Attachment sites form large bilobate imprints
- [Ilium] Reduction of ischial peduncle
- [Ischium] Anteroposterior widening of shaft constriction
- [Pubis] Mediolateral narrowing of peduncle

10
- [Ilium] Further reduction of acetabular perforation and preacetabular process
- [Ilium] Dorsal and ventral margins of ilium parallel
- [Ischium] Widening of peduncle bridge
- [Ischium] Shortening of anterior process (hook)
- [Pubis] Strong reduction of pubic diaphysis
- [Pubis] Widening of pubic peduncle

11
- [Ilium] Widening of preacetabular process
- [Ilium] Attachment sites form shallow bilobate scars
- [Ilium] Ventral margin of ilium strongly undulating:
  pubic peduncle is convex whereas ischial peduncle is concave
- [Ilium] Dorsal and posterior margins form a protruding corner
- [Pubis] Widening of pubic peduncle and strong constriction of shaft
- [Pubis] Narrowing of pubic apron
- [Pubis] Angle between pubic symphysis and distal blade ~145°
- [Pubis] Angle between pubic symphysis and median of shaft ~30°

12
- [Ischium] Further widening of distal blade
- [Ischium] Development of posterior corner between shaft and posterior process
- [Pubis] Widening of pubic apron

13
- [Ilium] Widening of preacetabular process
- [Ilium] Ventral margin of ilium strongly undulating:
  pubic peduncle is convex whereas ischial peduncle is concave
- [Ilium] Attachment sites form shallow scars ventrally and deeper indentations dorsally
- [Ilium] Dorsal and posterior margins form a protruding corner
- [Ischium] Further widening of peduncle bridge
- [Ischium] Further widening of shaft
- [Ischium] Reduction of posterior peduncle mediolateral width
- [Pubis] Buldging of distal margin and development of lateral protuberance
- [Pubis] Angle between pubic symphysis and distal blade ~110°
- [Pubis] Angle between pubic symphysis and median of shaft ~35°

14
- [Ischium] Long and slender shaft
- [Ischium] Strong widening of posterior process of distal blade
- [Ischium] Development of posterior corner between shaft and posterior process
- [Ischium] Strong thinning and enlargement of anterior process (hook) of distal blade
- [Ischium] Strong thinning and enlargement of peduncle bridge
- [Ischium] Strong enlargement of acetabular perforation
- [Ischium] Reorientation mediolaterally of acetabular perforation

Fig. 77. — Phylogeny of Metriorhynchoidea (Part 3). Figure modified from Young *et al.* (2020b) for the global phylogeny; relationships of *Cricosaurus suevicus* (Fraas, 1901), *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021) and *Cricosaurus bambergensis* (Sachs, Young, Abel & Mallison, 2019) modified from Sachs *et al.* (2021). Color alternating for readability.

Pissarrachampsa sera (Godoy *et al.* 2016), *Araripesuchus tsangatsangana* (Turner 2006), *Baurusuchus albertoi* (Nascimento & Zaher 2010), *Stratiotosuchus maxhechti* (Riff & Kellner 2011)).

The preacetabular process of terrestrial mesoeucrocodylians is relatively short and thick (e.g. *Sebecus icaeorhinus* (Pol *et al.* 2012), *Araripesuchus tsangatsangana* (Turner 2006), *Baurusuchus*

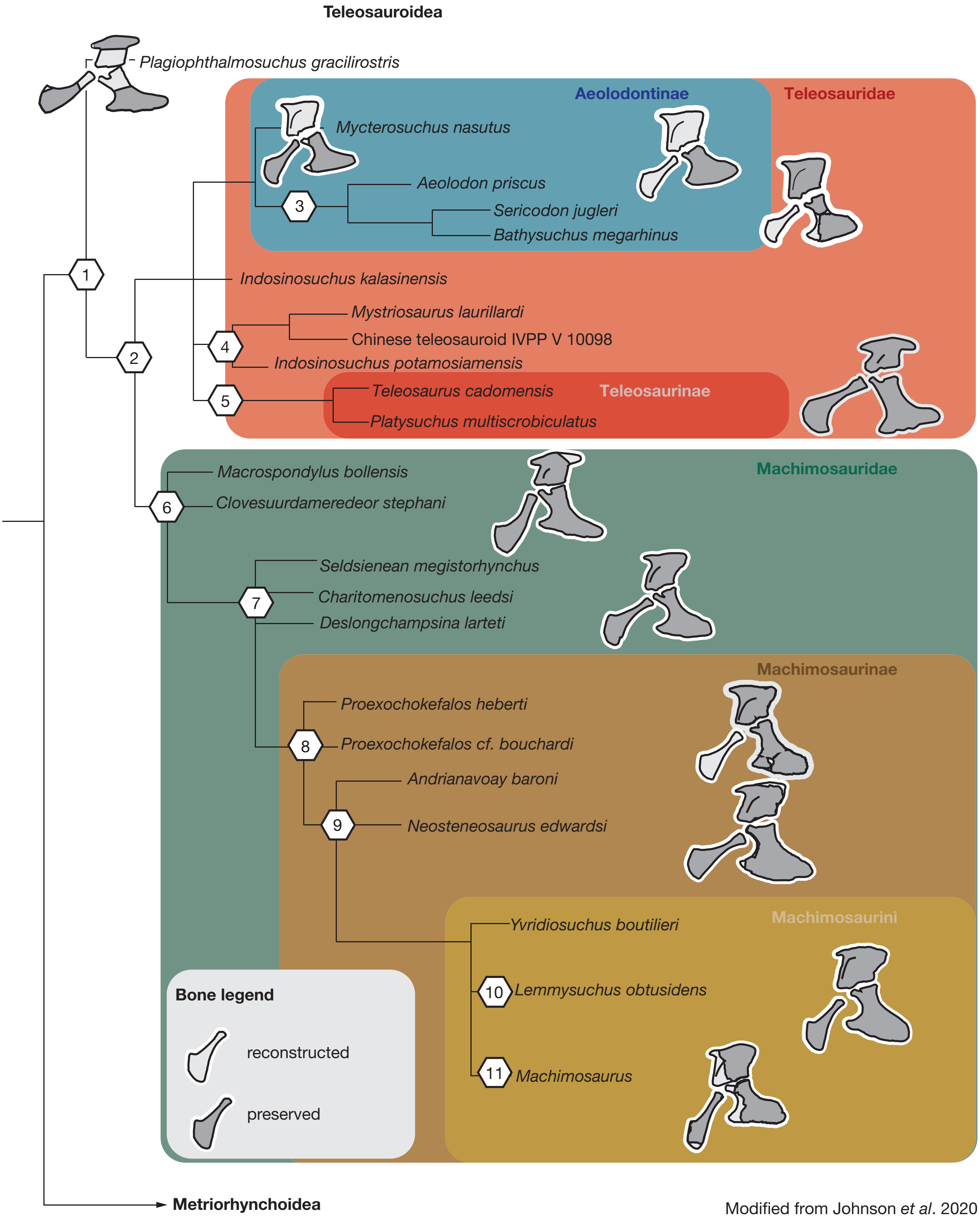


Fig. 78. — Phylogeny of Teleosauroidea (Part 1). Numbers highlight acquisition of morphologies based on our morphological observations. Figure modified from Johnson *et al.* (2020).

albertoi (Nascimento & Zaher 2010)), as in dyrosaurids and as opposed to most thalattosuchians. Still, the most remarkable feature of the ilium of terrestrial mesoeucrocodylians is the presence of a medially deep bony acetabulum, dorsally covered by a laterally prominent supraacetabular crest which forms a ‘roof’ (e.g. *Notosuchus terrestris* (Fiorelli & Calvo

1

- [Ilium] Short and slender postacetabular process
- [Ilium] Preacetabular process and iliac crest in line
- [Ilium] Large bony acetabulum
- [Ilium] Two attachments sites centered on medial surface (presumed)
- [Ischium] Acetabular perforation laterally obstructed
- [Ischium] Flat distal blade of ischium
- [Ischium] Long and slender posterior process
- [Ischium] Slender anterior process (hook) in line with posterior process
- [Pubis] Long pubic diaphysis (1/3 of total length)
- [Pubis] 150° angle pubic symphysis - distal blade
- [Pubis] Strongly concave pubic apron
- [Pubis] 27°-30° angle shaft - pubic symphysis

2

- [Ilium] Nonalignment of preacetabular process and iliac crest
- [Ilium] Development of a mediolaterally thick preacetabular process
- [Ischium] Slender shaft (anteroposteriorly thin and dorsoventrally long)
- [Ischium] Orientation of anterior process is anterodorsal
- [Pubis] Thin shaft (mediolaterally) shorter than the proximal peduncle
- [Pubis] Development of lateral protuberance

3

- [Ilium] Dorsoventral widening of postacetabular process
- [Ilium] Enlargement of acetabular perforation
- [Ischium] Shaft becomes thicker anteroposteriorly than dorsoventrally
- [Ischium] Thick posterior process on ischium
- [Ischium] Thick and short anterior process on ischium

4

- [Ilium] Development of an elongated and slender precetabular process
- [Ischium] Strong shaft constriction
- [Ischium] Short and sharp posterior process
- [Ischium] Elongated and slender anterior process
- [Ischium] Elongated and slender peduncle bridge
- [Ischium] Enlargement of acetabular perforation + no lateral osbstruction

5

- [Ilium] Lengthening of already slender postacetabular process
- [Ilium] Lengthening of already thick preacetabular process
- [Ilium] Alignment of preacetabular process and iliac crest
- [Ischium] Lengthening of already slender shaft (dorsoventrally longer than anteroposteriorly)
- [Ischium] Shortening of anterior process (P*latysuchus multiscrobiculatus*)
- [Ischium] Anterior process in line with posterior process (*Platysuchus multiscrobiculatus*)
- [Pubis] Widening of pubic apron and shortening of proximal peduncle (*Platysuchus multiscrobiculatus*)

6

- [Ischium] Enlargement of acetabular perforation + no lateral osbstruction
- [Ischium] Lengthening of shaft (equally long anteroposteriorly and dorsoventrally)
- [Pubis] Reduction of pubic diaphysis (<< 1/3 of total length)
- [Pubis] Reduction of pubic apron (and loss of lateral protuberance)
- [Pubis] Strong thinning of shaft constriction and enlargement of proximal peduncle

7

- [Ilium] Anterior inclination of ilium
- [Ilium] Dorsoventral and mediolateral thinning of already long preacetabular process
- [Ilium] Deep scars for attachment sites
- [Ilium] Dorsoventral widening of postacetabular process (still long and relatively slender)
- [Ilium] Convex anterior margin of ilium due to supraacetabular crest (to accommodate acetabulum?)
- [Ilium] Nonalignment of preacetabular process and iliac crest
- [Ischium] Dorsoventral lengthening and anteroposterior thinning of shaft
- [Ischium] Bowing of distal blade (convex)
- [Ischium] Broadening of posterior process
- [Pubis] Reduction of pubic shaft to 1/4 of total length
- [Pubis] Relative thickening of shaft constriction and slimming of proximal peduncle
- [Pubis] Lengthening of pubic symphysis (1/3 of total length)

Fig. 79. — Phylogeny of Teleosauroidea (Part 2). Numbers highlight acquisition of morphologies based on our morphological observations. Color alternating for readability.

2008), *Sebecus icaeorhinus* (Pol *et al.* 2012), *Pissarrachampsa sera* (Godoy *et al.* 2016), *Baurusuchus albertoi* (Nascimento & Zaher 2010), *Stratiotosuchus maxhechti* (Riff & Kellner 2011)).

The hypertrophied supraacetabular crest enables the femur to produce large retraction and protraction movements (Riff & Kellner 2011).

8
- [Ilium] Dorsoventral enlargement of the preacetabular process at its base
- [Ilium] Postacetabular process reduces in size
- [Ischium] Slender and elongated shaft, with overall dorsoventral stretching of ischium
- [Ischium] Anterior and posterior peduncles reduce in overall size
- [Ischium] Shortening of anterior process
- [Ischium] Dorsoventral widening of posterior process extremity

9
- [Ilium] Lengthening of base of acetabular perforation
- [Ilium] Reduction of ischial peduncle and parallel development of pubic peduncle
- [Ilium] Dorsoventral widening of postacetabular process
- [Ilium] Alignment of preacetabular process and iliac crest
- [Ischium] Anteroposterior thickening of shaft (equally long anteroposteriorly and dorsoventrally)
- [Ischium] Slimming/refinement of posterior process
- [Ischium] Acetabular perforation laterally obstructed
- [Pubis] Lengthening of pubic shaft to 1/3 of total length
- [Pubis] Decrease to 120-130° angle between pubic symphysis - distal blade
- [Pubis] Increase (slight) to 30° angle between shaft - pubic symphysis

10
- [Ilium] Relative anteroposterior shortening of preacetabular process
- [Ilium] Third attachment site for last lumbar
- [Ilium] Shallow scars for attachment sites
- [Ischium] Dorsoventral widening of posterior process extremity
- [Ischium] Flattening and inclination of distal blade
- [Pubis] Increase to 130-140° angle between pubic symphysis - distal blade

11
- [Pubis] Narrowing of proximal peduncle
- [Pubis] Lengthening of pubic symphysis (35% of total length)
- [Pubis] Decrease to 22° angle between shaft - pubic symphysis and consequently narrow pubic apron
- [Pubis] Decrease to 120-130° angle between pubic symphysis - distal blade
- [Pubis] Development of medial protuberance

Fig. 80. — Phylogeny of Teleosauroidea (Part 3). Numbers highlight acquisition of morphologies based on our morphological observations. Color alternating for readability.

In extant crocodylians, most of the distal blade of the ischium is occupied by hip adductor and hip extensor muscles, whereas the posterior process is anchored with muscles involved in the hepatic respiration and with muscles connecting the ilium and ischium to the ventral side of the tail (Table 5; Romer 1923; Otero *et al.* 2010; Allen *et al.* 2014). Similar to the ilium, it is possible that the ischium of thalattosuchians and dyrosaurids possessed muscles filling comparable functions to that of extant crocodylians (Fig. 90). The ischium of dyrosaurids closely resembles that of extant crocodylians (minus the enlarged 'pubic knob') whereas thalattosuchians present a relatively larger distal blade due to greater anterior and posterior processes. In comparison, the ischium of terrestrial and semi-aquatic mesoeucrocodylians also displays an appearance closer to that of dyrosaurids and extant crocodylians than thalattosuchians (e.g. *Mahajangasuchus insignis* [Buckley & Brochu 1999], *Stratiotosuchus maxhechti* [Riff & Kellner 2011], *Pissarrachampsa sera* [Godoy *et al.* 2016], *Yacarerani boliviensis* [Leardi *et al.* 2015], *Sebecus icaeorhinus* [Pol *et al.* 2012]).

The relative surface available on the thalattosuchian ischium does not appear drastically different than in dyrosaurids or extant crocodylians, and hence presumably presented a similar muscle architecture with large hip adductor and hip extensor muscles. Still, the larger posterior process of thalattosuchians may convey the presence of greater muscles in size and/or number connecting the ischium to the ventral portion of the tail. In addition, we hypothesise that the interlocking ischia of thalattosuchians may convey an additional support role during aquatic locomotion (transmission of forces) and preservation of movement strength. This could presume that thalattosuchians as a whole were good swimmers, potentially better than extant crocodylians. However, the relative reduction of dorsal girdle elements and increase of ventral ones is presumably linked to the drop in gravitational pressure underwater, similar to turtles and sauropterygians, and hence does not directly imply a certain swimming mode of locomotion (Krahl 2021).

The most impressive role of the extant crocodylian pubis is its contribution to the hepatic piston pump, which is achieved through the combined movements of the liver and the pubis (plus gastralia) propelled by the actions of the diaphragmaticus, abdominal, intercoastal muscles and pelvic muscles (i.e. RABD, PIFE 1 and PIFE 2) (Gans & Clark 1976; Carrier 1987; Farmer & Carrier 2000b; Munns *et al.* 2012). In extant crocodylians (e.g. *Alligator mississippiensis*), the distal portion of the pubis is covered with a relatively important cartilaginous portion (Romer 1923), which extends to the last gastralia (Romer 1923; Farmer & Carrier 2000b; Uriona & Farmer 2008). The prepubic cartilage is connected to the last gastralia anteriorly and laterally, and the last gastralia are connected to the *diaphragmaticus* muscle (Farmer & Carrier 2000a). This cartilage grants the pubis an extended length and secures the pubic symphysis, but also bears muscles involved in hepatic respiration (Munns *et al.* 2012): the origin and insertion of the *rectus abdominis* muscles (Romer 1923; Claessens & Vickaryous 2012), and *M. pubo-ischio-femoralis externus 1 & 2* (see Table 6). The former is found at the cranial extremity of the prepubic cartilage and also covers the last gastralia (Romer 1923). The ischiopubic muscles (*M. pubo-ischio-femoralis externus 1 & 2*) occupy most of the crocodylian pubic plate and its cartilaginous extension (prepubic cartilage or cranial pubic cartilage) (Romer 1923; Otero *et al.* 2010; Claessens & Vickaryous 2012; Allen *et al.* 2014). These muscles serve as hip adductors (Otero *et al.* 2010; Allen *et al.* 2014), but also rotate the pubis ventrally during inspiration (Farmer & Carrier 2000a). In contrast, the pubis of thalattosuchians and dyrosaurids is more ossified than that of extant crocodylians (Romer 1923; Claessens & Vickaryous 2012), but their pitted distal margin indicates the existence of a cartilage cap *in vivo*. Presumably, the pubis of thalattosuchians and dyrosaurids extended into and likely connected to the thoracic region like that of extant crocodylians (Farmer & Carrier 2000a), through soft tissues (including muscles and cartilaginous structures) and gastralia (e.g. *Lemmysuchus obtusidens* see Johnson *et al.* (2017), *Hyposaurus natator* NJSM 23368). The pubis of crocodylians is peculiar and adapted to a pumping mechanism unique within archosaurs (Brocklehurst *et al.* 2020). We assume that the pubis of thalattosuchians and dyrosaurids served as attachment site for muscles homologous in function and position to those of extant crocodylians (see Table 6). Putatively, most of the shaft, distal blade and prepubic cartilage were covered with hip adductors, and the distal-most extremity of the pubis bore a muscular connection with the last gastralia or equivalent. However, because the relative mobility of the pubis is not an osteological correlate for hepatic respiration due to no strict correlation between the visceral shift initiated by the shortening of the *diaphragmaticus* muscle and the pubic rotation (Claessens 2009; Claessens & Vickaryous 2012; Brocklehurst *et al.* 2020), it is unknown whether thalattosuchians and dyrosaurids possessed their own version of the crocodylian *M. diaphragmaticus* (Munns *et al.* 2012) or not. For these reasons, we will only discuss the possible movements of the pubis and its presumed impact (i.e. pelvic aspiration; Brocklehurst *et al.* 2020). Hence, it is fully possible that the action of some of the muscles induced a movement of the pubis, with some pulling it anterodorsally and others posteroventrally. If thalattosuchians and dyrosaurids possessed a similar muscular framework to that of crocodylians, then their hip adductors would pull the pubis posteroventrally and their *M. rectus abdominis* would provoke the opposite motion.

Body size and shape influence manoeuvrability, with small bodies, flexible axial skeleton and wide limbs showing the greatest scores (Webb 2002; Gutarra & Rahman 2022). Extant crocodylians can control their posture, pitch and roll in water by shifting the position of their centre of buoyancy in relation to their centre of mass (Uriona & Farmer 2008). To initiate diving, extant crocodylians simultaneously incline both their head (ventrally) and tail (dorsally), and shift their centre of buoyancy caudally through the use of several muscles notably involved in the respiration (i.e. *M. diaphragmaticus, M. pubo-ischio-femoris, M. rectus abdominis*, and the internal intercostals). The unilateral activity of some of these muscles have also been recorded during rolling, namely right or left *M. diaphragmaticus* and *M. rectus abdominis* depending on the direction (Uriona & Farmer 2008).

Even if the existence of a *M. diaphragmaticus* in thalattosuchians and dyrosaurids is unknown, the highly mobile pelvis suggests that pelvic muscles played a role in manoeuvrability and stability (control posture, pitch and roll; as in extant crocodylians [Uriona & Farmer 2008]) by impacting at least the centre of mass through (even subtle) displacement of viscera by pubis and gastralia movements alone. Extinct crocodyliforms sharing an anguilliform body shape (i.e. cylindrical body shape, anteroposteriorly elongated but relatively limited in other directions) presumably employed an axial swimming mode. With the forelimb reduction in pelagic metriorhynchoids (e.g. rhacheosaurines), swimming mode requiring the use of four limbs (i.e. paraxial and hybrid swimming) becomes harder to perform. Presumably, those taxa (e.g. geosaurines and rhacheosaurines) used body undulations as a thrusting force, with hindlimbs possibly displaying crucial role in stabilisation or rapid change in direction assisted by the displacement of viscera and centre of mass. This is consistent with the interpretations of Hua (1994) in which metriorhynchids are sustained swimmers. The forepaddles of metriorhynchids were presumably exclusively used for balance (Fraas 1902; Hua 1994).

The presence of *M. diaphragmaticus* appears almost necessary for extinct aquatic crocodyliforms, especially if they belong to the slow swimmer and ambush predators categories like extant crocodylians, as it gives the necessary kick to initiate diving (Uriona & Farmer 2008). Furthermore, having a long and heavy tail (as is also the case in dyrosaurids, and metriorhynchoids to a lesser extent) would also require an increased activity of the pelvic and thoracic muscles to dive (i.e. M. pubo-ischio-femoralis externus, *M. rectus abdominis* and internal intercostal muscles plus a *M. diaphragmaticus* equivalent), as it is the case for extant crocodylians (Uriona & Farmer 2008); it is thus likely that thalattosuchians and dyrosaurids had a similar mechanism helping them initiate diving without propulsion (which does not create additional surface ripples). Indeed, extant cetaceans exhibit a similar behaviour where they collapse their lungs to plunge without external force (Ridgway & Howard 1979). In addition, the presence of a *M. diaphragmaticus* and *M. rectus abdominis* in Thalattosuchia and Dyrosauridae would also assist rolling mechanisms as in Crocodylia (Uriona & Farmer 2008), and presumably play a role in underwater manoeuvrability.

In comparison, the marine iguana *Amblyrhynchus cristatus* Bell, 1825 displays a highly diverging swimming mechanism. Indeed, marine iguanas keep their lungs inflated when diving and hence must overcome their own buoyancy to descend. To do so, marine iguanas swim using powerful body undula-

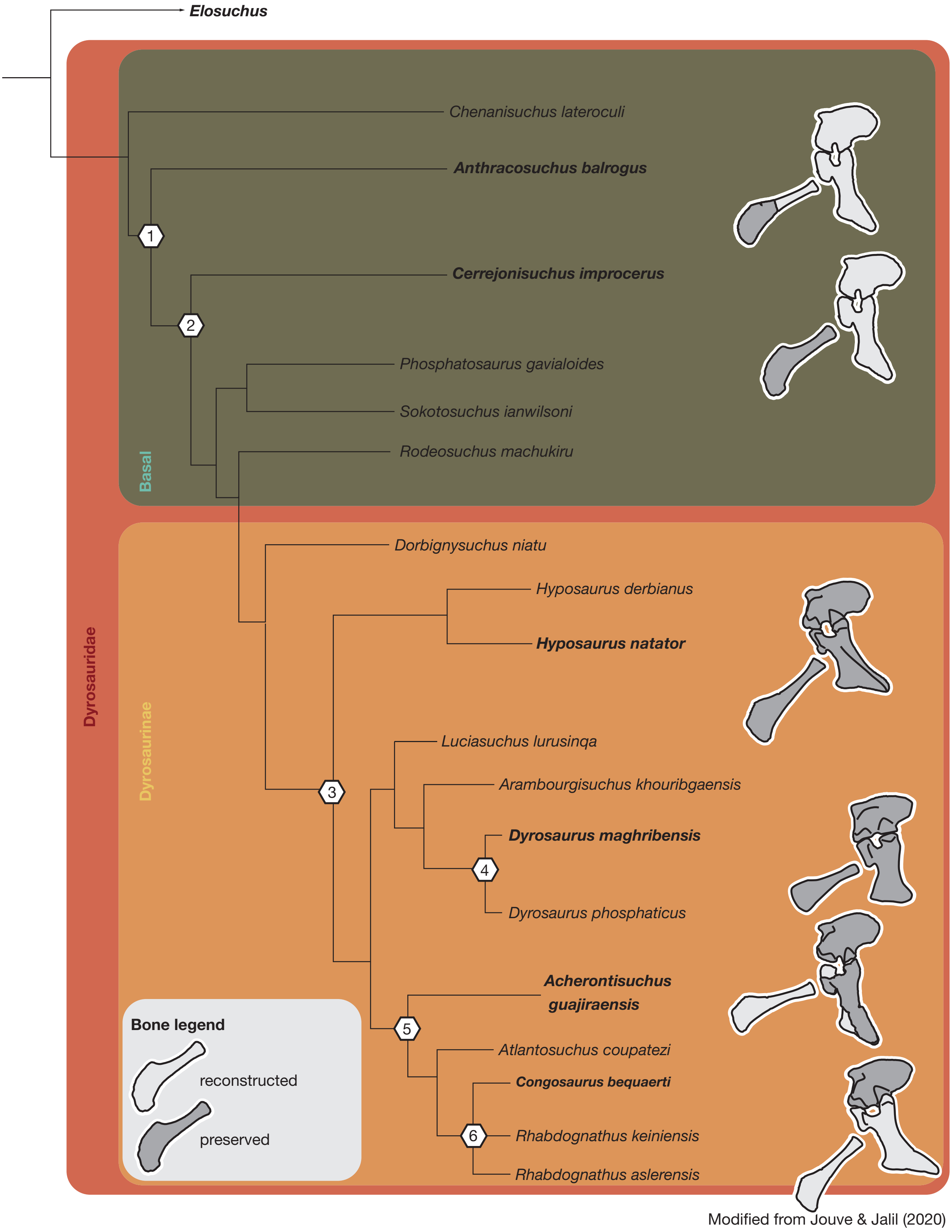


FIG. 81. — Phylogeny of Dyrosauridae (Part 1). Numbers highlight acquisition of morphologies based on our morphological observations. Figure modified from Jouve & Jalil (2020).

1 - [Pubis] 136° angle pubic symphysis - distal blade
- [Pubis] Long pubic symphysis
- [Pubis] Presumably slender pubis with narrow apron (incilination of pubic shaft media, ~25° angle with pubic symphysis)

2 - [Pubis] Lengthening of pubic symphysis (2/5 of total length)
- [Pubis] Straightening of pubic shaft (about 20° angle with pubic symphysis)
- [Pubis] Development of lateral protuberance
- [Pubis] 125° angle pubic symphysis - distal blade

3 - [Ilium] Short preacetabular process
- [Ilium] Large dome-shaped postacetabular process
- [Ilium] Large acetabular perforation
- [Ilium] Large and deep bony acetabulum (with strongly protruding ischial peduncle)
- [Ilium] Proportionally short supraacetabular crest
- [Ischium] Mediolateral twisting of distal blade
- [Ischium] Short anterior hook of distal blade
- [Ischium] Posterior hook of distal blade set further ventrally than anterior hook
- [Ischium] Anterior peduncle with large ‘pubic knob’
- [Ischium] Large acetabular perforation with strict lateromedial orientation
- [Pubis] Shortened pubic symphysis (1/5 of total length)
- [Pubis] 118* angle pubic symphysis - distal blade
- [Pubis] Shortened pubic apron and overall slender aspect of pubis

4 - [Ilium] Shortening of preacetabular process
- [Ilium] Lengthening of supraacetabular crest
- [Ilium] Anteroposterior widening of bony acetabulum
- [Ilium] Reduction of postacetabular process
- [Ischium] Shortening of distal blade
- [Ischium] Anteroposterior widening of shaft
- [Ischium] Posterior and anterior hooks are aligned anteroposteriorly
- [Pubis] Further shortening of pubic apron which displays triangular outline
- [Pubis] Proportional reduction of pubis compared to other pelvic girdle elements

5 - [Ilium] Elongation of preacetabular process (with pointed tip)
- [Ilium] Enlargment of postacetabular process
- [Ilium] Anteroposterior narrowing of bony acetabulum
- [Ilium] Shortening of supraacetabular crest
- [Ilium] Inclination of pubic peduncle
- [Ilium] Reorientation of ischial peduncle lateromedially increasing depth of acetabulum
- [Ilium] Reduction of acetabular perforation
- [Ischium] Ventral extension of posterior hook of distal blade
- [Ischium] Shaft anteroposteriorly slender

6 - [Ilium] Thickening of preacetabular process
- [Ilium] Postacetabular process is less bulged
- [Ilium] Further reduction of acetabular perforation

Fig. 82. — Phylogeny of Dyrosauridae (Part 2). Numbers highlight acquisition of morphologies based on our morphological observations. Figure modified from Jouve & Jalil (2020).

tions at a downward angle of approximately 30°. When diving, the tail plays an essential role in the thrust production and individuals missing portions of the tail are not capable of submergence. Marine iguanas switch to a vertical descent after swimming for a couple of meters obliquely. Once submerged, they may release some air on occasion. In shallow waters, marine iguanas must swim to stay submerged. When feeding in shallow waters, marine iguanas use their claws to cling on rocks and algae so their buoyancy is not an issue (Bartholomew *et al.* 1976). In deeper waters, the pressure causes the air in their lungs to compact, and their buoyancy becomes neutral (Hobson 1965, 1969). All iguanids (i.e. marine and terrestrial) present higher compactness values in their forelimbs in relation to the hindlimbs. However, marine iguanas show a higher compactness value of their limb bones compared to their terrestrial counterpart, so that the forelimbs of marine iguanids might be used as ballast for buoyancy control (Hugi & Sanchez-Villagra 2012).

In extant crocodylians the pubic plate possesses a large cartilaginous cap which extends its flexibility plus its area of effect, and bears the origin of the *rectus abdominis* muscles (Romer 1923; Claessens & Vickaryous 2012). In the case of extant crocodylians, it is possible that the cartilaginous portion gradually took over the bony pubic plate following metabolic demands; the downsizing of their pubis presumably happened through the reduction of the pubic symphysis (Claessens & Vickaryous 2012). In extant crocodylians, ossification of the pelvis starts in embryonic development and continues through posthatchling development. At about one year of age, all three elements are ossified except for a small dorsal portion of the ischium (Claessens & Vickaryous 2012). Hence, it is possible that ossification is relatively 'delayed' in extant crocodylians which could at least partly explain their short pubic symphysis. Thereby, it is possible that the short pubic symphysis constitute a potential paedomorphic characteristic of extant crocodylians.

With cartilage being a relatively flexible connective tissue (Claessens & Vickaryous 2012; Tsai & Holliday 2015), it is possible that the greater proportion of cartilage in extant crocodylians impacts the way the viscera are pulled (anteriorly) by naturally absorbing or dispersing shocks, and by easily allowing pubic rotation (Farmer & Carrier 2000a); the flexibility of the cartilage cap presumably impacts the way the force is transmitted throughout the bone when the abdominal muscles shorten. Hence, the overall reduction of the bony pubic plate in extant crocodylians compared to thalattosuchians and dyrosaurids does not constitute a drawback in the shifting of visceral masses, all the more so that extant crocodylians show mediolaterally wide pubes due to an impressive flaring distally (e.g. *Palaeosuchus palpebrosus* [Fig. 7]; *Mecistops cataphractus* [Fig. 8]; *Caiman crocodilus* [Fig. 9]). This breadth along with their absolute and relative (to one another) mobility presumably allow them to efficiently encompass and shift visceral masses. It is possible that the shorter pubic symphysis of extant crocodylian constitutes a paedomorphic trait, but this hypothesis would need to be thoroughly investigated.

In comparison to extant crocodylians, extinct crocodyliforms such as thalattosuchians and dyrosaurids possess massive pubes, mainly due to a longer pubic symphysis and a larger pubic plate. The terrestrial mesoeucrocodylians *Yacarerani boliviensis* (Leardi *et al.* 2015) and *Araripesuchus tsangatsangana* (Turner 2006), and semi-aquatic *Mahajangasuchus insignis* (Buckley & Brochu 1999) also display relatively mediolaterally wide pubic apron with a larger symphysis than extant crocodylians. However, their overall triangular shape, emphasized by their short pubic symphysis, brings them closer to extant crocodylians than to what is observed in dyrosaurids and most thalattosuchians. Hence, with their large pubic apron and well-developed pubic symphysis, thalattosuchians (excluding basal metriorhynchoids, most rhacheosaurines and geosaurines, *Plagiophthalmosuchus gracilirostris*, and *Macrospondylus bollensis* see paragraph below) and even more dyrosaurids appear predisposed to displace visceral masses.

The overall size of the pubic apron in dyrosaurids and most thalattosuchians implies that pubic muscles had more extensive bony attachments compared to extant crocodylians (Romer 1923, Claessens & Vickaryous 2012). Hypothetically, a more ossified pubic apron would transmit forces at a faster rate, thus allowing for quicker responses. The large ossified pubic plates of thalattosuchians and dyrosaurids are connected together along the pubic symphysis. The latter is set at relatively constant angle with the median of the shaft within the clades (about 20° for dyrosaurids, 30° for most thalattosuchians, and 40-45° within Metriorhynchinae Fitzinger, 1843). The differences in angular relation presumably reflect differences in pelvic cross-section (which depends notably on sacral ribs) and also in overall inclination of the pubis regarding the sagittal plane at rest (the pubis of thalattosuchians is more tilted than that of dyrosaurids). In thalattosuchians, amid the resting stance, the dorsal surface of the pubes are tilted medially (i.e. towards the sagittal plane; Fig. 91). During forward motion, the pubes gradually rise dorsally and their dorsal surface becomes more dorsally facing than medially. This motion also causes the rotation of the pubic peduncle on the anterior peduncle of the ischium, and at a certain point lateral dislocation of the bony articulations could occur in thalattosuchians. Indeed, pubis rotation in the American alligator shows a range of 3.2° to 18.9°, with an average of 10.2°. The amount of pubic rotation varies depending on the effort and also between sequential breath (Claessens 2004, 2009). In our tests with 3D models (Fig. 91), the total amplitude of movement shown is about 18° for both cases. It shows that Thalattosuchia presumably did not reach the upper limit of the crocodilian range of motion (18.9°) because this limit already shows lateral dislocation of the pubic peduncle. However, lower angular rotations of the crocodilian pubis could be more easily achieved for Thalattosuchia. In parallel, since the pubis in included in a synchondrosis cartilage with the ischium, it is also possible that pubic dislocation did not constitute an issue like the femoral dislocation. Still, pubic movements are accessory components of the aspiration pump in extant crocodylians (Farmer & Carrier 2000a; Claessens 2004). Pubic movements make up about 5% and less of pulmonary tidal volume whereas visceral movement account for more than 60% of pulmonary tidal volume, and no strict correlation exists between both (Claessens 2009).

In dyrosaurids, the different stages are similar with the exception that the lateral excursion of the peduncle of the pubis would not happen. Indeed, in dyrosaurids the circular shape of both the pubic 'knob' on the anterior peduncle of the ischium and the peduncle of the pubis allow them to stay in contact throughout the rotation of the pubis (Fig. 91). Compared to Thalattosuchia and Crocodylia, dyrosaurids are the only ones to possess such a prominent articulation between the pubis and the ischium. In Crocodylia, this area does not protrude anteriorly and corresponds to the anteroventral surface of the anterior peduncle, like other crocodylomorphs (e.g. *Sebecus icaeorhinus* [Pol *et al.* 2012]; *Terminonaris robusta* [Wu *et al.* 2001]; *Oceanosuchus boecensis* [Hua *et al.* 2007]; *Sarcosuchus imperator* [Sereno *et al.* 2001]; *Stratiotosuchus maxhechti* [Riff & Kellner 2011]; *Shamosuchus djadochtaensis* [Pol *et al.* 2009]; *Knoetschkesuchus langenbergensis* [Schwarz *et al.* 2017]; *Amphicotylus lucasii* [Yoshida *et al.* 2021]). In Teleosauroidea, and even more spectacularly in Metriorhynchoidea, the anterior peduncle of the ischium is reduced and does not match with the shape of the peduncle of the pubis, which implies the presence of a more extensive cartilage cap. The development of a 'pubic knob' as in dyrosaurids is pre-

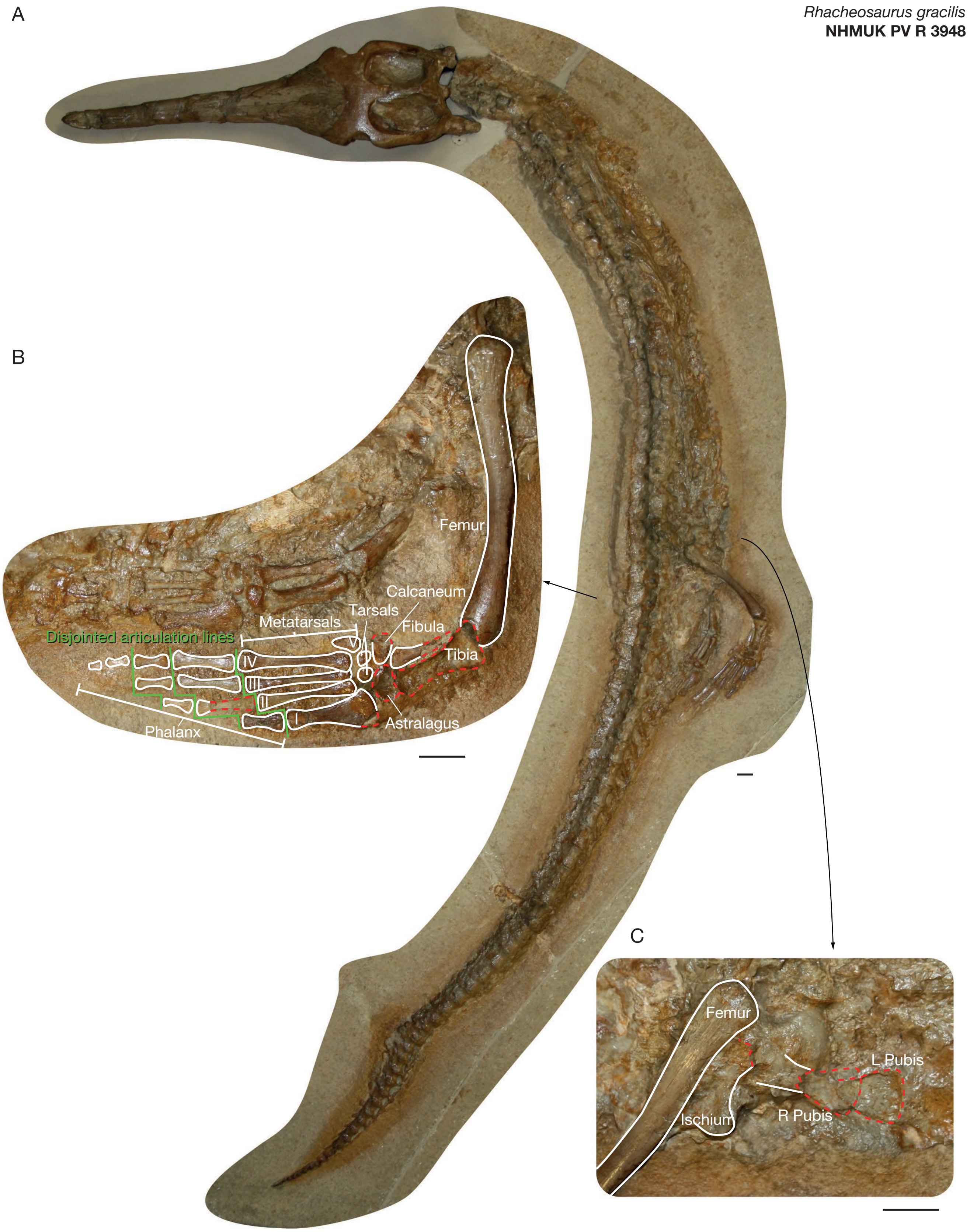


FIG. 83. — *Rhacheosaurus gracilis* Von Meyer, 1831, NHMUK PV R 3948: **A**, entire skeleton; **B**, hindlimb detail; **C**, pubis detail. Note the skin impression as the darker tone surrounding the body. Scale bar: 1 cm.

Table 12. — Relative length (in mm) of the pubis in relation to the presacral length (estimated) in *Dyrosaurus maghribensis* (OCP DEK-GE 252), *Thalattosuchus superciliosus* (NHMUK PV R 2054), and *Platysuchus multiscrobiculatus* (SMNS 9930). Abbreviations: **PR.L**, presacral length (estimated); **P.H**, total proximodistal height of the pubis; **P.R**, ratio of the pubis and total presacral length; **P.%**, percentage of total length accounted by the pubis. *, estimated.

Taxon	Inventory number	PR.L*	P.H	P.R	P.%
Dyrosaurus maghribensis	OCP DEK-GE 252	3738 to 3843	583	6.41 to 6.59	15.59 to 15.17
Thalattosuchus superciliosus	NHMUK PV R 2054	1074	109	9.85	10.14
Platysuchus multiscrobiculatus	SMNS 9930	870	99*	8.78	11.37

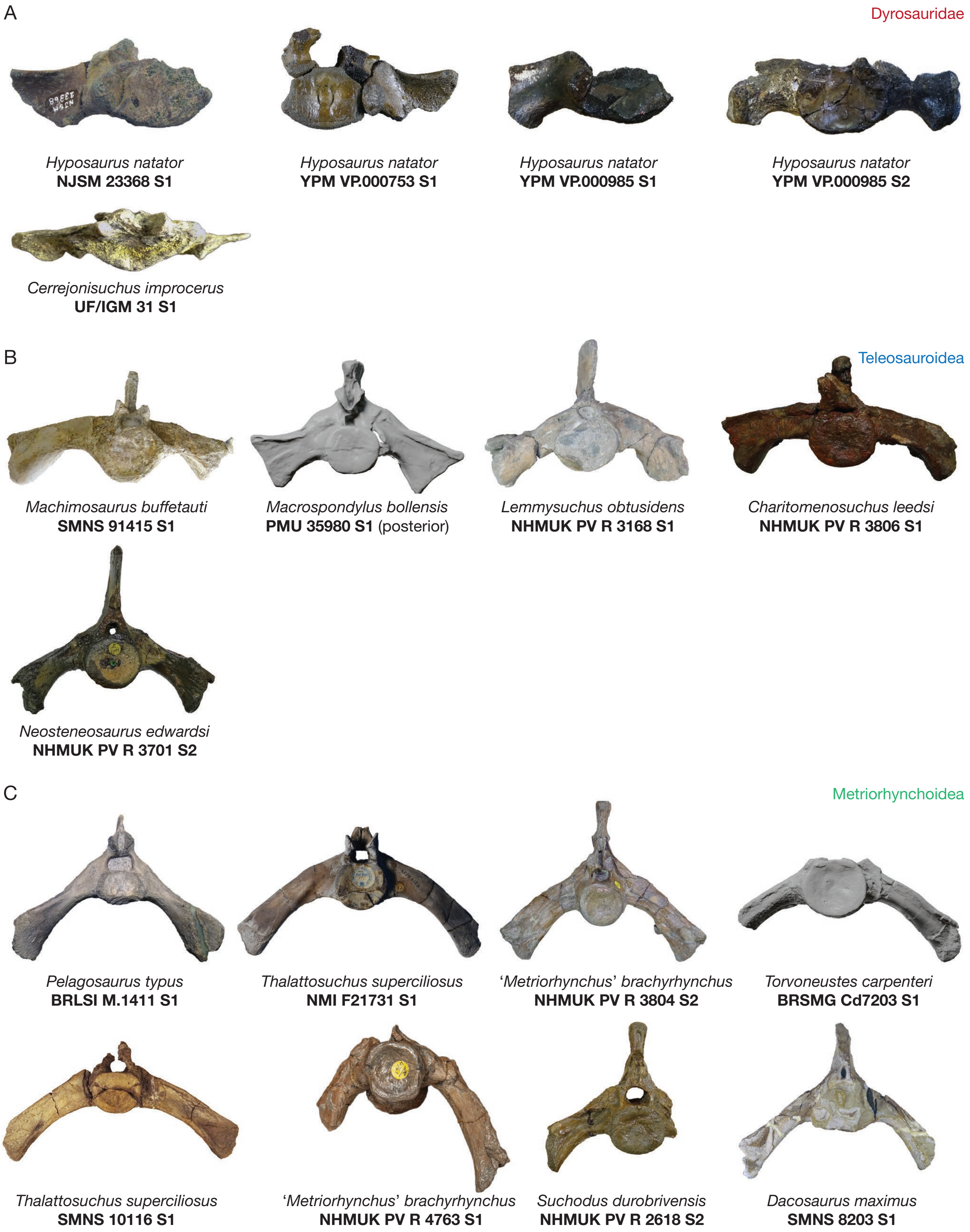
sumably not an isolated case, as the notosuchian *Yacarerani boliviensis* (Sphagesauridae; Leardi *et al.* [2015]) also possesses a similar structure, in which the size of the anterior peduncle of the ischium is enlarged anteroventrally.

During the motion of the pubis, the pubic symphysis of thalattosuchians and dyrosaurids presumably acted as an axis of rotation allowing for less overall flexibility than the crocodylian configuration (i.e. relative rotational flexibility between the pubes and soft deformation of the pre-pubic cartilage) (Claessens 2004). In addition, the relative length of the pubic symphysis in Thalattosuchia (with the exception of basal metriorhynchoids, most rhacheosaurines and geosaurines, *Plagiophthalmosuchus gracilirostris*, and *Macrospondylus bollensis*) and Dyrosauridae also comes with a proportionally narrower pubic plate in the mediolateral direction (which reflects their more oblong cross-section) and possibly a less pronounced inclination towards the sagittal plane. Comparatively, thalattosuchians present dorsally concave pubic plates whereas in dyrosaurids these are dorsally convex. These differences impact the way visceral masses are shifted, with convex pubic aprons presumably necessitating less rotational movement than concave ones to propel the viscera. It is possible that the dorsal convexity of the dyrosaurid pubic apron as well as the smaller angular relation (20°) of the pubic symphysis evolved to counterbalance the length of their pubic rod. The variation in the relative length of the pubic rod among thalattosuchians and dyrosaurids supposedly reflects a difference in trunk length (see Table 12). Hence, the overall geometry of the pubis has an influence over the total amplitude of movements of the pubes before lateral dislocation (Fig. 15). In the case of an important angle between the pubic symphysis and the axis of the pubic rod, pubes with a long pubic symphysis are capable of little relative rotation when pulled anteroposteriorly, otherwise it would cause the excursion of the pubic peduncle. If the concavity between the pubes is not flattened by the relative rotation of both pubes, then it would have little impact on the visceral masses, restricting the displacement of the masses strictly to the anterior posterior motion of both pubes.

Compared to what is observed in other thalattosuchians, the pubic symphysis of the basal metriorhynchoid *Pelagosaurus typus* is rudimentary (yet still relatively developed compared to the narrow appearance of the pubic apron), hinting at the independent evolution of a long bony pubic symphysis in Metriorhynchoidea and Teleosauroidea. In addition, basal teleosauroids like *Plagiophthalmosuchus gracilirostris* and *Macrospondylus bollensis* also show a relatively short pubic symphysis compared to more derived teleosauroids. Strictly pelagic forms within metriorhynchoids (i.e. rhacheosaurines and geosaurines) display shorter pubic symphysis and pubic aprons compared to other thalattosuchians and dyrosaurids (Figs 87-89). More precisely, the pubic plates of those rhacheosaurines and geosaurines display a relatively significant mediolateral breadth for a short proximodistal length and pubic symphysis, which give their pubis the axe head appearance usually displayed by extant crocodylians. Presumably, the distal extremity of the pubis of rhacheosaurines and geosaurines (Figs 87; 88) was topped with a relatively large cartilaginous cap similar to extant crocodylians. In parallel, the ischium of rhacheosaurines and geosaurines displays an enlarged acetabular perforation and posterior process compared to other methriorhynchoids. The former could have allowed a greater range of movement of the femur whereas the latter implies greater strength in the hindlimbs. Hence, the intense aquatic adaptations of rhacheosaurines also entailed the reduction of their pubis and widening of their ischium, whereas the ilium was already reduced in metriorhynchoids due to decreased terrestrial activity Krahl (2021).

In extant crocodylians (e.g. *Palaeosuchus palpebrosus* [Fig. 7], *Mecistops cataphractus* [Fig. 8], *Caiman crocodilus* [Fig. 9]), the well-developed and rounded articular surface of the anterior peduncle of the ischium plus its relatively short and mediolaterally twisted distal blade do not hamper the anteroposterior movements of the pubis. The distal blade of the dyrosaurid ischium is similarly shaped, however its anterior peduncle bears an additional articular surface for the peduncle of the pubis: the pubic 'knob' (Fig. 69) (e.g. *Hyposaurus natator* [Figs 66-68], *Dyrosaurus maghribensis* [Fig. 69], *Acherontisuchus guajiraensis* [Fig. 70]). In turn, the peduncle of the pubis displays an almost circular outline which closely hugs the shape of the pubic knob. In *Dyrosaurus maghribensis* and *Hyposaurus natator*, the presence of the pubic 'knob' on the ischium along with the shape of the pubis (i.e. elongated pubic rod, relatively short pubic symphysis, circular pubic peduncle, narrow pubic apron) suggests the possibility of combined anteroposterior motion and mediolateral rotation of the pubic plate not unlike extant crocodylians.

On the contrary, thalattosuchians markedly depart from the dyrosaurid and crocodylian configuration due to their untwisted interlocking ischia (almost forming a plastron like mentioned by Fraas [1902]), their anteriorly protruding sharp process and relatively reduced anterior peduncle. Hence, at first glance, thalattosuchians (and especially metriorhynchoids) appear to display a less functional or even dysfunctional ischiopubic articulation compared to crocodylians and dyrosaurids. Thalattosuchians are strongly disparate in the shape of their anterior peduncle of the ischium and overall form of their pubis: metriorhynchoids show an even more reduced anterior



Hyposaurus natator
NJSM 23368 S1

Hyposaurus natator
YPM VP.000753 S1

Hyposaurus natator
YPM VP.000985 S1

Hyposaurus natator
YPM VP.000985 S2

Cerrejonisuchus improcerus
UF/IGM 31 S1

Machimosaurus buffetauti
SMNS 91415 S1

Macrospondylus bollensis
PMU 35980 S1 (posterior)

Lemmysuchus obtusidens
NHMUK PV R 3168 S1

Charitomenosuchus leedsi
NHMUK PV R 3806 S1

Neosteneosaurus edwardsi
NHMUK PV R 3701 S2

Pelagosaurus typus
BRLSI M.1411 S1

Thalattosuchus superciliosus
NMI F21731 S1

'*Metriorhynchus*' *brachyrhynchus*
NHMUK PV R 3804 S2

Torvoneustes carpenteri
BRSMG Cd7203 S1

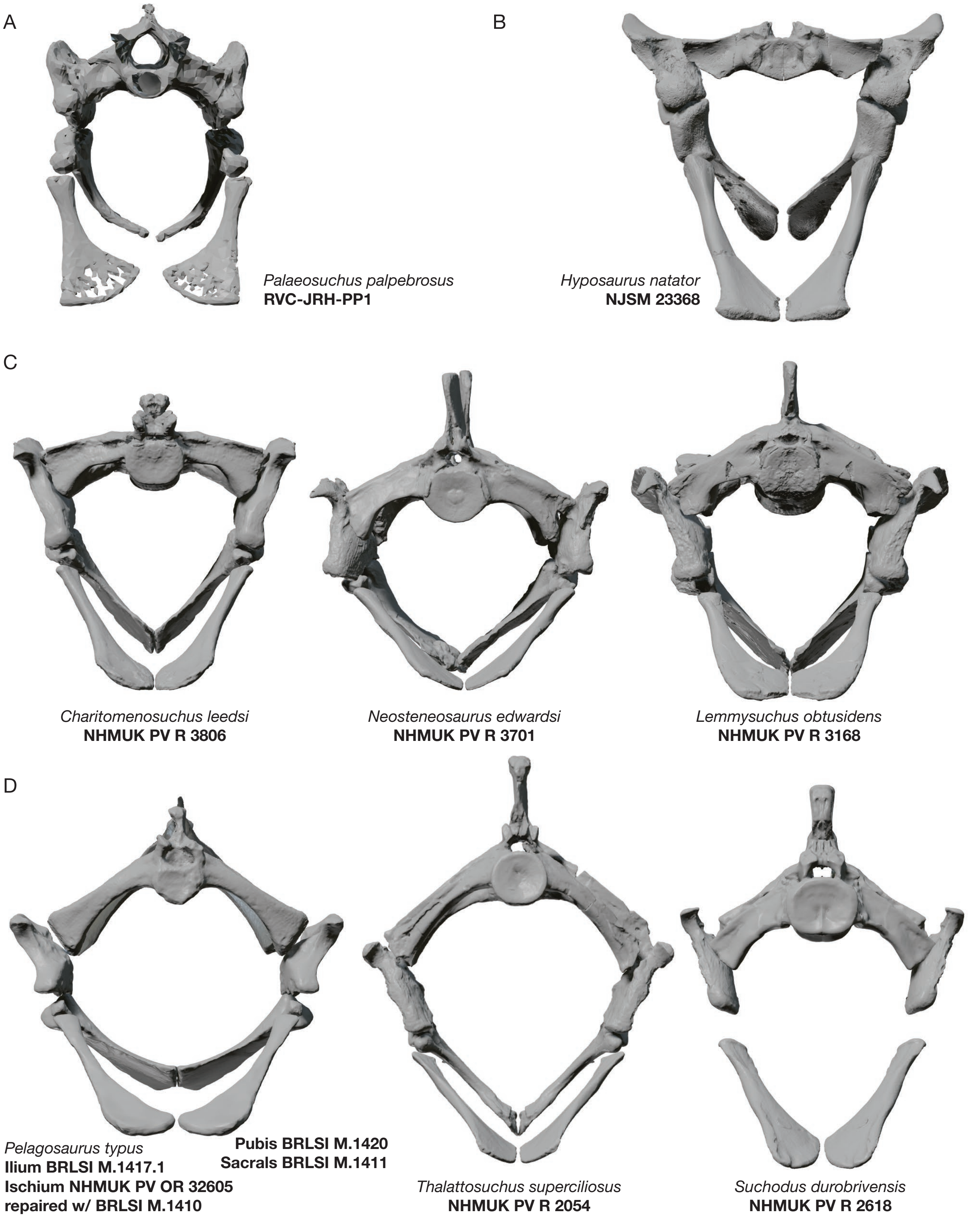
Thalattosuchus superciliosus
SMNS 10116 S1

'*Metriorhynchus*' *brachyrhynchus*
NHMUK PV R 4763 S1

Suchodus durobrivensis
NHMUK PV R 2618 S2

Dacosaurus maximus
SMNS 8203 S1

FIG. 84. — Comparison of thalattosuchian and dyrosaurid sacral vertebra: **A**, Dyrosauridae de Stefano, 1903; **B**, Teleosauroidea Geoffroy SaintHilaire, 1831; **C**, Metriorhynchoidea Fitzinger, 1843. The sacrals are placed in either anterior or posterior view. The order of each vertebrae is indicated in each case: **S1**, first sacral; **S2**, second sacral. For scale bars, see the other Figures in the article.



Palaeosuchus palpebrosus
RVC-JRH-PP1

Hyposaurus natator
NJSM 23368

Charitomenosuchus leedsi
NHMUK PV R 3806

Neosteneosaurus edwardsi
NHMUK PV R 3701

Lemmysuchus obtusidens
NHMUK PV R 3168

Pelagosaurus typus
Ilium BRLSI M.1417.1
Ischium NHMUK PV OR 32605
repaired w/ BRLSI M.1410
Pubis BRLSI M.1420
Sacrals BRLSI M.1411

Thalattosuchus superciliosus
NHMUK PV R 2054

Suchodus durobrivensis
NHMUK PV R 2618

Fig. 85. — Comparison of the pelvic area among Thalattosuchia: **A**, Crocodylia; **B**, Dyrosauridae; **C**, Teleosauroidea; **D**, Metriorhynchoidea. Girdles in anterior view. For scale bars, see the other Figures in the article.

Fig. 86. — Comparison of crocodyliformes ischia: **A**, Dyrosauridae de Stefano, 1903; **B**, Teleosauroidea Geoffroy SaintHilaire, 1831; **C**, Metriorhynchoidea Fitzinger, 1843. Ischia are placed on a flat surface in either medial or lateral view. For scale bars, see the other Figures in the article.

peduncle compared to teleosauroids, whereas rhacheosaurines and geosaurines have shortened their pubic symphysis and widened their pubic apron. These differences are presumably linked to a difference in habitat; strictly pelagic lifestyles may have entailed the further reduction of the anterior peduncle of the ischium as the load-bearing constraints are diminished on the pelvic girdle (Krahl 2021).

In Thalattosuchia, the medial position of both ischia (interlocked) and their protruding anterior process presumably hampered the posterior motion of the pubes compared to Crocodylia and Dyrosauridae. Indeed, the distal blade of the ischium lies in the trajectory of the pubes and their posterior displacement would result in soft tissues pinching or perforation, so that the area could not have registered the retraction and recoil of the pubis without suffering additional obstruction (Figs 15; 18; 25; 47; 49; 60) . For this reason, the posterior extension of the pubis was presumably more limited in thalattosuchians than in crocodylians. It is possible that the resting position of the pubis was set further anteriorly in thalattosuchians to counter this issue (Fig. 91), or that the mobility of the pubis was used differently in thalattosuchians than in crocodylians with only the anterior motion being active in the pelvic pump of the former.

At first glance, the small size of the anterior peduncle of thalattosuchians does not appear able to serve as a sound structure for accommodating pubic movements and resisting forces (e.g. rapid excursion of the pubic peduncle, or body weight lying or standing). In particular, the short dorsoventral height of the anterior peduncle of the ischium of thalattosuchians appears to offer a limited range of motion for the pubis compared to extant crocodylians and dyrosaurids (for which the anterior peduncle is even more developed than in crocodylians; Fig. 91). The pubic peduncle of thalattosuchians may have glided more mediolaterally than rotated on the anterior peduncle of the ischium due to the size of the anterior peduncle of the ischium combined with the shape of the peduncle of the pubis (i.e. ovoid outline with greatest axis parallel with the section of the shaft). In addition, the pubic symphysis acting as an axis of rotation constraints the possible movements of the pubis in Thalattosuchia (as in Dyrosauridae) and causes the lateral dislocation of the pubis if overdone. Within Thalattosuchia, the relatively mediolaterally wider anterior peduncle in teleosauroids (Figs 47; 49; 60) offers a slightly greater gliding surface for the pubic rotation before lateral excursion of the bone (unlike metriorhynchoids; Figs 15, 18, 25). The difference in shape of the peduncle of the pubis compared to the anterior peduncle of the ischium implies the presence of an extended cartilage cap to encompass the entire ischio-pubic articulation in Thalattosuchia compared to Crocodylia and Dyrosauridae. It is possible that the cartilaginous cover was slightly greater in metriorhynchoids compared to teleosauroids due to the difference in size of their anterior peduncle of the ischium.

To sum up, thalattosuchians presumably possessed a pelvic pump that slightly differed from dyrosaurids and the hepatic pump of extant crocodylians due to different bony constraints. Comparatively, both teleosauroids and metriorhynchoids possessed a more developed ischio-pubic cartilage than in extant crocodylians (and presumably dyrosaurids) to counter the absolute small size of their anterior peduncle of the ischium.

Articulations

In addition to the shape of the ilium, the shape of the femur (i.e. degree of anteversion and sigmoid aspect) will result in marked differences of femoral excursion between Crocodylia, Dyrosauridae and Thalattosuchia. Even though most thalattosuchian remains are strongly flattened dorsoventrally, it is unlikely that the compression markedly twisted the distal condyles to align them to the femoral head (Fig. 92). In thalattosuchians, the femoral anteversion (Table 13; Figs 93-98) aligns the greater axes of both distal condyles close to that of the femoral head, making the femur planar. This condition places the zeugopodia in line with the stylopodium, and also results in a knee oriented laterally in Thalattosuchia rather than anterolaterally for the same position of the femoral head as in Crocodylia and Dyrosauridae (Fig. 93). Furthermore, Dyrosauridae and Crocodylia show a strong difference in the overall position of their distal condyles, with the lateral condyle extending further distally than the medial condyle (Figs 93 to 96). Unfortunately this difference is lost when projecting the orientation of the condyles on a plane (see Table 13).

The planar disposition of the zeugopodium and stylopodia of thalattosuchians conveys a relatively different resting position of the hindlimb than in extant crocodylians, where the zeugopodium and autopodium of thalattosuchians are automatically placed further posteriorly for a similar orientation of the femoral head in the acetabulum. The configuration of the thalattosuchian hindlimb presumably impacted its range of motion and rendered terrestrial locomotion more difficult, especially for metriorhynchoids in the light of their *bauplan* (Hua 1994; Herrera *et al.* 2017). For example, in the sprawling posture, placing the zeugopodia perpendicular to the ground in Thalattosuchia requires a more anteriorly and dorsally flexed position of the femur than in Dyrosauridae and Crocodylia (Fig. 93) (Otero *et al.* 2010; Grigg & Kirshner 2015). Also, to achieve the high walk posture, they would have to bring their femur closer to their abdomen (greater adduction) than what is observed in Dyrosauridae and Crocodylia, which would in return cause a relatively greater femoral excursion. Whereas the degree of accommodation of the articular capsule and acetabular membrane is unknown, the high ratio of soft tissues to bone forming the acetabulum could potentially allow a vertical positioning of the femur. Indeed, the hip articulation of thalattosuchians was certainly cartilaginous and relatively flexible, similar to that of Crocodylia (Kuznetsov & Sennikov 2000; Tsai & Holliday 2015; Tsai *et al.* 2019), hence accommodating a wide array of femoral movements. Moreover, the presence of an acetabular perforation, even if reduced, suggests the existence of intrinsic joint ligaments and also of a soft inner wall in the acetabulum (Tsai & Holliday 2015) which presumably enabled them to reach certain degrees of femoral rotation and abduction (movement which provokes the femoral excursion; Fig. 93). Hence, the femur in Thalattosuchia thus presumably did not occupy the same

FIG. 87. — Comparison of thalattosuchian pubes; the pubes are placed on a flat surface in either anterior or posterior view to illustrate their geometry: **A**, Metriorhynchoidea Fitzinger, 1843; **B**, Metriorhynchinae Fitzinger, 1843; **C**, Rhacheosaurini Young, Bell & Brusatte, 2011; **D**, Geosaurinae Lydekker, 1889; **E**, Geosaurini Lydekker, 1889. For scale bars, see the other Figures in the article.

FIG. 88. — Comparison of thalattosuchian pubes; the pubes are placed on a flat surface in either anterior or posterior view to illustrate their geometry: **A**, Teleosauroidea Geoffroy Saint-Hilaire, 1831; **B**, Aeolodontinae Johnson, Young & Brusatte, 2020; **C**, Teleosaurinae Vignaud, 1995; **D**, Machimosauridea Jouve, Mennecart, Douteau & Jalil, 2016; **E**, Machimosaurinae Jouve, Mennecart, Douteau & Jalil, 2016; **F**, Machimosaurini Jouve, Mennecart, Douteau & Jalil, 2016. Picture of NHMW 1882C/0026/4082 courtesy of Alice Schumacher (NHMW) and Ursula Göhlich (NHMW). For scale bars, see the other Figures in the article.

FIG. 89. — Comparison of dyrosaurid and crocodylian pubes; the pubes are placed on a flat surface in either anterior or posterior view to illustrate their geometry: **A**, basal Dyrosauridae de Stefano, 1903; **B**, derived Dyrosauridae; **C**, Crocodylia Owen, 1842. For scale bars, see the other Figures in the article.

Table 13. — Angles in degrees formed between the major axes of the femoral head and lateral condyle (alpha); and between the femoral head and medial condyle (beta). The major axes of the femoral head, medial condyle and lateral condyle are projected onto a flat surface perpendicular to the long axis of the femur. Negative angle values reflect an inversion of the orientation of the major axis of the medial condyle in relation to the major axis of the femoral head.

Taxon	Inventory number	alpha	beta
Charitomenosuchus leedsi	NHMUK PV R 3806	15.52	36.53
Congosaurus bequaerti	MRAC 1817	19.72	47.32
Dakosaurus maximus	SMNS 8203	20.84	48.84
Hyposaurus natator	NJSM 23368	35.79	46.68
Palaeosuchus palpebrosus	RVC-JRH-PP1	14.90	44.08
Lemmysuchus obtusidens	NHMUK PV R 3168	–6.51	15.58
Machimosaurus hugii	SMNS 81608	15.07	12.41
Mecistops cataphractus	RBINS 18374	26.42	58.11
'*Metriorhynchus*' *brachyrhynchus*	NHMUK PV R 3804	11.38	27.13
'*Metriorhynchus*' *brachyrhynchus*	NHMUK PV R 4763	21.04	33.91
Neosteneosaurus edwardsi	NHMUK PV R 2076	19.37	39.86
Neosteneosaurus edwardsi	NHMUK PV R 2865	7.17	28.35
Pelagosaurus typus	SMNS 52034	–8.38	8.25
Suchodus durobrivensis	NHMUK PV R 2618	18.67	25.64
'*Thalattosuchus*' *superciliosus*	GLAHM V1005	18.90	41.70
'*Thalattosuchus*' *superciliosus*	GLAHM V960	14.99	39.00
Thalattosuchus superciliosus	NHMUK PV R 1530	18.31	38.48
Thalattosuchus superciliosus	NHMUK PV R 2032	3.78	31.67
Thalattosuchus superciliosus	NHMUK PV R 2054	2.73	26.04
Torvoneustes carpenteri	BRSMG Cd7203	–5.47	10.57
Tyrannoneustes lythrodectikos	GLAHM V1145	14.99	24.46

locomotor positions as in Crocodylia. Moreover, the femoral anteversion of thalattosuchians could mean that their femoral head resting stance was positioned more dorsally (within the acetabulum) than in Crocodylia and Dyrosauridae, and that Thalattosuchia diverged from the group prior to the evolution of the double sigmoid of the femur. Indeed, Thalattosuchia is often recovered at the base of the crocodyliform (Wilberg 2015a; Jouve & Jalil 2020) or crocodylomorph radiation (Wilberg *et al.* 2023).

In comparison, the femur of terrestrial mesoeucrocodylians also displays a lesser sigmoid profile due to a relatively straight shaft (e.g. *Araripesuchus tsangatsangana* [Turner 2006], *Stratiotosuchus maxhechti* [Riff & Kellner 2011], *Yacarerani boliviensis* [Leardi *et al.* 2015], *Pissarrachampsa sera* [Godoy *et al.* 2016], *Sebecus icaeorhinus* [Pol *et al.* 2012]). In addition, their femur shows a distal twisting of the condyles (about 45° for *Araripesuchus tsangatsangana* [Turner 2006], and *Yacarerani boliviensis* [Leardi *et al.* 2015]) ; about 36° for *Stratiotosuchus maxhechti* [Riff & Kellner 2011]) inferior to what is observed in some extant crocodylians (about 65°; Parrish 1986). The overall shape of the femur of terrestrial mesoeucrocodylians impacts the orientation of proximal muscles compared to extant crocodylians (Romer 1923; Turner 2006; Riff & Kellner 2011; Pol *et al.* 2012; Leardi *et al.* 2015; Godoy *et al.* 2016).

The femora of *Araripesuchus tsangatsangana* Turner (2006), *Sebecus icaeorhinus* (Pol *et al.* 2012) and *Yacarerani boliviensis* (Leardi *et al.* 2015) display a gracile shape, whereas the femur of *Stratiotosuchus maxhechti* (Riff & Kellner 2011) has a stouter aspect (due to a thick shaft and large proximal and distal extremities). Several traits further differentiate the terrestrial mesoeucrocodylians, some of which are listed below. For example in *Araripesuchus tsangatsangana* the proximal head is anteromedially titled (about 25°) and shows a marked constriction directly underneath it, plus it displays a prominent fourth trochanter and a 'cranial flange' (Turner 2006); in *Yacarerani boliviensis* the constriction and fourth trochanter are less marked, and the 'cranial flange' is not present (Leardi *et al.* 2015); in *Sebecus icaeorhinus* the proximal head shows a large medial proximal crest giving a bulged aspect to the proximal head, the 'cranial flange' is absent and the fourth trochanter is also reduced (Pol *et al.* 2012); in *Stratiotosuchus maxhechti* the femoral head is anteromedially tilted and the fourth trochanter is reduced Riff & Kellner (2011); in *Pissarrachampsa sera* the proximal head is medially tilted and shows a strong constriction underneath it (Godoy *et al.* 2016).

In the semi-aquatic mesoeucrocodylian *Mahajangasuchus insignis*, the sigmoid shape of the femur is more pronounced dorsally and ventrally, and the femoral head does not show an anteromedial inclination and thus appears more similar to extant crocodylians. The fourth trochanter is well-developed, and the shaft presents a strong constriction between the femoral head and fourth trochanter. In addition, the distal twisting of the condyles appears closer to extant crocodylians (Buckley & Brochu 1999).

The derived metriorhynchoid hindlimb greatly differs from that of teleosauroids and dyrosaurids as it depicts extreme modifications from the crocodyliforms *bauplan* (Steel 1973; Grigg & Kirshner 2015; Ristevski 2019), which are correlated with aquatic adaptations in other groups (like the reduction of the dorsal elements of the girdles, or the ventral deflection of the pelvic girdle; Krahl 2021). Indeed, the metriorhynchoid zygopodium and autopodium constitute together what can be interpreted as a seemingly rigid flipper according to the following traits: a stout and posteriorly arched tibia, a slightly shorter and thinner fibula, a reduced calcaneal tuberosity (i.e. heel), a reduced astralagus/intermedium, reduced tarsals (both in size and shape), a widened and blade-like first metatarsal, and a difference in the length of each metatarsal and phalanx causing a shift between the joint surfaces mediolaterally, similar to otariids (Hocking *et al.* 2018). In addition, the femur of some metriorhynchoids (and teleosauroids) shows a slight dorsoventral curvature in addition to the relative ventral deflection of their femoral head (e.g. '*Metriorhynchus*' *brachyrhynchus* NHMUK PV R 4763, *Dakosaurus maximus* SMNS 8203, *Suchodus durobrivensis* NHMUK PV R 2618, etc.). Putatively, the curvature of the femur prevents its anterior movements from meeting the abdomen. Metriorhynchoids (with the exception of basal members) presumably lacked the ability to travel across land *contra* teleosauroids or dyrosaurids. This hypothesis stems from first the imbalance between their long and distally stiff tail and their short overall limbs (Herrera *et al.* 2017), but also from the whole limb morphology. Indeed, the metriorhynchoid femur lacks the typical crocodyliform dorsoventral sigmoid curve (as it is dorsoventrally convex), has extremely reduced distal condyles (both forming a convex dome without a trochlea), and a femoral anteversion. These traits make it unlikely for a functional knee to be present,

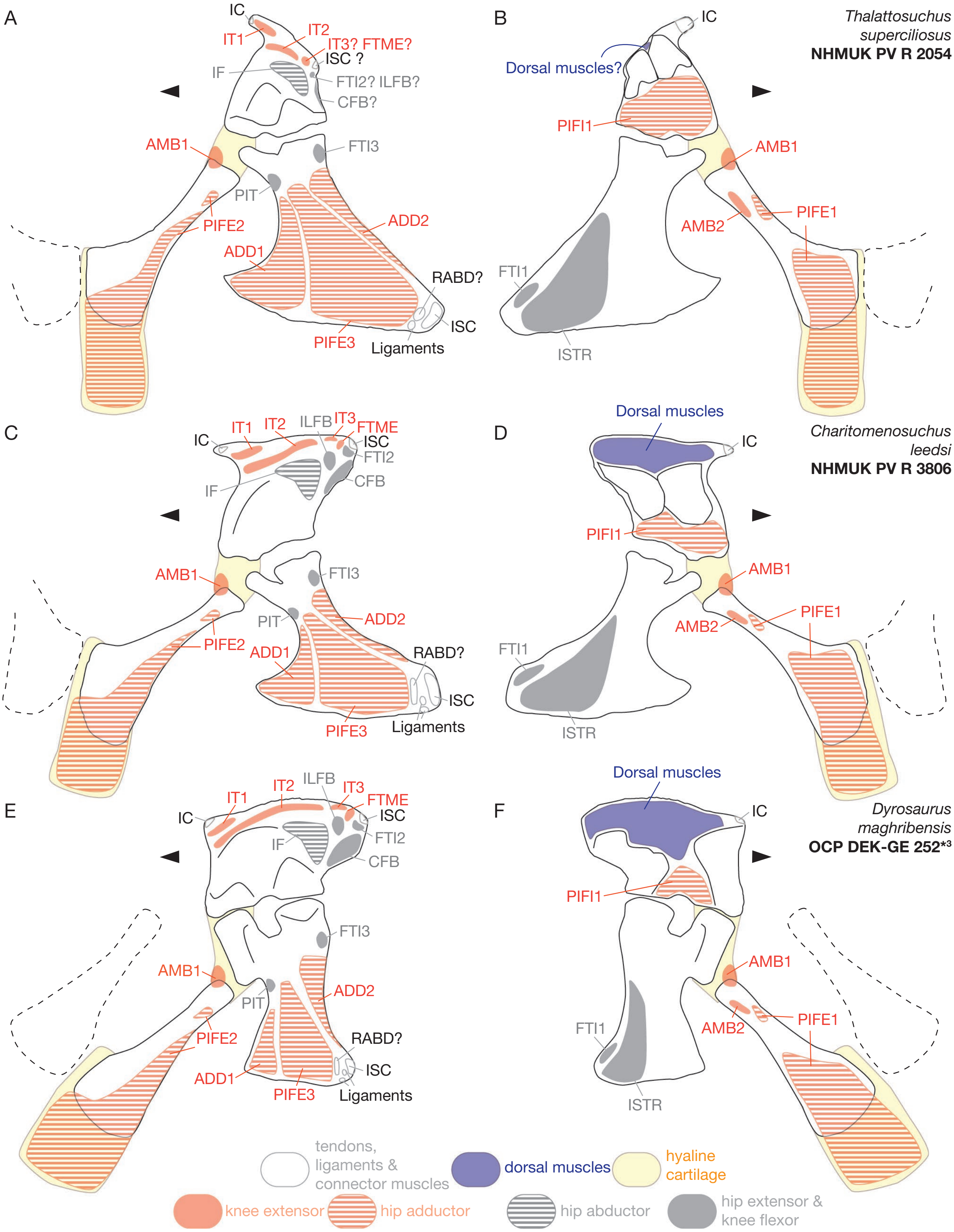


FIG. 90. — Hypothetical generalized reconstruction of the pelvic girdle musculature of extinct crocodyliformes. Drawings based on: **A**, **B**, *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852), NHMUK PV R 2054; **C**, **D**, *Charitomenosuchus leedsi* (Andrews, 1909), NHMUK PV R 3806; **E**, **F**, *Dyrosaurus maghribensis* Jouve, Iarochène, Bouya & Amaghzaz, 2006, OCP DEK-GE 252; **A**, Metriorhynchoidea in lateral view; **B**, Metriorhynchoidea in medial view; **C**, Teleosauroidea in lateral view; **D**, Teleosauroidea in medial view; **E**, Dyrosauridae in lateral view; **F**, Dyrosauridae in medial view. Muscle reconstructions based on the works of Romer (1923), Otero *et al.* (2010) and Allen *et al.* (2014). For scale bars, see the other Figures in the article.

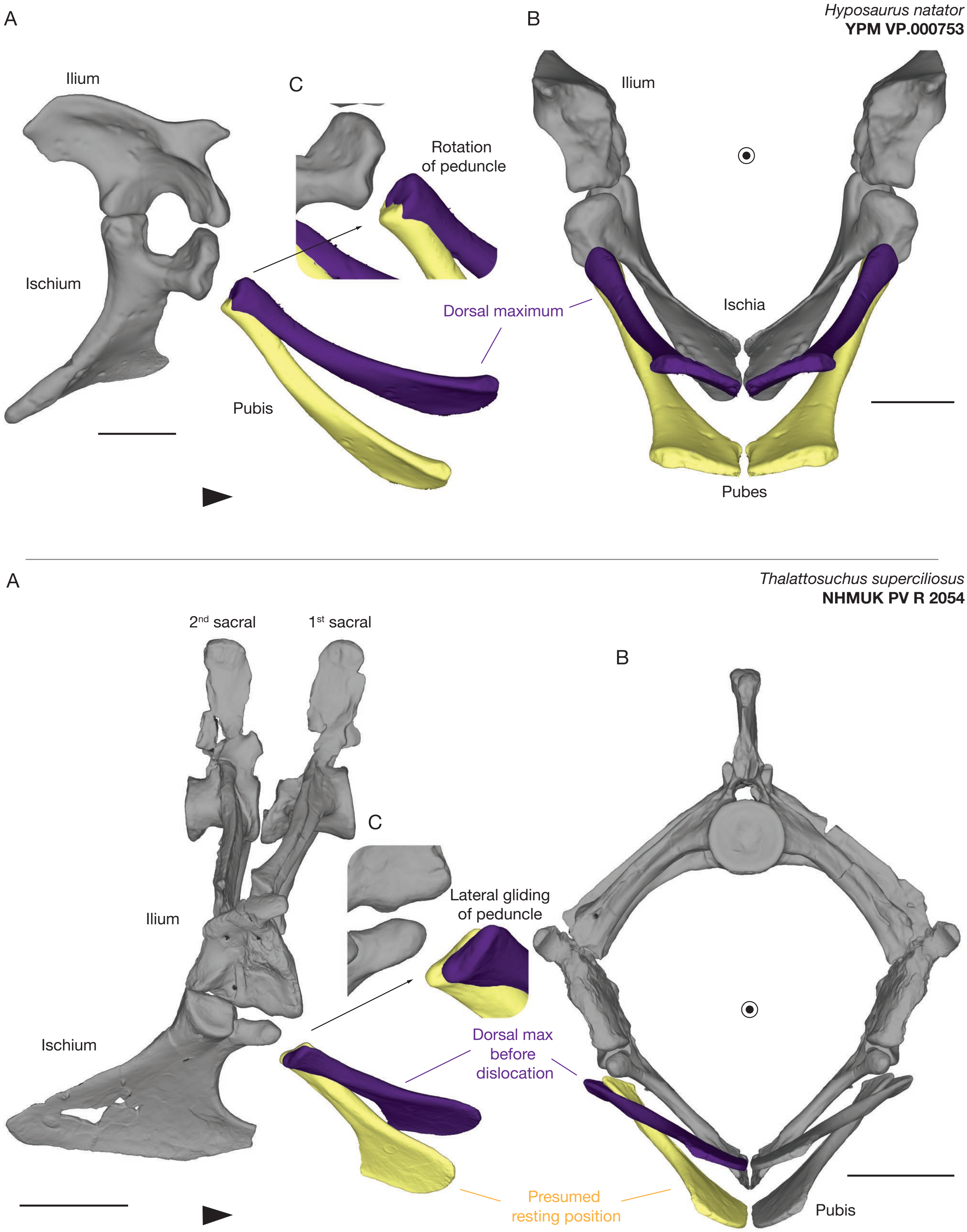


Fig. 91. — Pelvic girdle of *Hyposaurus natator* (Troxell, 1925), YPM VP.000753 and *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852), NHMUK PV R 2054, showing the possible motion of the pubis. **Yellow** represents the resting stance; **purple** represents the maximum dorsal position. **A**, lateral view; **B**, anterior view; **C**, detail of the pubic peduncle. **Target** indicates anterior. **Arrow** points anteriorly. The left ilium, ischium and pubis of *Hyposaurus natator* are mirrored. The ischium of of *Hyposaurus natator* has been partially reconstructed. The right ilium, ischium and pubis of *Thalattosuchus superciliosus* are mirrored. Scale bars: 5 cm.

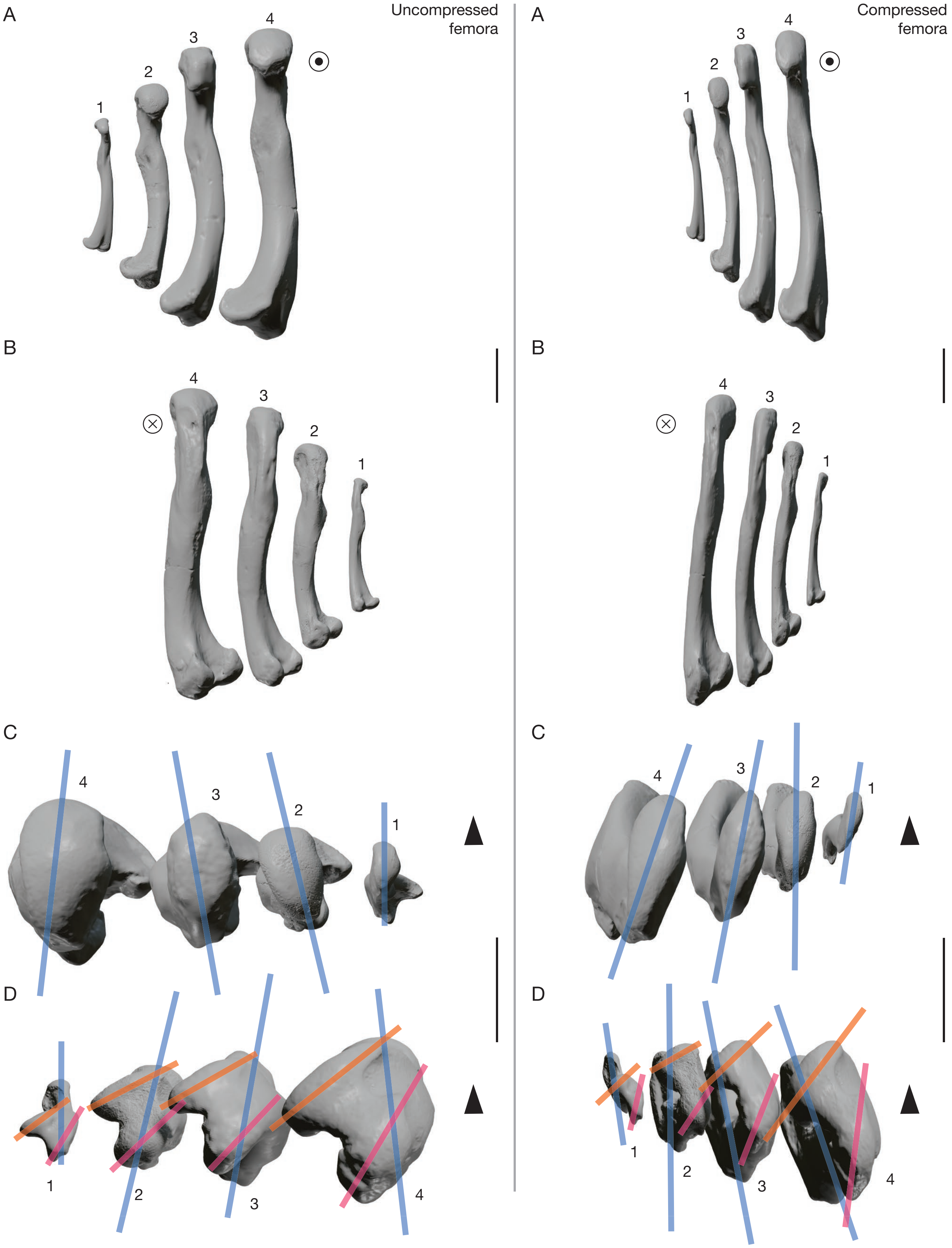


FIG. 92. — Comparative figures illustrating the dorsoventral compression Crocodyliformes femora using the unidirectional scaling tool in Blender (version 3.6.2). In the compressed femora, the distal condyles appear further squashed, not reoriented: **1**, *Mecistops cataphractus* Cuvier, 1825, RBINS 18374; **2**, *Hyposaurus natator* (Troxell, 1925), NJSM 23368; **3**, *Hyposaurus natator,* YPM VP.000753 ;4: *Congosaurus bequaerti* Dollo, 1914, MRAC 1817; **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view. **Blue line** represents main axis of femoral head; **orange line** indicates main axis of medial distal condyle; **fuchsia line** indicates main axis of lateral distal condyle. **Target** indicates anterior. **Cross** indicates posterior. **Arrow** points anteriorly. Scale bars: 5 cm.

meaning that metriorhynchoids presumably still had a working articulation between the femur and tibia-fibula, but they could not rely on it to carry their weight. Furthermore, the zygopodium and autopodium of metriorhynchoids (e.g. *Cricosaurus suevicus* [Fig. 19], *Cricosaurus albersdoerferi* [Fig. 20], *Rhacheosaurus gracilis* [Fig. 83]) appear to have formed a relatively stiff paddle fin which was probably unable to support the body vertically or even propel it horizontally due to a lack of a working ankle joint and an unbendable fin (see below). Indeed, in metriorhynchoids, the astralagus/intermedium and calcaneum/fibulare are reduced (e.g. see *Cricosaurus albersdoerferi* on Fig. 20) both in size and shape, which impacts the flexibility, rotation, and support of the ankle compared to that of Crocodylia (Grigg & Kirshner 2015). Hence, terrestrial locomotion seems unlikely for metriorhynchoids (Herrera *et al.* 2017), even though the length of their femur might evoke the possibility (Motani & Vermeij 2021).

On the contrary, most teleosauroids (e.g. especially *Lemmysuchus obtusidens*, *Platysuchus multiscrobiculatus*, and *Mycterosuchus nasutus* Johnson *et al.* (2022)) and basal metriorhynchoids (e.g. *Pelagosaurus typus*, *Magyarosuchus fitosi* [Ősi *et al.* 2018]) were presumably able to wander over land, although pre-″ sumably not as efficiently as most extant crocodylians, due to both the size of their limbs and their functional articulations. Indeed, the distal extremity of their femur is relatively well-developed as it presents two distinct condyles separated by the trochlea posteriorly. Still, the distal condyles of teleosauroids are less developed than in crocodylians or dyrosaurids (Fig. 93). In teleosauroids, the medial condyle is smaller and less protruding than the lateral condyle which slightly tilts the whole articular surface ventrally and helps counter the femoral anteversion. Another feature in favour of the relative terrestriality of teleosauroids and basal metriorhynchoids (Ősi *et al.* 2018) are the shape of the ilium and the shorter and stouter sacral ribs which place the pelvic girdle almost on the same level as the axial skeleton as opposed to Metriorhynchidae. As mentioned earlier, the anteversion of the femur in teleosauroids and basal metriorhynchoids presumably impacted the orientation of the femur (and knee) during terrestrial locomotion. Nevertheless, it is highly unlikely that adult teleosauroids and basal metriorhynchoids could perform either the sprawling nor high walk due to their elongated hindlimbs but short forelimbs, similar to adult gharials which only use a 'sprawling belly slide' locomotion mode (Grigg & Kirshner 2015). The anteversion of the teleosauroid and basal metriorhynchoid femur appears most efficient for this type of locomotion, with the zeugopodia and stylopodia directly in line with the greatest axis of the femur.

The caiman (alligatoroid) *Palaeosuchus palpebrosus* displays an anteversion of the femur superficially comparable to what is observed in teleosauroids (Table 13; Figs 94, 95), and thus differs from the higher angular values of *Mecistops cataphractus* and hyposaurine dyrosaurids (Table 13; Fig. 94). However, teleosauroid femora show a greater dorsal sigmoid curvature, a ventrally deflected femoral head, and also lack the presence of a well-developed fourth trochanter. Still, crocodylians, dyrosaurids and most teleosauroids display a functional ankle which allowed them to set their autopodium perpendicular to their zeugopodium on the ground and lean on it (Grigg & Kirshner 2015). In teleosauroids, the latter is also notably reflected in the degree of anteversion of their femur and in the relative development of their articular distal facets compared to metriorhynchoidea.

HIND FIN SHAPE

Fin shape in ichthyosaurians vs plesiosaurians vs thalattosuchians (Fig. 83; *Rhacheosaurus gracilis* NHMUK PV R 3948).

There is no osteological evidence in the stylopodium and zygopodium of metriorhynchoids and teleosauroids that would suggest the existence of a posterior thinning – or trailing edge – of the fin in that area. Hence, the thalattosuchian hindlimb does not appear teardrop -shaped in cross section, unlike ichthyosaurians or plesiosaurians (Fischer *et al.* 2012; Gutarra & Rahman 2022). In metriorhynchoids, the portion of the leg encompassing the zeugopodium and stylopodium seems fleshy and rod-like (Fig. 99), and does not seem to contribute to a teardrop profile either (e.g. *Cricosaurus albersdoerferi* [Fig. 20]; *Rhacheosaurus gracilis* [Fig. 83]; see also Ammon [1905]). In comparison, the autopodium forms a svelte structure with little tissue filling it out (e.g. *Cricosaurus albersdoerferi* [Fig. 20]; *Rhacheosaurus gracilis* [Fig. 83]). In relatively complete slab-specimens of derived metriorhynchoids, both hindlimbs display a symmetrical and posteriorly curved stance with differing positions of the femur ranging from perpendicular to parallel to the axial skeleton. This conveys a potentially high mobility of the limb in the sagittal plane posteriorly. Different degrees of inclination between the femur and the zeugopodium are also observed, hinting at a relatively functional knee articulation allowing some flexion of the distal fin (i.e. the stylopodium and autopodium). The autopodium is directly in line with the zeugopodium and formed a rigid flipper due to the disjointed articulation lines of the phalanges and the smooth shape plus planar orientation of tarsal and ankle elements (i.e. calcaneum/fibulare and astralagus/intermedium). In comparison, the forelimb of derived metriorhynchoids constitutes a short fin close to the body, with a rounded outline. The autopodium and zeugopodium of the forelimb are modified to form a tightly packed and curved paddle, whose fleshy portion was presumably limited to the surrounding of the humerus.

In teleosauroids, the thigh and calf were relatively thicker as seen in SMNS 10985 (*Macrospondylus bollensis*) where soft tissues are finely preserved (Fig. 100). Hence, it is possible that teleosauroids possessed a certain amount of blubber deposits, similar to other aquatic tetrapods (Gutarra & Rahman 2022). Skin details on this specimen also show an array of fine scales, relatively smaller than those of extant crocodylians (Grigg & Kirshner 2015). This smoother skin could be seen as a step towards drag reduction similar to metriorhynchoids, but to a lesser extent. The skin also appears to wrinkle alongside major scale pattern ramifications, which conveys the idea of a relative softness and presumably elasticity of the skin (which also helps reduce drag by absorbing energy deformations; see Gutarra & Rahman 2022).

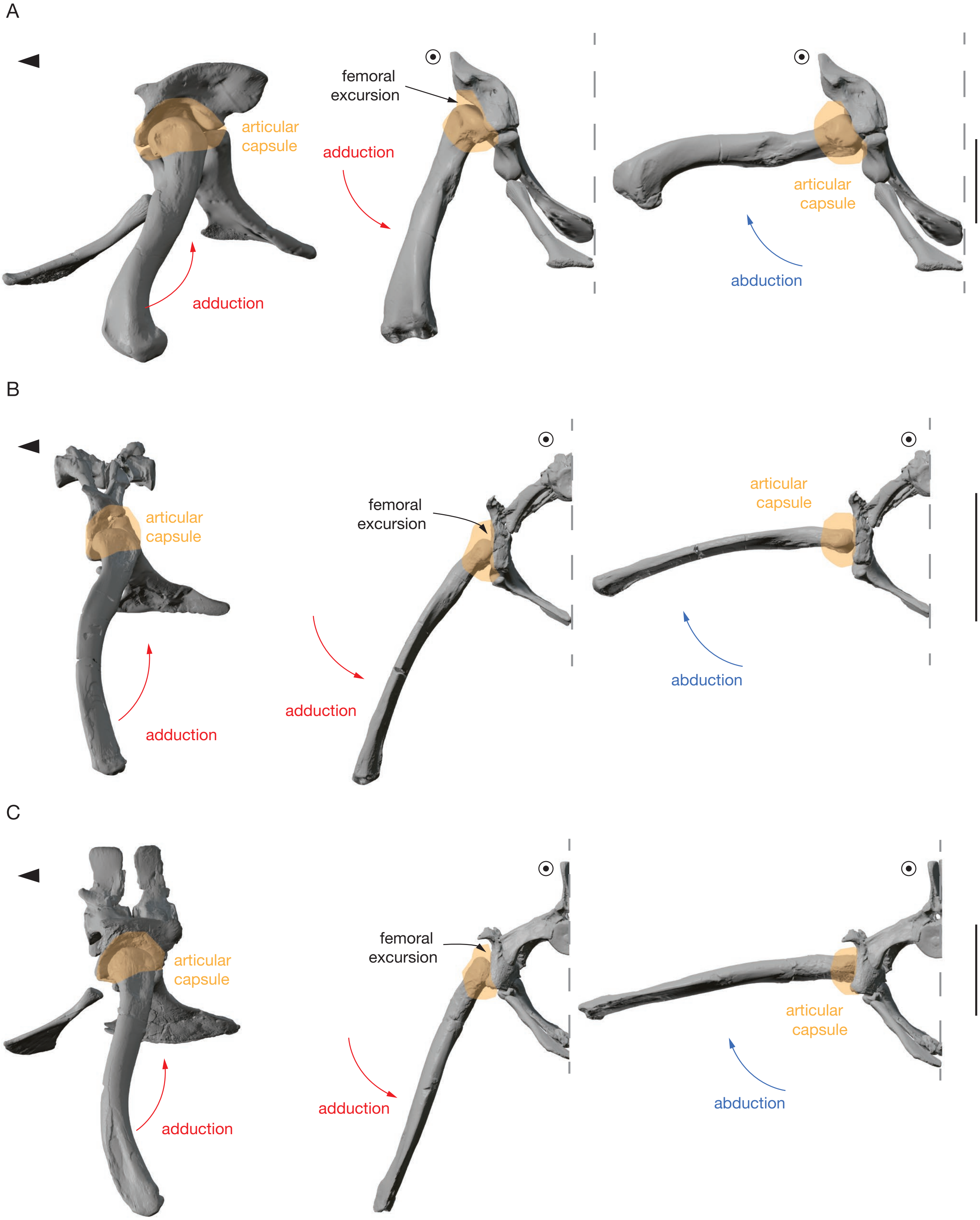


FIG. 93. — Comparison of the adduction and abduction movements with similar femoral head orientation between Dyrosauridae, Metriorhynchoidea and Teleosauroidea in lateral and anterior views: **A**, *Congosaurus bequaerti* Dollo, 1914 (holotype); **B**, '*Metriorhynchus*' *brachyrhynchus* (Eudes-Deslongchamps, 1867), NHMUK PV R 4763; **C**, *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 3701. **Target** indicates anterior. **Arrow** points anteriorly. Scale bars: 10 cm.

The autopodium of teleosauroids (Fig. 100) presumably resembled the webbed paws of extant crocodylians (Grigg & Kirshner 2015). On the contrary, the hands and feet of metriorhynchoids formed a rigid paddle, incapable of folding due to the arrangement of their phalanges (e.g. *Rhacheosaurus gracilis* and *Cricosaurus albersdoerferi* [Figs 20; 100]).

SUMMARY

In this contribution, we thoroughly compare and revise the terminology of the pelvic anatomy of thalattosuchians and dyrosaurids with extant crocodylians. Here is a summary of the major differences and innovations in those lineages.

Compared to dyrosaurids and extant crocodylians, thalattosuchians display relatively longer and more ventrally deflected sacral ribs. Within Thalattosuchia, metriorhynchoids bear their pelvic girdle generally more ventrally (i.e. the ilium is ventral to the sacral vertebrae) than teleosauroids, overall resulting in proportionally more tilted and elongated sacral ribs. Still, there are exceptions to this general trend, like for example the metriorhynchid *Suchodus durobrivensis* which has short sacral ribs. The lengthening of the sacral ribs and ventral shifting of the pelvic girdle increases the available space in the abdominal cavity, and also creates a relatively circular cross-section. By reducing the pelvic constriction, it also produces a smoother and less abrupt thoracic to pelvic transition, which further helps the thoracic ribs shape the trunk into a compact cylinder in extreme pelagic forms (e.g. *Rhacheosaurus gracilis* and *Cricosaurus* species). In teleosauroids, the overall position of the ilium is slightly variable, with more derived taxa (e.g. *Neosteneosaurus edwardsi*, *Lemmysuchus obtusidens*, and *Machimosaurus*) bearing their ilium more ventrally in relation to the sacral vertebrae. The relatively longer ribs of teleosauroids compared to dyrosaurids and extant crocodylians also increases the relative mediolateral width of their pelvic area, without reaching metriorhynchoid levels. Still, the proportionally shorter sacral ribs of teleosauroids compared to metriorhynchoids supposedly reflects their ability to carry their own mass on land. In comparison, the ilium of extant crocodylians and dyrosaurids is more centred with respect to the axial skeleton due to their relatively more horizontal sacral ribs. In addition, their attachment sites are not adjacent as in thalattosuchians, which presumably conveys more stability for terrestrial locomotion.

In metriorhynchids, the dorsal element of their pelvic girdle – the ilium – is reduced, as in other pelagic reptilians, presumably as a consequence of a fully pelagic lifestyle and the subsequent loss of load-bearing requirements for the pelvic girdle. The ilium of metriorhynchids got reduced in size while still maintaining the parts involved in the hip articulation – the bony acetabulum and peduncles. This reflects the necessity to keep a certain hindlimb flexibility, either for steering or active swimming (e.g. paraxial swimming, rowing or underwater flight). The most noticeable expression of this reduction concerns the 'loss' of the postacetabular process, which results in a lower muscle density on the ilium through the diminution in size or number of muscle attachments. The latter presumably had a direct impact on the strength and/or rapidity of execution of limb movements compared to other thalattosuchians, dyrosaurids and extant crocodylians. The reduction of the ilium also happened at the expense of the acetabular perforation. As a result, the acetabular perforation of metriorhynchids is markedly diminished and sometimes only forms a subtle notch along the ventral margin of the ilium. Another consequence of the shortening of the ilium and acetabular perforation is the coalescence of both peduncles, which form a continuous structure and are not clearly separated by the acetabular perforation. Hence, in metriorhynchids, the transition between the pubic and ischial peduncle is indicated by the emergence of a dorsally tall triangular shape along their lateral outline (usually preceded by a recess) and the concomitant indentation of the acetabular perforation along the ventral margin of the bone. Besides its coalescence with the pubic peduncle, the ischial peduncle of the ilium of metriorhynchids displays its common triangular shape whose posterior half is laterally protruding as well, as in other crocodylomorph clades (e.g. Teleosauroidea, Crocodylia, and Dyrosauridae). In comparison, the pubic peduncle shows a varying array of small triangular peaks (usually two) which are always dorsoventrally shorter than the ischial peduncle. Other major modifications of the ilium of metriorhynchids concern the diminution of the dorsal margin and the migration of the sacral ribs attachment sites. Indeed, the dorsal margin of the ilium is shortened and also markedly tilted in relation to the ventral margin, which leads to the anterodorsal reorientation of the preacetabular process.

The latter is well-developed and forms a relatively slender process as in other thalattosuchians, unlike extant crocodylians and dyrosaurids which present a bulkier process. The preacetabular process of metriorhynchids would potentially host most of the knee extensor muscles, which would otherwise be spread across the dorsal margin and postacetabular process. On the medial side of the ilium, the attachment sites of the sacral ribs are found along the dorsal margin, rather than centred as in other thalattosuchians, dyrosaurids and extant crocodylians, which also considerably decreases the available space for dorsal muscles and the overall stability of the pelvic girdle.

In comparison, the ilium of basal metriorhynchoids and teleosauroids is more similar to extant crocodylians and dyrosaurids, namely in possessing a well-developed postacetabular process as well as centred sacral ribs attachment sites on the medial side of the bone (even though differing in sacral rib's lengths). In teleosauroids, the attachment sites are adjacent and share a moderately long margin, as in metriorhynchoids but unlike dyrosaurids and extant crocodylians. In the large and relatively more terrestrial teleosauroid *Lemmysuchus obtusidens*, the ilium shows an additional attachment site anteriorly for the first caudal vertebra, which presumably granted more stability to the girdle during terrestrial locomotion. The centred position of the sacral rib attachment sites offers a large area for dorsal muscles, which connect the trunk and tail to the ilium and sacral ribs in extant crocodylians. In addition, the

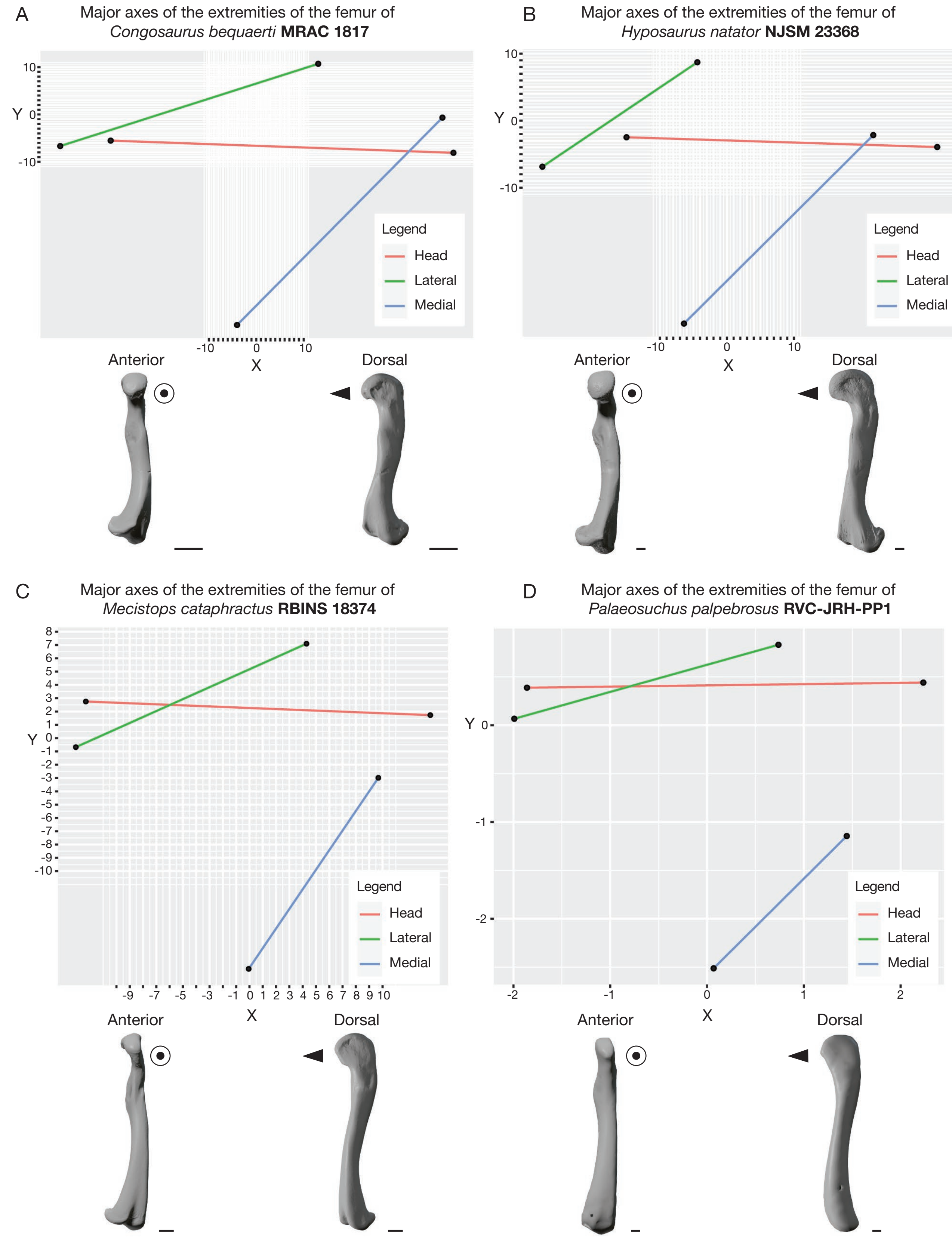
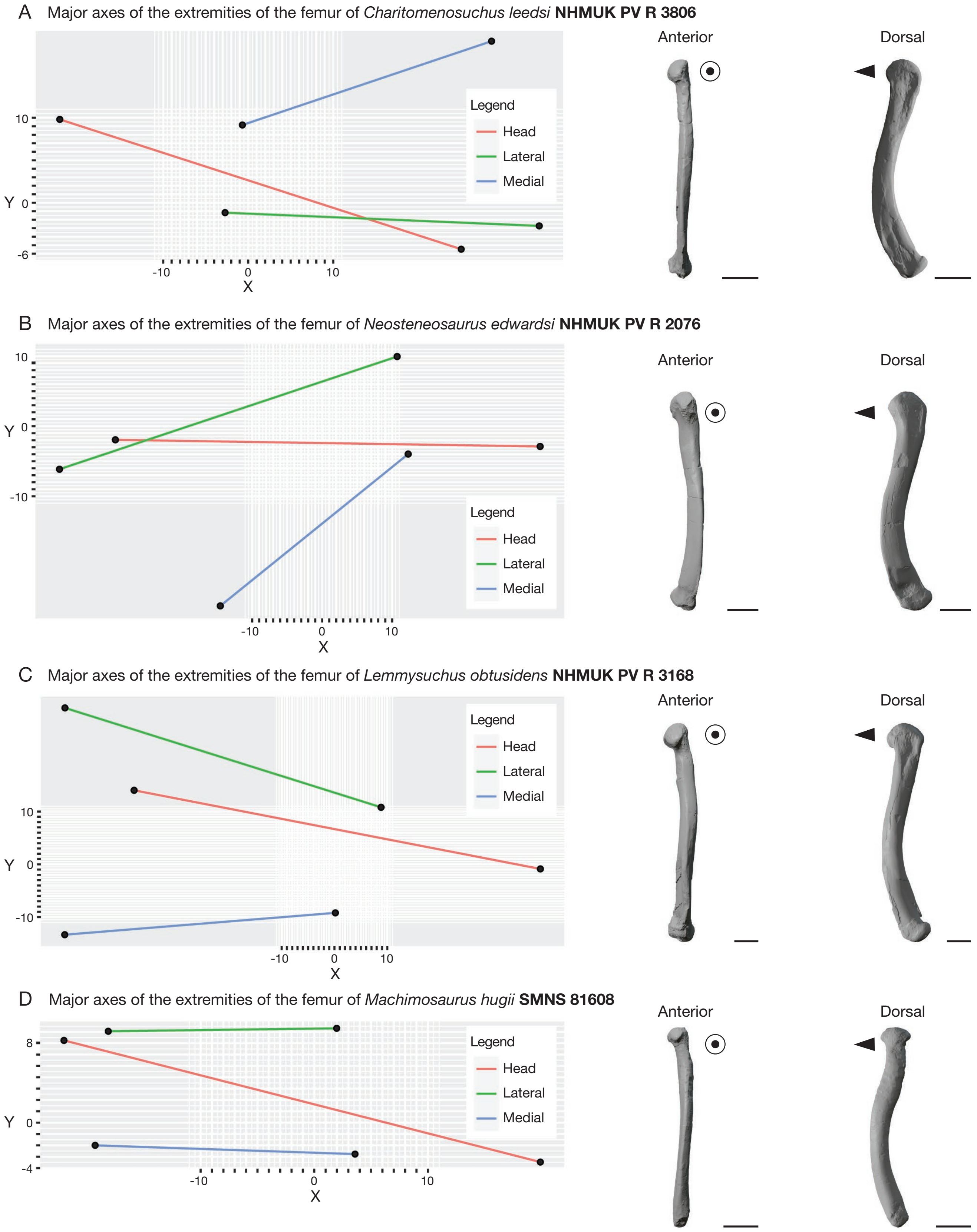


FIG. 94. — Projected great axes of the femoral condyles and head onto a X-Y plane perpendicular to the greatest axis of the femur: **A**, *Congosaurus bequaerti* Dollo, 1914, MRAC 1817; **B**, *Hyposaurus natator,* NJSM 23368; **C**, *Mecistops cataphractus* Cuvier, 1825, RBINS 18374; **D**, *Palaeosuchus palpebrosus* Cuvier, 1807, RVC-JRH-PP1. Femora with anteversion will display similar orientations of the greatest axis of the distal condyles and the femoral head. Scale bars: A, 5 cm; B-D, 1 cm.



A Major axes of the extremities of the femur of *Charitomenosuchus leedsi* **NHMUK PV R 3806**

B Major axes of the extremities of the femur of *Neosteneosaurus edwardsi* **NHMUK PV R 2076**

C Major axes of the extremities of the femur of *Lemmysuchus obtusidens* **NHMUK PV R 3168**

D Major axes of the extremities of the femur of *Machimosaurus hugii* **SMNS 81608**

Fig. 95. — Projected great axes of the femoral condyles and head onto a X-Y plane perpendicular to the greatest axis of the femur: **A**, *Charitomenosuchus leedsi* (Andrews, 1909), NHMUK PV R 3806; **B**, *Neosteneosaurus edwardsi* (Eudes-Deslongchamps, 1868), NHMUK PV R 2076; **C**, *Lemmysuchus obtusidens* (Andrews, 1909), NHMUK PV R 3168; **D**, *Machimosaurus* sp., SMNS 81608. **Target** indicates anterior. **Arrow** points anteriorly. Femora with anteversion will display similar orientations of the greatest axis of the distal condyles and the femoral head. Scale bars: 5 cm.

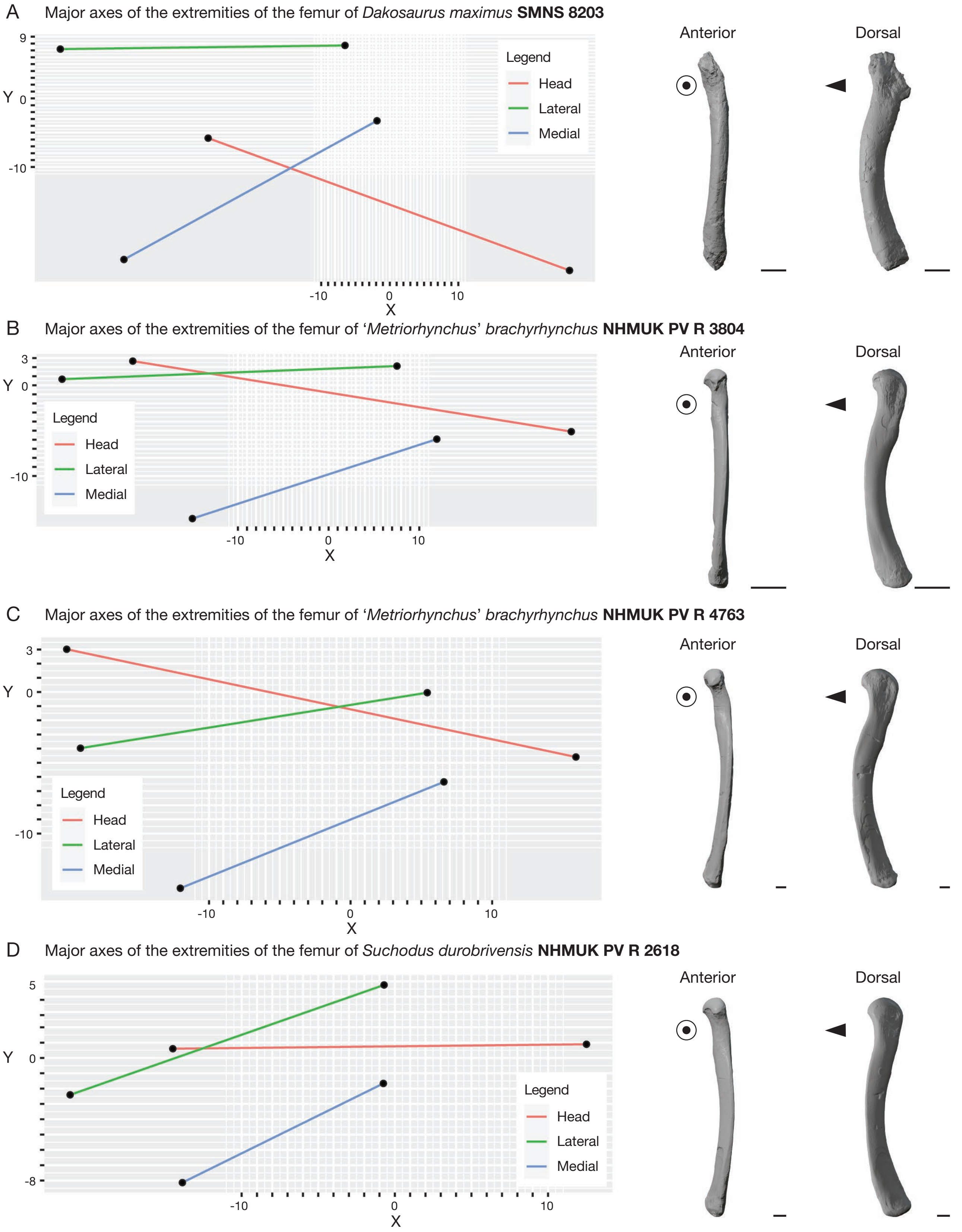


FIG. 96. — Projected great axes of the femoral condyles and head onto a X-Y plane perpendicular to the greatest axis of the femur: **A**, *Dakosaurus maximus* (Plieninger, 1846), SMNS 8203; **B**, ‘*Metriorhynchus*’ *brachyrhynchus* (Eudes-Deslongchamps, 1867), NHMUK PV R 3804; **C**, ‘*Metriorhynchus*’ *brachyrhynchus,* NHMUK PV R 4763; **D**, *Suchodus durobrivensis* Lydekker, 1890, NHMUK PV R 2618. **Target** indicates anterior. **Arrow** points anteriorly. **Femora** with anteversion will display similar orientations of the greatest axis of the distal condyles and the femoral head. Scale bars: A, B, 5 cm; C, D, 1 cm.

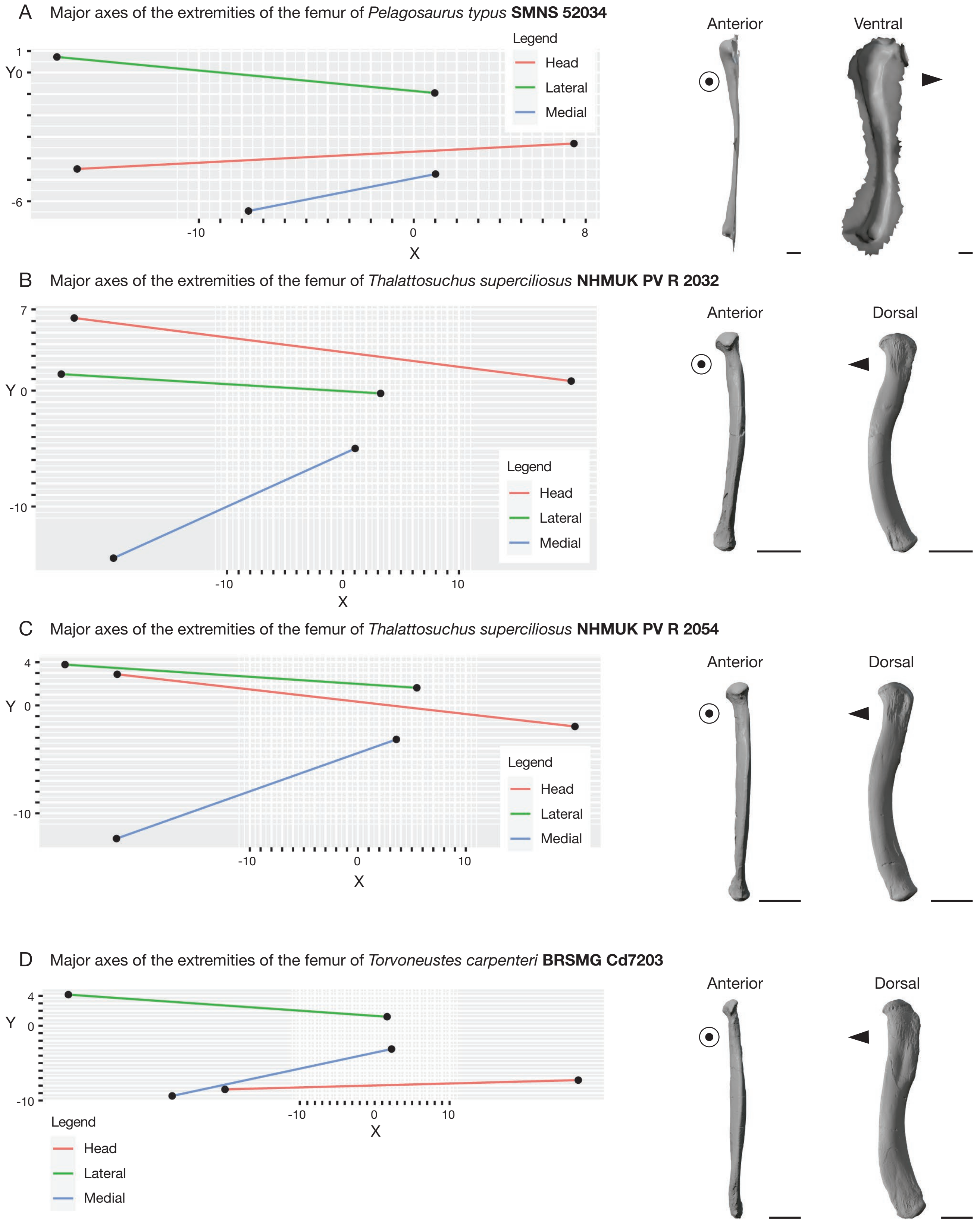
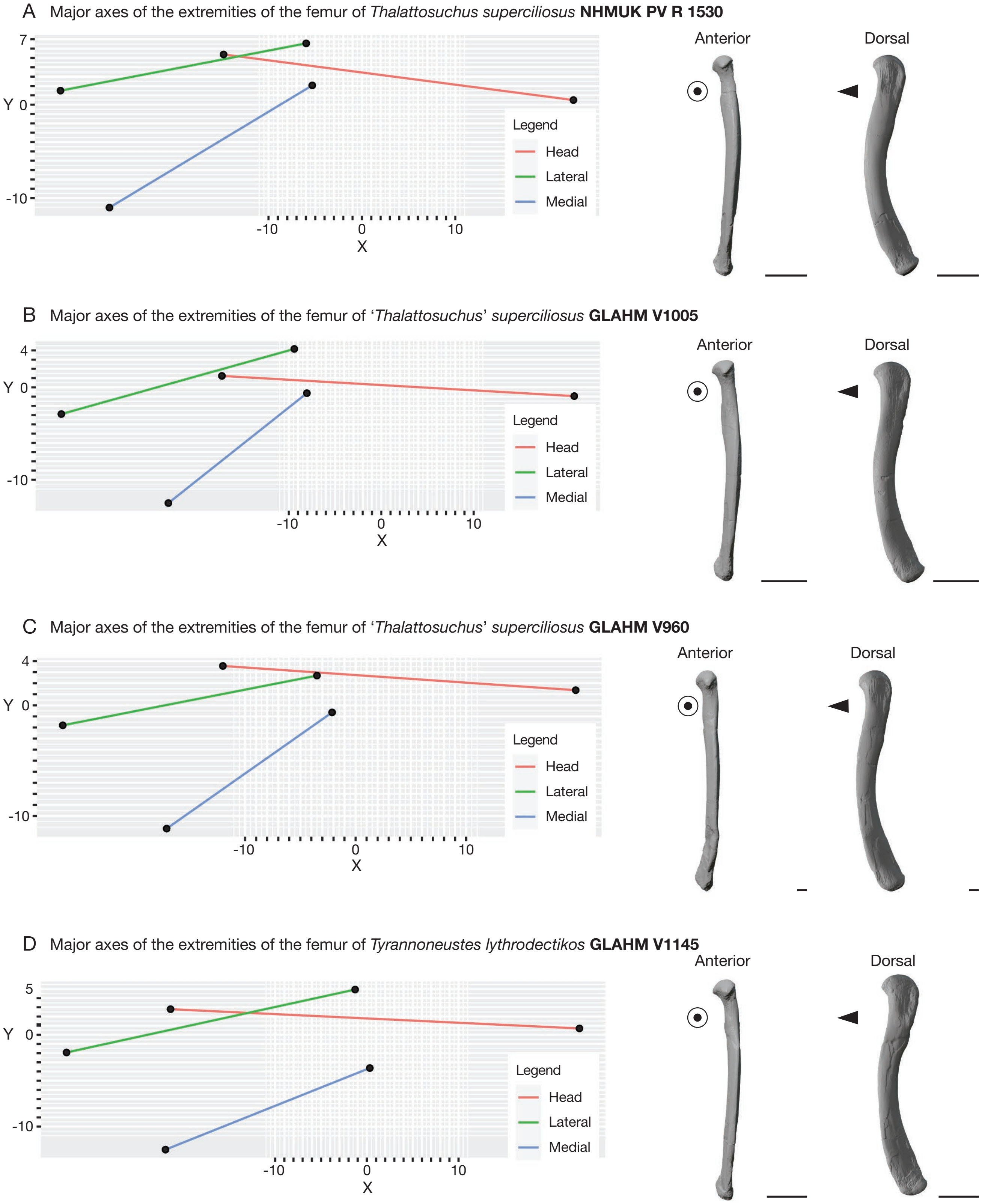


FIG. 97. — Projected great axes of the femoral condyles and head onto a X-Y plane perpendicular to the greatest axis of the femur: **A**, *Pelagosaurus typus* Bronn, 1841, SMNS 52034; **B**, *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852), NHMUK PV R 2032; **C**, *Thalattosuchus superciliosus,* NHMUK PV R 2054; **D**, *Torvoneustes carpenteri* (Wilkinson, Young & Benton, 2008), BRSMG Cd7203. **Target** indicates anterior. **Arrow** points anteriorly. Femora with anteversion will display similar orientations of the greatest axis of the distal condyles and the femoral head. Scale bars: A, 1 cm; B-D, 5 cm.



A Major axes of the extremities of the femur of *Thalattosuchus superciliosus* **NHMUK PV R 1530**

B Major axes of the extremities of the femur of ‘*Thalattosuchus*’ *superciliosus* **GLAHM V1005**

C Major axes of the extremities of the femur of ‘*Thalattosuchus*’ *superciliosus* **GLAHM V960**

D Major axes of the extremities of the femur of *Tyrannoneustes lythrodectikos* **GLAHM V1145**

FIG. 98. — Projected great axes of the femoral condyles and head onto a X-Y plane perpendicular to the greatest axis of the femur: **A**, *Thalattosuchus superciliosus* (Blainville in Eudes-Deslongchamps & Blainville, 1852), NHMUK PV R 1530; **B**, ‘*Thalattosuchus*’ *superciliosus,* GLAHM V1005; **C**, ‘*Thalattosuchus*’ *superciliosus,* GLAHM V960; **D**, *Tyrannoneustes lythrodectikos* Young, de Andrade, Brusatte, Sakamoto & Liston, 2012, GLAHM V1145. **Target** indicates anterior. **Arrow** points anteriorly. Femora with anteversion will display similar orientations of the greatest axis of the distal condyles and the femoral head. Scale bars: A, B, D, 5 cm; C, 1 cm.

welldeveloped postacetabular process of basal metriorhynchoids and teleosauroids creates more space for hip abductors and extensors as well as knee extensor and flexor muscles compared to metriorhynchids. The size and shape of the postacetabular process fluctuates depending on the taxa, for example relatively basal teleosauroids (e.g. *Plagiophthalmosuchus gracilirostris*, *Platysuchus multiscrobiculatus*, and *Macrospondylus bollensis*) show a tubular postacetabular process whereas it has a more wider base in more derived machimosaurids and aeolodontines (e.g. *Sericodon jugleri*). In parallel, the more pelagic teleosauroids *Sericodon jugleri* and *Machimosaurus* show a slightly shortened postacetabular process, possibly in the early stages of reduction. Teleosauroids and basal metriorhynchoids further differ from metriorhynchids in displaying distinctly separated pubic and ischial peduncles. However, the dimensions of the acetabular perforation strongly vary between taxa, with some bearing deep semi-circular indentations (e.g. *Pelagosaurus typus* and *Sericodon jugleri*) and others showing shallower gaps (e.g. *Neosteneosaurus edwardsi* and *Lemmysuchus obtusidens*) or even more reduced notches (e.g. *Charitomenosuchus leedsi* and *Proexochokefalos* cf. *bouchardi*).

The ilium of dyrosaurids appears more similar to extant crocodylians than thalattosuchians due to its bulkier preacetabular process, large peduncles, well-developed acetabular perforation and spaced sacral ribs attachment sites. In comparison, the latter are relatively close in extant crocodylians but do not share an extended margin as in thalattosuchians. The gap between the sacral rib attachment sites of dyrosaurids is due to their position along the anterior and posterior borders of the ilium. This position and the relatively straight sacral ribs of dyrosaurids presumably offered more stability to the girdle during terrestrial locomotion compared to thalattosuchians. The bony acetabulum of dyrosaurids is slightly more compressed anteroposteriorly and possibly slightly medially deeper than extant crocodylians, due to the different orientation of the pubic and ischial peduncles. The latter are distinct and separated by the acetabular perforation, which forms a relatively marked notch along the ventral margin of the ilium. Still, its dimensions vary depending on the taxon, with *Congosaurus bequaerti* showing the smallest indentation compared to *Hyposaurus natator*, *Dyrosaurus maghribensis*, and *Acherontisuchus guajiraensis*. The most remarkable trait of the dyrosaurid ilium is the enlarged postacetabular process forming a thick Lancet arch shape, which conveys a greater muscle density in terms of size or number of muscle attachments. These presumably offered increased stability to the pelvic girdle, as well as increased strength and rapidity of execution of limb movements. The enlarged area for dorsal muscles on the medial side of the ilium mirrors the massive axial musculature of dyrosaurids.

The overall shape of the thalattosuchian ischium strongly stands out from dyrosaurids and extant crocodylians. The thalattosuchian ischium shows a dorsoventrally shortened anterior peduncle, which is further reduced mediolaterally in metriorhynchoids. This shape seems to provide a more restricted range of motion for the pubis compared to extant crocodylians and dyrosaurids, which possibly glided mediolaterally rather than rotating. In parallel, it also suggests the existence of a larger cartilaginous structure encompassing the ischio-pubic articulation in Thalattosuchia, which was presumably even more developed in metriorhynchoids. The thalattosuchian ischium bears most of the acetabular perforation of the pelvic girdle, whereas the ilium proportionally displays a greater participation in dyrosaurids and extant crocodylians. The acetabular perforation is an osteological evidence for the presence of intrinsic ligaments (i.e. ligaments fused to the articular capsule of the hip and found within the synovial cavity, like the anterior and posterior ligamentum capitis). The acetabular perforation of dyrosaurids and thalattosuchians was presumably covered by a soft membrane, capable of accommodating the femoral movements causing the deformation of the soft articular capsule. The proportionally larger acetabular perforation of dyrosaurids presumably enabled a greater accommodation of femoral movements compared to thalattosuchians, which also depend on the overall shape of the femur and limb proportions. The shape and size of the acetabular perforation greatly varies within Thalattosuchia, but most taxa present it as a medially tilted sulcus with the peduncle bridge more or less obstructing it laterally. Overall, teleosauroids display a proportionally large acetabular perforation, greater than metriorhynchoids (e.g. *Sericodon jugleri*, *Indosinosuchus potamosiamensis*, *Macrospondylus bollensis*, *Charitomenosuchus leedsi*, *Neosteneosaurus edwardsi*, and *Lemmysuchus obtusidens*). This increased the surface of the membrane covering the perforation medially and presumably offered a better accommodation to femoral movements, supposedly reflecting the relative terrestrial capabilities of teleosauroids or a increased use of the femur for locomotion. Likewise, derived metriorhynchoids show a relative expansion in size of their acetabular perforation, implying a potentially greater range of movement of the femur. Another major trait of the thalattosuchian ischium is the elongated and untwisted distal blade with enlarged anterior and posterior processes. The prominent anterior process of the ischium in thalattosuchians could potentially hamper posterior motion of the pubis. Along the medial side, the ischial blade presents a scarred area – the ischial suture – throughout its length where it connected to the other blade, forming a large bony shield ventrally. The latter presumably improved the transmission of forces as well as the preservation of movement strength, offering an additional support function during locomotion. The width and overall inclination of the ischial suture varies across Thalattosuchia, as well as the length and thickness of the anterior and posterior process. Still, the large ischial blade of thalattosuchians supposes the presence of greater quantity of hip adductor and extensor muscles in terms of size and/or number of muscles attachments bridging the ischium and the ventral portion of the tail compared to dyrosaurids and extant crocodylians.

The dyrosaurid ischium possesses a twisted distal blade and a well-developed peduncles as in extant crocodylians. Still, the distal blade of dyrosaurids is proportionally larger, with more prominent anterior and posterior processes and subsequent increased area for hip adductors. In addition, the anterior

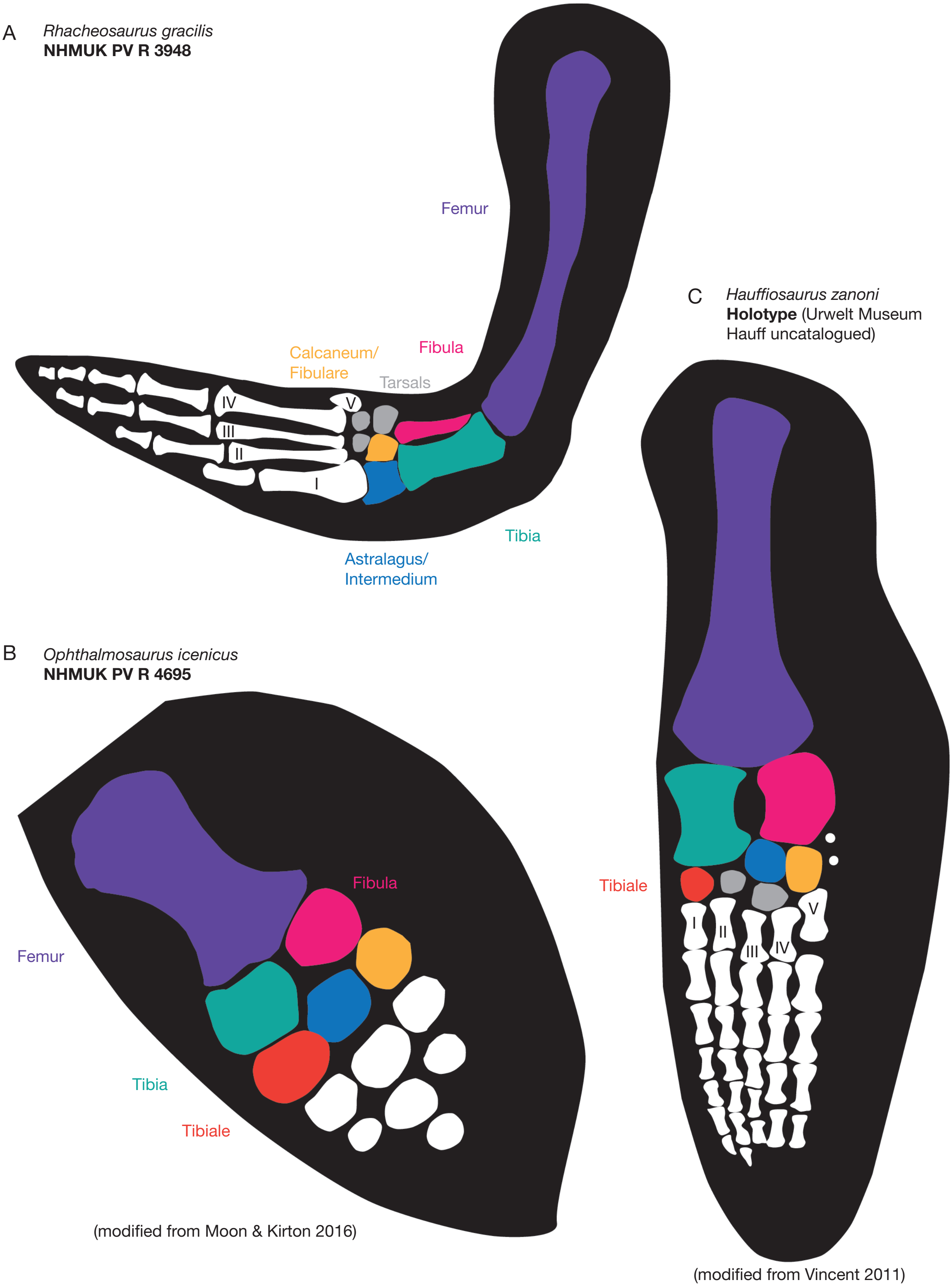


Fig. 99. — Comparison of hind fin shapes in three different clades of marine reptiles: **A**, Thalattosuchia; **B**, Ichthyosauria; **C**, Plesiosauria.

peduncle of dyrosaurids is larger than in extant crocodylians; it presents an extended articular facet anteroventrally – the pubic knob – to receive the pubis. Furthermore, the shape of the 'pubic knob' matches that of the peduncle of the pubis, which allowed them to stay in contact during pubic movement as opposed to thalattosuchians. This configuration presumably enabled a mix of anteroposterior motion and mediolateral rotation of the pubis, as in extant crocodylians.

Extant crocodylians possess a comparatively short pubic symphysis, which strongly contrasts with the enlarged pubic symphysis of dyrosaurids and most thalattosuchians. The latter presumably evolved it independently as basal metriorhynchoids and teleosauroids (namely *Plagiophthalmosuchus gracilirostris*, and *Macrospondylus bollensis*) have a shortened pubic symphysis. Some rhacheosaurines and geosaurines possess a proportionally reduced pubic symphysis as well, with a relatively broad pubic apron for a short overall proximodistal length. This configuration is similar to extant crocodylians, and their pubis was presumably covered with a relatively large cartilaginous cap distally. Those rhacheosaurines and geosaurines (as well as *Macrospondylus bollensis*) also show a proportionally greater acetabular perforation, enabling a wide range of motion for the femur. The peduncle of the pubis in dyrosaurids is more circular as in extant crocodylians, whereas it is markedly elliptic in thalattosuchians. The outline of the peduncle of the pubis do not match the anterior peduncle of the ischium in thalattosuchians, which possibly presented a more extensive cartilage cap. In addition, thalattosuchians possess a proportionally mediolaterally wider pubic apron, longer pubic symphysis and greater degree of inclination of the shaft in relation to the symphysis. These traits constitute important mechanical constraints during pubic movements, reducing the possible range of motion of the pubis before dislocation in Thalattosuchia. The thalattosuchian pubis is also proportionally shorter than in dyrosaurids, which places the pubic apron directly in line with the anterior process of the ischium, which presumably hampered potential posterior retractions of the pubis. In dyrosaurids, the pubic apron and anterior process of the ischium are set on different levels, due to the relative length of the pubis and its more ventral anchor on the anterior peduncle of the ischium ('pubic knob'). The dyrosaurid pubis possesses a relatively mediolaterally narrow apron, and its shaft is set at a lower angle to the pubic symphysis than in thalattosuchians, which enables a larger amplitude of movements before dislocation. The peduncle of the pubis is relatively circular and possesses a distinct anchoring surface of similar shape on the ischium which would promote axial rotation of the pubis, unlike in thalattosuchians. The pubic apron of dyrosaurids is also dorsally convex rather than concave like thalattosuchians, which would presumably require less rotational movement to mobilize the viscera. Whereas the existence of a highly mobile pubis is not an osteological correlation for hepatic respiration, it suggests that pelvic muscles of Thalattosuchia and Dyrosauridae presumably played a role in manoeuvrability and stability (control, posture, pitch and roll), as in extant crocodylians.

The femur of Dyrosauridae and Crocodylia shows a marked fourth trochanter, as well as a strongly protruding lateral condyle which extends further distally than the medial condyle, whereas those traits are more subtle in Thalattosuchia. Likewise, the articular facets of the distal condyles of Dyrosauridae and Crocodylia are bulbous (mediolaterally thick and markedly rounded) with a large trochlear gap; teleosauroids possess similar features but to a lesser extent.

The femoral head of thalattosuchians display an orientation closer to that of the distal condyles than what is observed in Crocodylia and Dyrosauridae, which we refer to as the femoral anteversion. The difference in the sigmoid shape of the femur between Crocodylia, Dyrosauridae and Thalattosuchia impacts the overall orientation of the femoral head during locomotion. It presumably resulted in different degree of femoral excursion in Thalattosuchia for a similar position of the femur than in Crocodylia and Dyrosauridae. In addition, the zeugopodia is directly in line with the stylopodium in Thalattosuchia, so that the knee displays a lateral orientation when that of Crocodylia and Dyrosauridae is oriented anterolaterally. This configuration impacted the range of motion of the hindlimb in Thalattosuchia, making terrestrial locomotion more difficult than in Crocodylia and Dyrosauridae. As a result, the thalattosuchian femur likely positioned differently than in Crocodylia and Dyrosauridae. The short forelimbs and long hindlimbs presumably prevented the sprawling or high-walk posture in adult teleosauroids and basal metriorhynchoids, as in adult gharials which solely employ the 'sprawling belly slide' locomotion mode.

In addition, the planar position of their hindlimbs appears most efficient for this type of locomotion.

Finally, the extreme pelagic metriorhynchids hindlimbs depicts extreme modifications from the crocodyliforms bauplan, with the zygopodium and autopodium forming a seemingly rigid flipper with no working ankle. Their femur displays the typical femoral anteversion, their distal condyles are strongly reduced, and their shaft is slightly arched dorsally (preventing anterior motion from encountering the abdomen). These features, along with their long and distally stiff tail plus their short overall limbs, presumably incapacitated metriorhynchids, making them unable to travel across land, unlike in teleosauroids or dyrosaurids.

Acknowledgements

We would like to thank all the museum staff for smoothly granting us the access of the crocodyliformes collections. We thank Dr Jonathan Bloch, Dr Richard Hulbert, and the rest of the staff at the Florida Museum (Florida Museum, Gainesville, United States); Dr David Parris and Dr Dana Ehret (New Jersey State Museum, Trenton, United States); collection manager Ned Gilmore (Academy of Natural Sciences of Drexel University, Philadelphia, United States); Dr Daniel Brinkman (Yale Peabody Museum, New Haven, United States); Dr Susannah Maidment (Natural History Museum, London, United Kingdom); Dr Fabienne Giraud (Joseph Fourier University, France); Dr Neil Clark (Hunterian Museum and Art Gallery, Glasgow, United

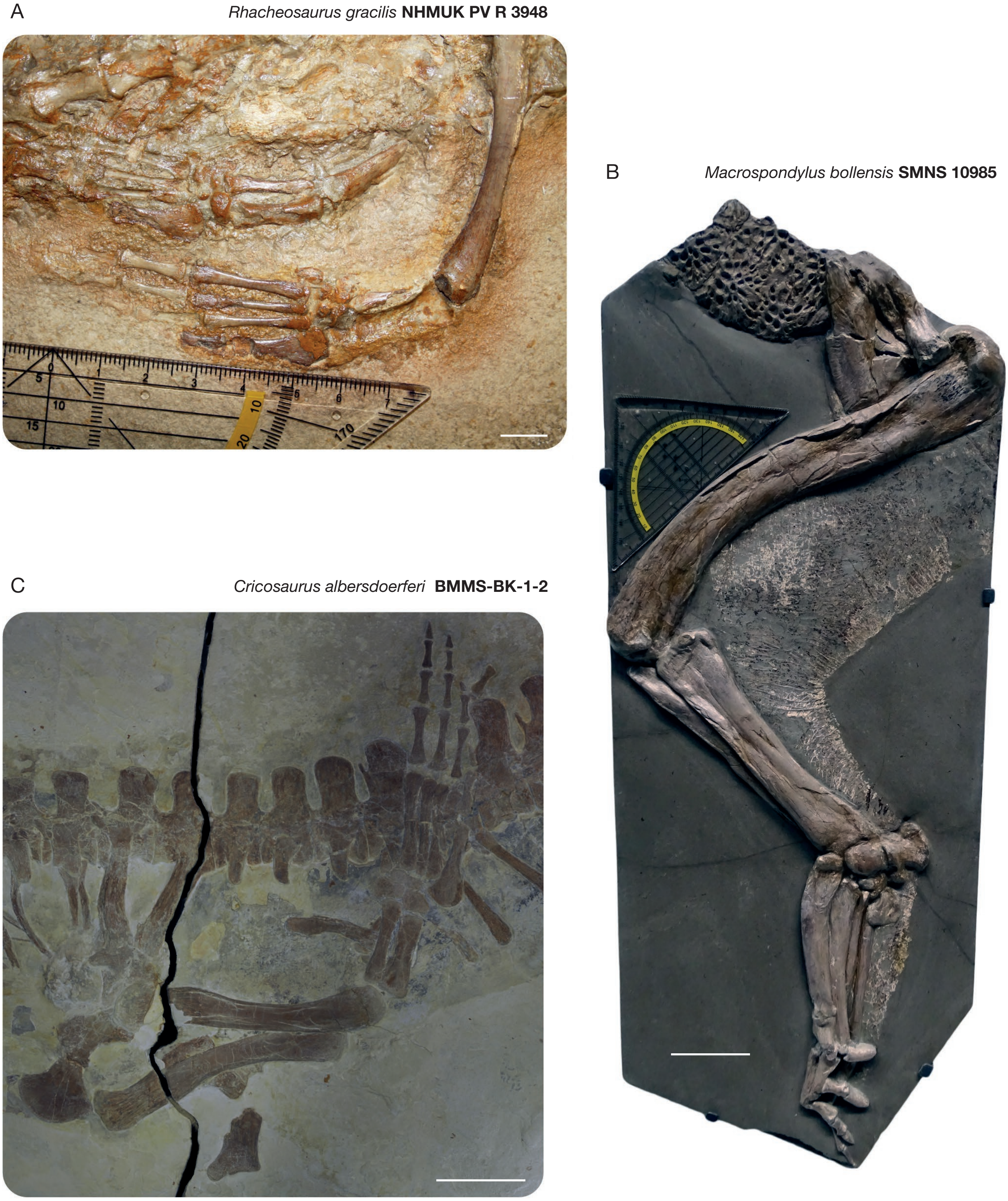


Fig. 100. — Comparison of fin impressions in Thalattosuchia: **A**, *Rhacheosaurus gracilis* Von Meyer, 1831, NHMUK PV R 3948; **B**, *Macrospondylus bollensis* (Jäger, 1828), SMNS 10985; **C**, *Cricosaurus albersdoerferi* (Sachs, Young, Abel & Mallison, 2021), BMMS-BK-1-2 modified from Sachs *et al.* (2021). Set square is in cm. Scale bars: A, 1 cm; B, C, 5 cm.

Kingdom); Dr Deborah Hutchinson (Bristol City Museum and Art Gallery, Bristol, United Kingdom); Matt Williams (Bath Royal Literary and Scientific Institute, Bath, United Kingdom); Dr Erin Maxwell (Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany); Dr Matthew Parkes (Natural History Museum of Ireland, Republic of Ireland); Dr Olivier

Pauwels (Royal Belgian Institute of Natural Sciences, Belgium) for the help and care. We thank Dr Yanina Herrera for her 3D models of *Cricosaurus araucanensis*; Dr Jérémy Anquetin for his 3D models of *Proexochokefalos cf. bouchardi* (MJSN SCR010-374) and *Sericodon jugleri* (MJSN SCR010-312); Dr Rebecca Bennion, Dr Narimane Chatar, Dr Christophe Mallet, Dr Roland Sookias, and Antoine Laboury for scanning specimens during their visits; and Candice Stephanic for sharing her scans of NJSM 23368. We would like to warmly thank Eric Wilberg and an anonymous reviewer for their kind and thorough review.

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Submitted on 17 January 2023;
accepted on 2 October 2023;
published on 2 May 2024.