Postcranial skeleton of Cricosaurus araucanensis (Crocodyliformes: Thalattosuchia): morphology and palaeobiological insights

Yanina Herrera , Marta S. Fernández & Zulma Gasparini
Published online: 16 May 2013.

PLEASE SCROLL DOWN FOR ARTICLE

Postcranial skeleton of *Cricosaurus araucanensis* (Crocodyliformes: Thalattosuchia): morphology and palaeobiological insights

YANINA HERRERA, MARTA S. FERNÁNDEZ and ZULMA GASPARINI

The metriorhynchid crocodyliform *Cricosaurus araucanensis* (Gasparini & Dellapé) has been documented from Tithonian (Upper Jurassic) strata of the Vaca Muerta Formation exposed in the Neuquén Basin, northwest Patagonia, Argentina. Postcranial components of this species were mentioned but not described in the original analysis. Subsequently, other authors described the forelimbs. The postcranial elements of metriorhynchids are poorly documented in comparison with their skulls, but new data from *C. araucanensis* reveal delayed ossification of the caudal neurocentral sutures indicating skeletal paedomorphosis affecting not only the appendicular skeleton but also the posterior region of the vertebral column. The morphology of the caudal region (transverse processes of the first caudal vertebrae ventrally deflected) and the reduction in the femur of the fourth trochanter suggest a reduction of the hypaxial musculature allowing increased epaxial musculature. This pattern of musculoskeletal arrangement is consistent with the swimming style and propulsion by lateral undulation of the tail, as proposed by previous authors.

Yanina Herrera [yaninah@fcnym.unlp.edu.ar], Marta S. Fernández [martafer@fcnym.unlp.edu.ar] and Zulma Gasparini [zgaspari@fcnym.unlp.edu.ar], División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n, W1900FWA La Plata, Argentina, CONICET. Received 23.7.2012; revised 16.10.2012; accepted 22.10.2012.

THE METRIORHYNCHIDAE are a family of Mesozoic marine crocodyliforms characterized by extensive skeletal and physiological adaptations to a pelagic lifestyle (see Fraas 1902, Andrews 1913, Hua 1994, Hua and de Buffrénil 1996, Fernández and Gasparini 2000, 2008, Young *et al.* 2010). The evolutionary history of metriorhynchids ranges from the Middle Jurassic (upper Bajocian–lowermost Bathonian; Cau and Fanti 2011) to Early Cretaceous (lower Hauterivian; Debelmas 1952), and it is expressed by a rich fossil record.

In recent years, a revival in studies of metriorhynchids has expanded our knowledge of this group's evolutionary relationships (Pol and Gasparini 2009, Young and Andrade 2009, Young *et al.* 2010, 2011a, b) and their palaeobiology, including putative niche partitioning within the clade (Pierce *et al.* 2009, Young et al. 2010), body-size variation (Young et al. 2011a) and soft anatomy of the snout and braincase (Fernández and Herrera 2009, Fernández et al. 2011, Herrera *et al.* in press a). In contrast to the diversity and abundance of metriorhynchid skulls, postcranial skeletons are scarce and limited to a few well-preserved remains from a few species, but many of them are disarticulated. The postcranial skeleton of metriorhynchids differs from that of other crocodyliforms, especially in its reduced and paddle-like forelimbs, loss of bony armour and hypocercal tail. These fundamental differences are classically attributed to adaptations to the marine environment (Fraas 1902, Andrews 1913, 1915, Hua 1994, Hua and Buffetaut 1997, Young *et al.* 2010).

The Late Jurassic/Early Cretaceous marine herpetofauna from northwestern Patagonia (Neuquén Basin, Argentina) is among the best-known and taxonomically diverse assemblages of Mesozoic marine reptiles from Gondwana. This fauna includes ichthyosaurs, plesiosaurs, turtles and thalattosuchian crocodyliforms (Gasparini and Fernández 2005, 2011). Exposures of the Tithonian–Berriasian levels of the Vaca Muerta Formation in northwestern Patagonia (Neuquén Basin) have yielded abundant and well-preserved metriorhynchid specimens that are assignable to *Purranisaurus potens* Rusconi, 1948, *Cricosaurus araucanensis* (Gasparini and Dellapé, 1976), *Dakosaurus andiniensis* Vignaud and Gasparini, 1996, and a new Patagonian species (Herrera, Gasparini & Fernández, in press). Most of the specimens are represented by three-dimensional skulls, whereas postcranial elements have been recovered only for the new Patagonian species and *C. araucanensis*. The latter is the best-known and documented species; its fossil record includes not only skeletal material but

also natural casts of the snout and braincase (Fernández and Gasparini 2000, 2008, Fernández and Herrera 2009, Herrera *et al.* in press a). Since its original description, *C. araucanensis* has not been revised in detail. Gasparini and Dellapé (1976) based their diagnosis mainly on cranial features and mentioned the existence of postcranial elements without describing them. The only contribution dealing with postcranial anatomy of this species (Herrera *et al.* 2009) describes exclusively its forelimbs.

Here, we describe the postcranial morphology of *Cricosaurus araucanensis* based on the holotype and several new specimens recovered during recent fieldwork. We also evaluate the palaeobiological aspects that can be inferred from the specimens.

Material and methods

The described material consists of three specimens of *Cricosaurus araucanensis* including the holotype and one new specimen, which could only be assigned to *Cricosaurus* sp. (MLP 86-XI-10-8) because of the elements preserved. The specimens MLP 72-IV-7-1 and MLP 73-II-27-6 are adult, whereas MLP 73-II-27-1 and MLP 86-XI-10-8 are sub-adult.

The holotype (MLP 72-IV-7-1) comprises: five postaxial cervical vertebrae, 16 dorsal vertebrae, two sacral and four caudal vertebrae, ribs, gastralia, haemal arches, incomplete pectoral girdle and forelimbs, and incomplete pelvic girdle and hind limbs (Figs 1–3, 4A–E, 5A–E, 6). Specimen MLP 73-II-27-1 comprises six dorsal vertebrae, a pectoral girdle and an incomplete left forelimb (Fig. 4F). Specimen MLP 73-II-27-6 consists of 11 dorsal vertebrae, two sacral vertebrae and 12 caudal vertebrae, an incomplete pelvic girdle and both femora (Fig. 7A, B). MLP 86-XI-10-8 consists of the posterior region of the vertebral column, the second sacral vertebra and 20 caudal vertebrae (Fig. 7C–E).

All specimens were recovered from lower Tithonian (Upper Jurassic) levels of the Vaca Muerta Formation exposed at Cerro Lotena (39°11′S; 69°40′W) and Bosque Petrificado (39°12′S; 69°42′W) in central western Argentina.

Institutional abbreviations. GPIT, Institut für Geowissenschaften Biogeologie, Tübingen, Germany; MLP, Museo de La Plata, La Plata, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Anatomical abbreviations. ac, acetabulum; a.pr, anterior process; ar.f, articular surface for the femur; ar.fi, articular surface for the fibula; ar.i, articular surface for the ilium; ar.r, articular surface for the radius; ar.s, articular surface for the sacral rib; ar.t, articular surface for the tibia; ar.u, articular surface for the ulna; ca.v, caudal vertebra; ce.v, cervical vertebra; co, coracoid; co.f, coracoid foramen; c.r, cervical rib; dc, deltopectoral crest; di, diapophysis; d.r, dorsal rib; d.v, dorsal vertebra; fe, femur; fi, fibula; ga, gastralia; h, humerus; ha, haemal arch, ha.a, haemal arch articulation; hy, hypapophysis;

is, ischium; mc, metacarpal; pa, parapophysis; ph, phalanx; pi, pisiform; PIFI2, M. puboischiofemoralis internus 2; prez, prezygapophysis; ps, pubic symphysis; pu, pubis; r, radius; ra, radiale; sc, scapula; s.r, sacral rib; s.v, sacral vertebra; ti, tibia; tr.p, transverse process; u, ulna; ul, ulnare; 4°tr, fourth trochanter.

Description

General preservation

The postcranial skeleton of MLP 72-IV-7-1 is preserved in four slabs, numbered 1 to 4. Slab 1 contains five articulated postaxial cervical vertebrae, four partially articulated dorsal vertebrae, a pectoral girdle and incomplete forelimbs (Fig. 1A, B). Slab 2 contains seven disarticulated dorsal vertebrae and ribs (Fig. 1C, D). Slab 3 has five disarticulated dorsal vertebrae, two sacral vertebrae and one caudal vertebra, pelvic girdle elements and an incomplete hind limb (Fig. 2A, B). Slab 4 is the smallest of the series and contains three disarticulated caudal vertebrae and haemal arches (Fig. 2C, D). The sacral vertebrae, pelvic girdle elements, the left humerus and the right femur were extracted from the matrix (Figs 3A, B, 4A–E, 5A–E, 6). In MLP 73-II-27–1 there are six articulated and partially preserved dorsal vertebrae in contact with the incomplete pectoral girdle and left forelimb (Fig. 4F). In MLP 73-II-27-6, the vertebral column is preserved articulated within the matrix, although incomplete. The pelvic girdle and left hind limb are disarticulated and partially preserved (Fig. 7A, B). In MLP 86-XI-10-8, the postcranial skeleton is preserved in one slab. The sacral vertebrae and the first eight caudal vertebrae are articulated. At this point, the vertebral column is disarticulated and rotated 180° with respect to the anterior portion of the column. Posteriorly, there are three articulated caudal vertebrae, one vertebra displaced from the vertebral column. Beyond this, there are eight other articulated caudal vertebrae (Fig. 7C–E).

Axial skeleton

Cervical vertebrae. The atlas–axis complex is not preserved in any of the specimens of *Cricosaurus araucanensis*. The description of the cervical vertebrae is based on MLP 72-IV-7-1. As in all metriorhynchids (see Fraas 1902, Andrews 1913, Wilkinson *et al.* 2008, Young *et al.* in press), there are five postaxial cervical vertebrae in *C. araucanensis* (Fig. 1A, B). In the first postaxial cervical vertebra, the shape of the centrum in anterior view is oval and slightly concave. In lateral view, the postzygapophysis extends beyond the posterior margin of the centrum. The parapophysis is short and positioned on the centrum ventral to the diapophysis. The parapophysis surface is anteroposteriorly oval in outline. The diapophysis is associated with the neural arch and is angled 45° downwards from the sagittal plane of the vertebra. The diapophysis is longer than

Fig. 1. Cricosaurus araucanensis (MLP 72-IV-7-1), photographs and drawings of slabs 1 and 2. **A**, Photograph (above) and drawing (below) of slab 1 (cervical and anterior dorsal vertebral region) in left lateral view. **B**, Photograph (above) and drawing (below) of slab 1 in right ventrolateral view. **C**, **D**, Photograph (above) and drawing (below) of slab 2 (middle dorsal vertebral region). Scale bars = 3 cm.

the parapophysis, and its articular surface is circular in outline. Both the parapophysis and diapophysis are borne on the anteromedial region of the centrum.

In lateral view, the prezygapophysis of the second postaxial cervical vertebra extends slightly beyond the anterior margin of the centrum, whereas the postzygapophysis extends markedly beyond the posterior margin of the centrum. In the third to fifth postaxial cervical vertebrae, the postzygapophysis is located at the same level as the posterior margin of the centrum. The
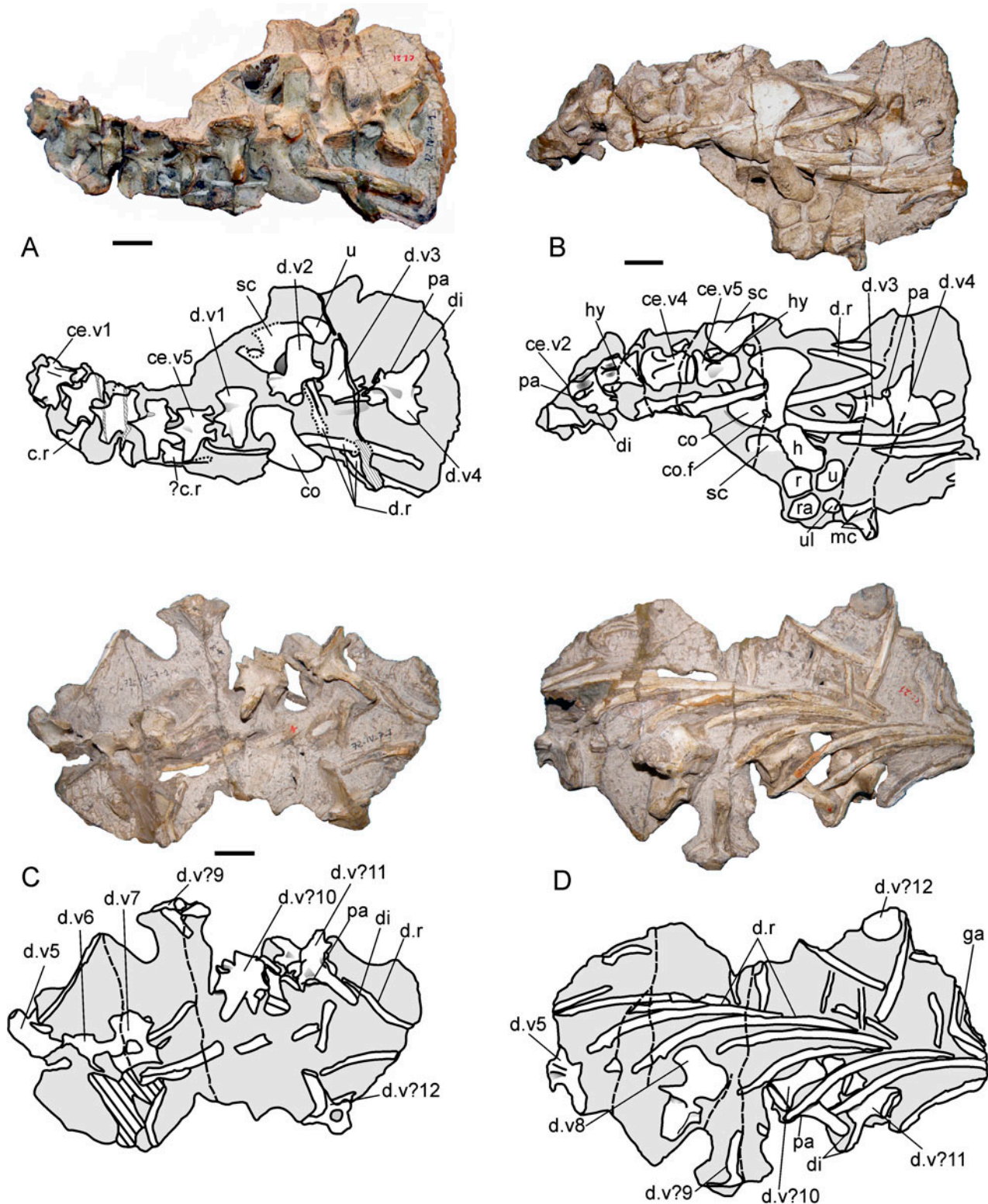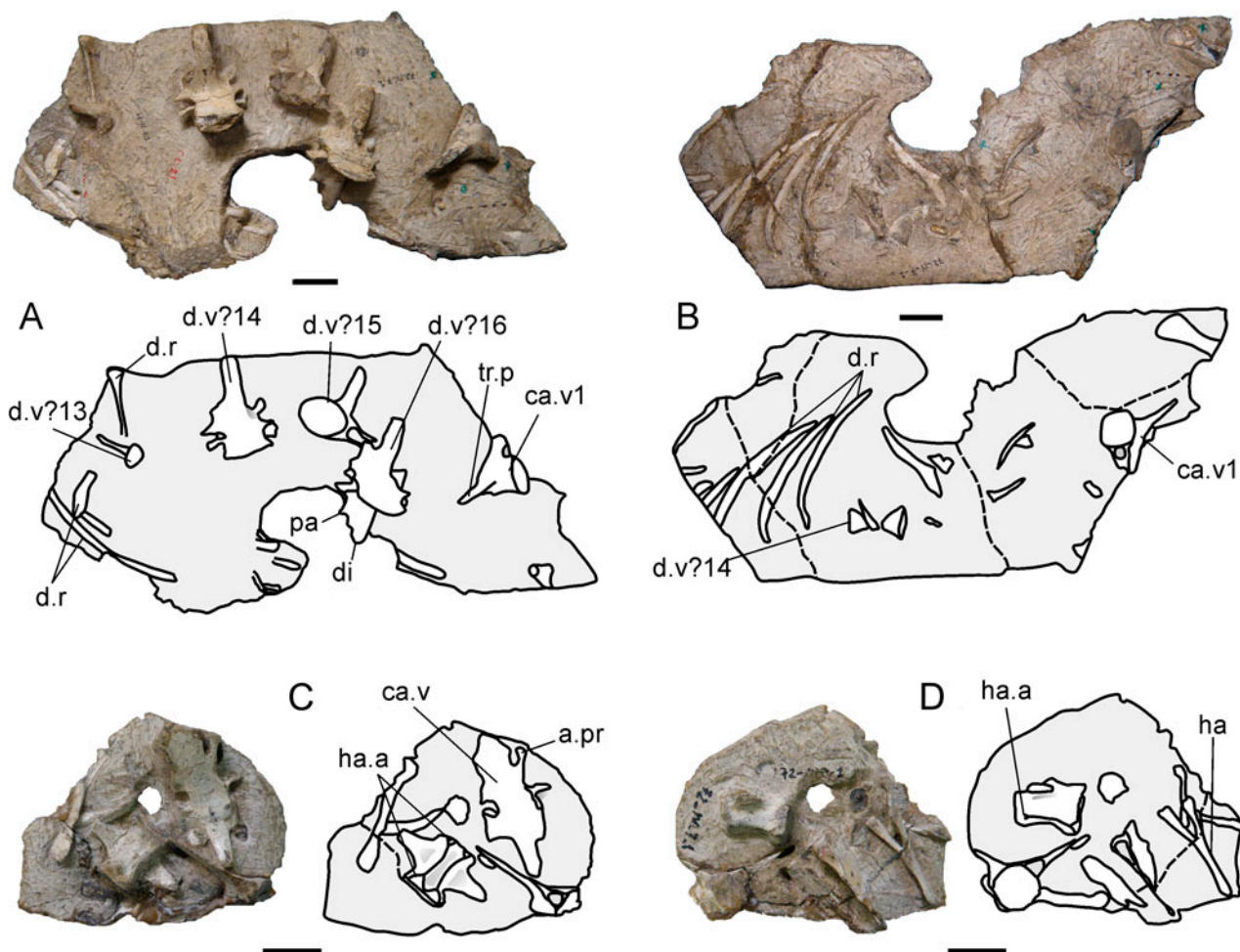
Fig. 2. Cricosaurus araucanensis (MLP 72-IV-7-1), photographs and drawings of slabs 3 and 4. **A**, **B**, Photograph (above) and drawing (below) of slab 3 (posterior dorsal vertebral region). **C**, **D**, Photograph (above) and drawing (below) of slab 4 (anterior caudal vertebral region). Scale bars = 3 cm.

hypapophysis of the first and second postaxial cervical vertebrae form a medial crest along the ventral surface of the centrum. The hypapophyses of both the fourth and fifth cervical vertebrae are more developed in the anterior portion of the centrum (Fig. 1B). In the first three postaxial cervical vertebrae, the parapophysis is evident in ventral view; lateral to the hypapophysis, in the fourth postaxial cervical vertebra, the parapophysis is not visible in ventral view (Fig. 1B).

The following changes are observed in these successive cervical vertebrae: (1) the centrum becomes increasingly longer and wider towards the end of the series; (2) the parapophysis moves from a lateroventral position in the centrum to a laterodorsal position in relation to the neural arch; and (3) the increased size of the centrum is related to an increased size of the parapophysis and diapophysis. The neurocentral suture is open in all cervical vertebrae.

Dorsal vertebrae. In MLP 72-IV-7-1, the most complete specimen of *Cricosaurus araucanensis*, 16 partially articulated dorsal vertebrae are preserved. The first dorsal vertebra is slightly disarticulated from the fifth cervical vertebra and totally disarticulated from the second dorsal vertebra. This latter is totally disarticulated, but the third and fourth dorsal vertebrae are articulated with each other (Fig. 1A, B). The 12 remaining dorsal vertebrae are disarticulated (Figs 1C, D, 2A, B). Due to disarticulation of the vertebral column, the exact number of dorsal vertebrae can not be determined. In MLP 73-II-27-1, six incomplete, articulated and lateromedially compressed dorsal vertebrae are preserved. In MLP 72-IV-7-1, the parapophysis of the first dorsal vertebra passes partially onto the neural arch, and on the remaining dorsal vertebrae, the parapophysis passes wholly onto the neural arch. The dorsal centra in anterior/posterior aspect are circular; they are hour-glass shaped in ventral view. As in *Cricosaurus suevicus* (Fraas 1902) and *Metriorhynchus* (Andrews 1913), the centra become more elongated towards the posterior region. The transverse processes are long and anteroposteriorly expanded at the base. The parapophysis forms a step-like prominence on the anterior margin of the transverse process; therefore, it is approximately 2.5 times shorter than the diapophysis. In the anterior dorsal vertebrae, the parapophysis surface is circular in outline and slightly concave, whereas it is oval in the posterior dorsal vertebrae. The diapophysis surface is oval and
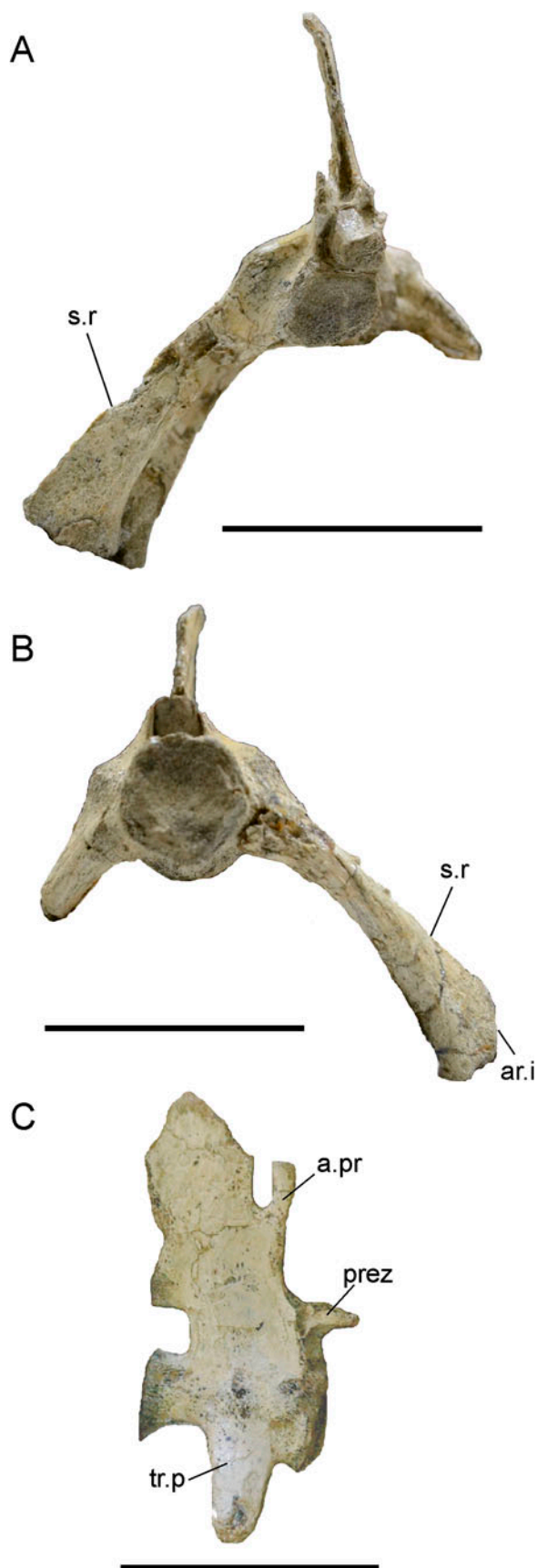
Fig. 3. Sacral and caudal vertebrae of *Cricosaurus araucanensis* (MLP 72-IV-7-1). **A**, First sacral vertebra in anterior view. **B**, Second sacral vertebra in posterior view. **C**, Caudal vertebrae in right lateral view. Scale bars = 5 cm.

larger than the parapophysis surface. In extant crocodiles, the hypapophysis is present in the first three or four dorsal vertebrae (Hoffstetter & Gasc 1969), whereas, in *C. araucanensis*, the hypapophysis is not developed in any of the dorsal vertebrae. The articular surfaces of pre- and postzygapophyses are dorsolaterally inclined forming an angle of 20–25° to the sagittal plane. The neural spines are incomplete except for the last dorsal vertebra. The dorsal margin of this neural spine is convex and mediolaterally broadened, as was described by Andrews (1913) for *Metriorhynchus*. The only complete dorsal vertebra in MLP 73-II-27-6 shows the same feature.

Sacral vertebrae. In MLP 72-IV-27-1 and MLP 73-II-27-6, both sacral vertebrae are partially preserved. In MLP 72-IV-27-1, the centrum of the first sacral vertebra is incompletely preserved, whereas the left sacral rib is not preserved (Fig. 3A). The second sacral vertebra lacks both the neural spine and the tip of the left sacral rib (Fig. 3B). In MLP 73-II-27-6, the centrum of the first sacral vertebra and the proximal portion of the sacral rib are not preserved, and the second sacral vertebra and sacral rib are partially preserved (Fig. 7A, B). The neural spine is completely preserved in the first sacral vertebra of MLP 72-IV-27-1 and in the second sacral vertebra of MLP 73-II-27-6. The neural spine of the first sacral vertebra of MLP 72-IV-7-1 is higher and narrower than the neural spine of the dorsal vertebrae. In MLP 72-IV-27-1, the centrum of the first sacral vertebra is almost flat posteriorly, whereas the centrum of the second sacral vertebra is circular, and slightly concave anteriorly and more concave posteriorly. In crocodyliforms, the centrum of the second sacral vertebra is shorter than the centrum of the first sacral vertebra (Hoffstetter & Gasc 1969). This character is not expressed in *Cricosaurus araucanensis* (MLP 72-IV-7-1), where the first sacral vertebra is 32 mm long, and the second is 33 mm long.

As in metriorhynchids (e.g., *Cricosaurus suevicus*, SMNS 9808; *Metriorhynchus superciliosus*, SMNS 10116; *Dakosaurus maximus*, Fraas 1902 and *Torvoneustes carpenteri*, Wilkinson *et al.* 2008), the sacral ribs are ventrally deflected (Figs 3A, B, 7A). This deflection is similar to *Dakosaurus maximus* figured by Fraas (1902, tafel III, Fig. 5) and more pronounced than in *Metriorhynchus superciliosus* and *Torvoneustes carpenteri*. The sacral rib of the first sacral vertebra is directed slightly backwards, whereas the sacral rib of the second vertebra is directed forwards. The first sacral rib does not reach further backwards than the posterior centrum face. In contrast, the rib of the second sacral vertebra extends further forwards than the anterior centrum face. The proximal portion of the right first sacral rib is mediolaterally wider and anteroposteriorly narrower than the second sacral rib. However, the distal end of the first sacral rib is less anteroposteriorly expanded than the second. In anterior view, the first sacral rib has
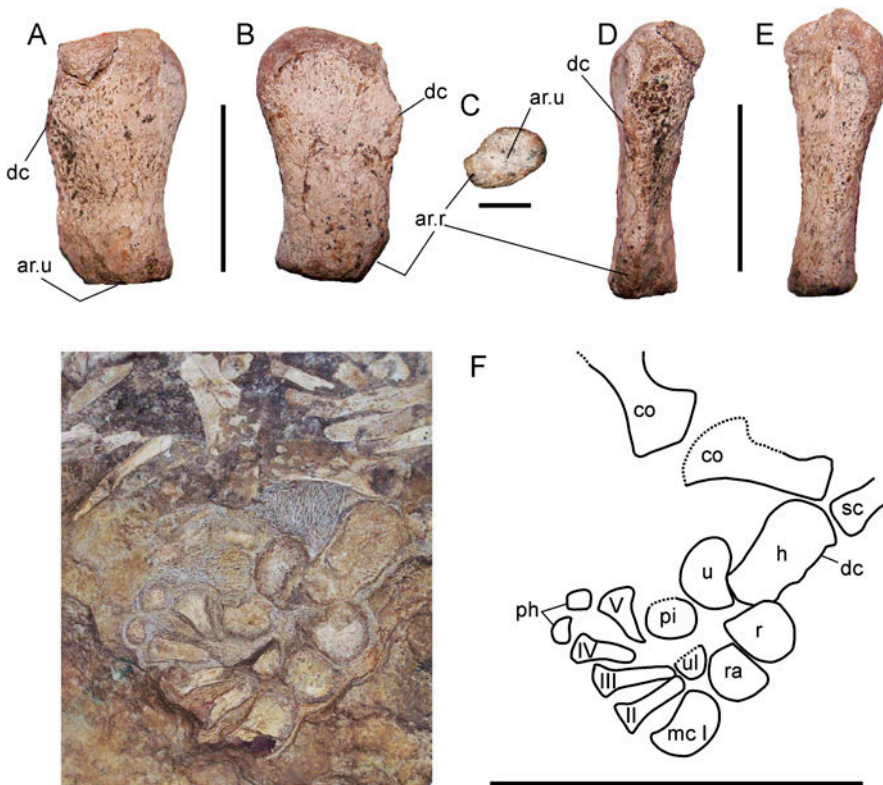
Fig. 4. Forelimb of *Cricosaurus araucanensis*. **A–E**, MLP 72-IV-7-1, **F**, MLP 73-II-27-1. **A**, Left humerus in dorsal view. **B**, Left humerus in ventral view. **C**, Distal articular surface of left humerus. **D**, Left humerus in anterior view. **E**, Left humerus in posterior view. **F**, Photograph (left) and drawing (rigth) of left forelimb in ventral view. Scale bars A–B, D–E = 3 cm, C = 1 cm, F = 5 cm.

a marked concavity over the length of the rib (Fig. 3A). In posterior view, this concavity is only on the proximal region of the rib, whereas towards the distal portion there is a triangular surface posteromedially oriented. This surface corresponds to the articulation with the second sacral rib. Anterior to this surface is the articular surface of the ilium. In anterior and posterior views, the second sacral rib is mediolaterally compressed.

Caudal vertebrae. In MLP 72-IV-7-1, only four disarticulated caudal vertebrae are preserved and exposed in different views (Fig. 2C, D). MLP 73-II-27-6 has 12 articulated caudal vertebrae (Fig. 7A, B) and MLP 86-XI-10-8, 20 (Fig. 7C). The vertebrae in both specimens are exposed in left lateral view. In MLP 73-II-27-6, the ribs are fused to the vertebral body only in the first two caudal vertebrae (Fig. 7A, B). The ribs are anteroposteriorly narrower and ventrally deflected, as described for the sacral ribs. In the caudal vertebrae of MLP 72-IV-7-1, the ribs are fused to the vertebral body and ventrally deflected (Figs 2C, 3C); we infer that these correspond to the first caudal vertebrae. The vertebrae are hourglass-shaped. In MLP 72-IV-7-1, the centrum of the supposed first caudal vertebra is shorter than the centrum of the second and third vertebrae, which is a feature described by Andrews (1913) for *Metriorhynchus*. However, in MLP 73-II-27-6 all centra are approximately equal in length. There are two anteroposteriorly directed crests in the ventral region of the vertebrae of MLP 72-IV-7-1. The articulation surfaces for the haemal arches are in the anterior and posterior portion of

these crests (Fig. 2C, D). These articulation surfaces are more developed in the anterior region. The neural spines are partially preserved in all specimens. The neural spine of the first vertebrae of MLP 73-II-27-6 is parallel to the anteroposterior axis of the vertebra, whereas at least from the ninth caudal vertebra, the neural spines slope posteriorly (Fig. 7A), which is a feature shared with *C. suevicus* (SMNS 9808). The anterodorsal portion of the neural spine has a marked notch. The neural spine thus formed by a small anterior process and posteriorly by the principal body of the neural spine (Figs 2C, 3C, 7A). This characteristic is shared with *Cricosaurus suevicus* (GPIT/Re/7322) from the third to the fifteenth caudal vertebrae. According to Fraas (1902), this characteristic is also present in *Rhacheosaurus gracilis*.

Ribs. The ribs associated with the atlas and axis are not preserved in any of the specimens. The second cervical rib is preserved in MLP 72-IV-7-1 (Fig. 1A). The shaft of the rib extends anteroposteriorly, parallel to the longitudinal axis of the vertebra. The capitular and tubercular processes are almost perpendicular to the rib shaft. The capitular process is shorter than the tubercular process. The dorsal ribs of MLP 72-IV-7-1 and MLP 73-II-27-6 are disarticulated and included in the matrix (Figs 1, 2A, B, 7A). The middle to posterior portion of MLP 72-IV-7-1 has 10 disarticulated dorsal ribs but arranged in the same orientation (Fig. 1D). The ribs are long, posteroventrally curved and subcircular in outline. The tubercular process is longer than the capitular process; the latter
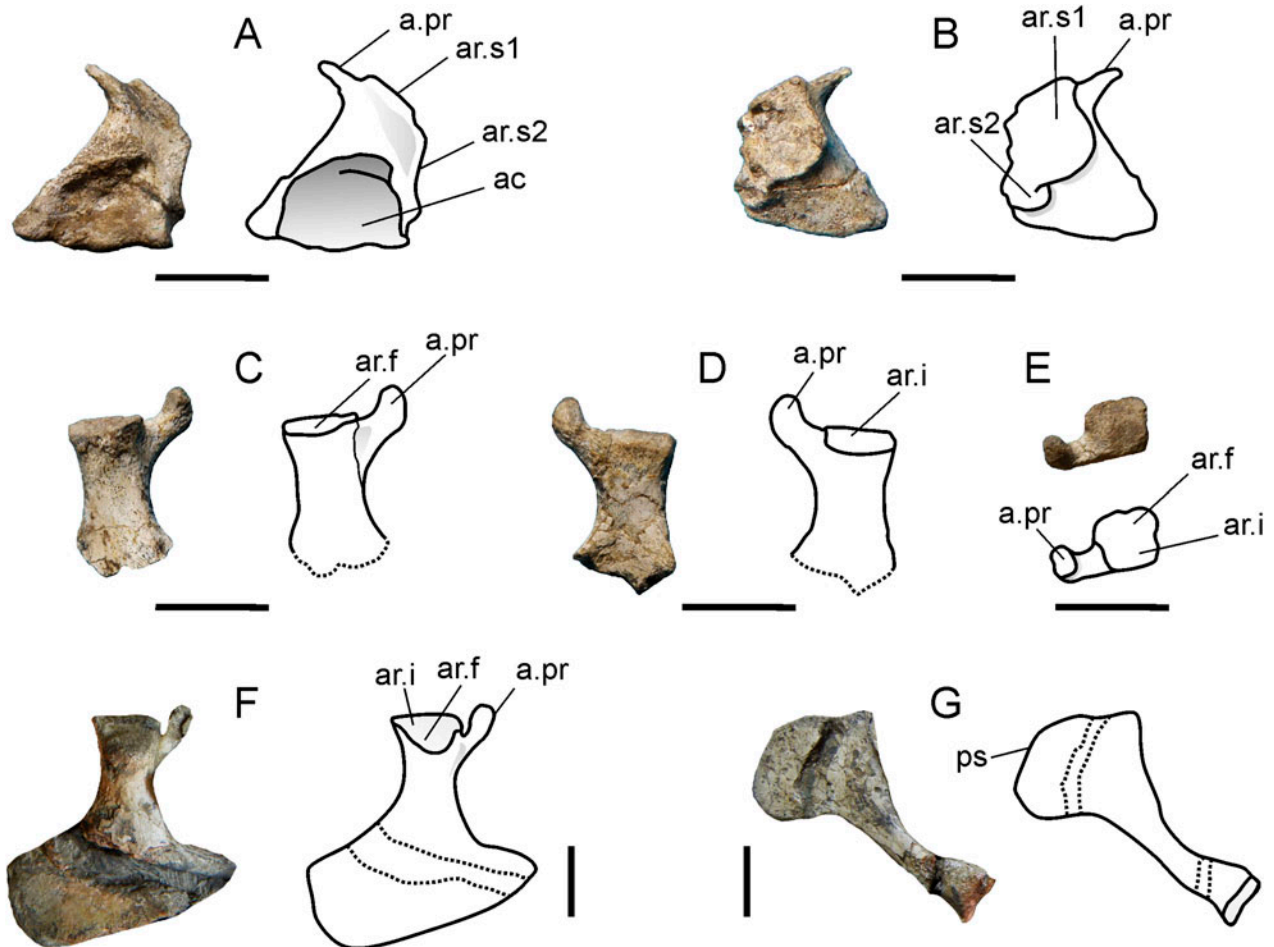
Fig. 5. Pelvic girdle of *Cricosaurus araucanensis*. **A–E**, MLP 72-IV-7-1, **F–G**, MLP 73-II-27-6 photographs and drawings of pelvic girdle. **A**, Left ilium in lateral view. **B**, Left ilium in medial view. **C**, Right ischium in lateral view. **D**, Right ischium in medial view. **E**, Right ischium in proximal view. **F**, Right ischium in lateral view. **G**, Right pubis. Scale bars = 3 cm.

is oval in cross-section. The length and thickness of the ribs decrease posteriorly.

Gastralia. The dorsal region of MLP 72-IV-7-1 bears some disarticulated elements that are not consistent with the orientation described for the ribs (Fig. 1D). These bones are slender and shorter than the dorsal ribs. One of them is V-shaped, and the remaining elements are slightly curved (Fig. 1D). According to Fraas (1902), the gastralia in *Cricosaurus suevicus* are formed by one medial V-shaped piece and two curved lateral elements. Based on this description, we interpret these elements to be gastralia.

Haemal arches. Some disarticulated anterior haemal arches are preserved in MLP 72-IV-7-1 and MLP 73-II-27-6 (Figs 2C, D, 7A). The haemal arches are articulated with the intervertebral region of the 9–11 caudal vertebrae in MLP 86-XI-10-8 (Fig. 7A). The anterior haemal arches are Y-shaped. The arms are shorter than the ventral process (Fig. 2D) and the articulation surface with the vertebra is slightly rounded. The proximal portion of the ventral process is rounded, whereas the distal portion is lateromedially compressed (Fig. 4F).

Appendicular skeleton

Scapulae. Both scapulae are incompletely preserved in MLP 72-IV-7-1 (Fig. 1A, B), whereas MLP 73-II-27-1 retains only the proximal portion of the left scapula articulated with the coracoid and the humerus (Fig. 4F). As in other metriorhynchids (e.g., *Cricosaurus suevicus*, GPIT/Re/43/97/3-4; *Dakosaurus maximus*, Fraas 1902 and *Metriorhynchus*, von Arthaber 1906), the scapula is flattened with expanded proximal and distal ends. These expansions are more developed at the anterior margin, whereas the posterior margin of the scapula is quite straight (Fig. 1A). The right scapula is approximately 55 mm long and is articulated with the coracoid and humerus in MLP 72-IV-7-1. These articulation surfaces are straight and thickened. In MLP 73-II-27-1, the proximal portion is not expanded (Fig. 4F).

Coracoid. The coracoid is dorsoventrally flattened with expanded proximal and distal ends (Figs 1A–B, 4F). The anterior margin is strongly concave, whereas the posterior is slightly concave. The right coracoid of MLP 72-IV-7-1 is 59 mm long, 42 mm wide on the proximal expansion and 43 mm wide on the distal

expansion. These measurements on the left coracoid are 55, 42 and 38 mm, respectively. The articulation surfaces with the humerus and scapula are dorsoventrally thickened. In MLP 73-II-27-1, only the proximal portion is expanded, and the distal region has the same width as the shaft (Fig. 4F). The coracoid is 40 mm long, 23 mm wide on the proximal expansion and 13 mm wide on the distal expansion. The distal expansion of the right coracoid in MLP 72-IV-7-1 bears a small coracoid foramen without a notch (Fig. 1B). According to Andrews (1913), the coracoid in *Metriorhynchus* is larger than the scapula; in *C. araucanensis* and *C. suevicus* (SMNS 9808), these bones are approximately equal in size.

Forelimb. The description is based on incomplete forelimbs of MLP 72-IV-7-1 (Figs 1B, 4A–E) and an incomplete left forelimb of MLP 73-II-27-1 (Fig. 4F). The right forelimb of MLP 72-IV-7-1 and the left one of MLP 73-II-27-1 are articulated, in contact with the pectoral girdle and exposed in ventral view.

Humerus. The humerus is short with the proximal end expanded; the distal end has approximately the same width as the shaft (Fig. 4A, B, F). The left humerus of MLP 72-IV-7-1 is 45 mm long, 26 mm wide at the proximal end and 15 mm wide at the distal end. In MLP 73-II-27-1, these measurements are 31, 15 and 12.5 mm, respectively. The humerus is dorsoventrally compressed (Fig. 4D, E); in dorsal view it is convex (Fig. 4A), whereas in ventral view it is concave at the proximal end and flat distally (Fig. 4B). The humeral head is very convex anteroposteriorly. The articular region is wide anteroposteriorly and narrow dorsoventrally. The deltopectoral crest is restricted to a small knob on the anterior margin of the humerus (Fig. 4A, B, F). The posterior margin of the humerus is concave. The distal articulation surface is on the distal margin and continues to the anterior margin (Fig. 4A, B), as in *Metriorhynchus* (Andrews 1915) and in the new Patagonian metriorhynchid (Herrera *et al.* in press b). The articular surface with the ulna is oval and slightly concave. The articular surface with the radius is subrectangular and flat (Fig. 4C). These articular surfaces are oriented at 45° to each other (Fig. 4A, B, F).

Radius. As in other metriorhynchids, the radius of *Cricosaurus araucanensis* is a flattened disk-like bone. The anteroposterior axis is equal to the proximodistal axis so that the anteroposterior/proximodistal ratio is approximately 1. In *Metriorhynchus superciliosus* sp. (Andrews 1913), *Metriorhynchus* sp. (Andrews 1915) and in the new Patagonian metriorhynchid (Herrera *et al.* in press b), the anteroposterior axis is shorter than the proximodistal axis. In MLP 72-IV-7-1, the anterior margin is strongly convex and the articular surfaces with the humerus, ulna and radiale are straight (Fig. 1B). The articular surface with the humerus is restricted to the

proximomedial margin. The articular surface with the ulna is shorter than the articular surface with the radiale. The sub-adult specimen, MLP 73-II-27-1, has ill-defined articular surfaces; therefore, the radius is rounded (Fig. 4F). The left radius of MLP 72-IV-7-1 has dorsoventrally thickened articular regions, as described by Andrews (1913) for *Metriorhynchus superciliosus*.

Ulna. The ulna is slightly larger than the radius in *Cricosaurus araucanensis* (Figs 1B, 4F). The ulna is subrectangular with a strongly convex posterior margin. The articular surfaces with the humerus and radius are straight. As described for the radius, the articular surfaces are better defined in the adult specimen (MLP 72-IV-7-1) than in the sub-adult (MLP 73-II-27-1). As in *C. suevicus* (SMNS 9808) and *Rhacheosaurus gracilis* (Ammon 1905), the anteroposterior axis is longer than the proximodistal axis. In MLP 72-IV-7-1, the anteroposterior axis is 21 mm and the proximodistal axis is 18 mm. These measurements in MLP 73-II-27-1 are 15 and 13 mm, respectively. In contrast, in *Metriorhynchus* from the Oxford Clay (Andrews 1915) and *Metriorhynchus superciliosus* (Andrews 1913), the ulna is more expanded proximodistally than anteroposteriorly; therefore, this bone has a columnar aspect.

Radiale. The radiale in *C. araucanensis* is subquadrangular (Figs 1B, 4F), as in *C. suevicus* (SMNS 9808) and *Cricosaurus* sp. (GPIT/Re/07285), and different from the new Patagonian metriorhynchid, in which it is circular (Herrera *et al.* in press b). The radiale has two straight articular surfaces; the articular surface with the radius is long and clearly defined, whereas the articular surface with the ulna is short. Distal and posterior margins are convex without defined articular surfaces (Figs 1B, 4F). The radiale and radius are similar in size in *C. araucanensis* (Figs 1B, 4F), the new Patagonian metriorhynchid (Herrera *et al.* in press b), *C. suevicus* (SMNS 9808), *Cricosaurus* sp. (GPIT/RE/07285) and *Rhacheosaurus gracilis* (Ammon 1905). Radial enlargement is probably a common characteristic associated with Rhacheosaurini (*sensu* Young *et al.* 2011b). However, this can not be confirmed until more complete and articulated metriorhynchid forelimbs are described.

Ulnare. The posterior half of the ulnare in MLP 72-IV-7-1 is broken, however its outline can be defined (Fig. 1B). As in the new Patagonian metriorhynchid (Herrera *et al.* in press b), *C. suevicus* (SMNS 9808) and *Metriorhynchus* (Andrews 1915), the ulnare is smaller than the radiale. The ulnare of MLP 72-IV-7-1 does not contact the radius, as in extant crocodiles (Müller and Alberch 1990). The ulnare contacts metacarpals II and III in MLP 73-II-27-1 (Fig. 4F).

Pisiform. The pisiform is preserved in MLP 73-II-27-1 and is discoidal and more developed than the ulnare (Fig. 4F). The central region is strongly ossified,

whereas the margins are poorly defined, suggesting poor ossification. The pisiform is preserved distal to the ulna and posterior to the ulnare. In *Cricosaurus suevicus* (SMNS 9808), the exposed forelimb is disarticulated; however, there is an element between the humerus and the ulna that may correspond to the pisiform displaced with respect to its natural position.

Metacarpals. All metacarpals are preserved in MLP 73-II-27-1 (Fig. 4F), whereas only metacarpal I and an unidentified metacarpal are preserved in MLP 72-IV-7-1 (Fig. 1B). In *C. araucanensis*, metacarpal I has the crescent shape typical of other metriorhynchids. The anterior margin is convex, whereas the posterior one is concave. The distal and proximal margins are straight. In MLP 73-II-27-1, the proximal margin contacts the radiale and ulnare. Metacarpals II to V are long and flattened with the distal margins expanded. In metacarpal V, this expansion is more pronounced. Metacarpals II and III contact the ulnare (Fig. 4F).

Phalanges. Distal to metacarpals IV and V, in MLP 73-II-27-1, there are two small and sub-pentagonal phalanges (Fig. 4F). The articular surfaces are straight; the anterior and posterior margins are convex.

Ilium. The left ilium is completely preserved in MLP 72-IV-7-1, whereas the right ilium lacks the anterior process. The outline of the ilium in *C. araucanensis* is subtriangular (Fig. 5A, B), as in other metriorhynchids (Fraas 1902, Andrews 1913, Herrera *et al.* in press b, Young *et al.* in press). The dorsal margin is quite straight and terminates approximately level with the midpoint of the acetabulum (Fig. 5A), as in *Metriorhynchus superciliosus* and *Suchodus brachyrhynchus* but unlike in Mr Leeds' specimen (Young *et al.* in press). The anterior process projects anteriorly by a short, thin process that is slightly curved ventrally and exceeds the anterior margin of the ilium (Fig. 5A, B). Ventral to this process, the anterior margin of the ilium is straight. In lateral view, the posterior half of the ilium corresponds approximately with the acetabulum (Fig. 5A). The acetabulum in *C. araucanensis* is shallower than in extant crocodiles. In medial view on the dorsal region, there is a rough area that corresponds to the articular surface for the sacral ribs. This area begins posterior to the anterior process of the ilium and is slightly constricted in the middle region. The constriction separates the rough area into two regions; the dorsoanterior area corresponds to the articular surface for the first sacral rib, whereas the posterior and slightly ventral one corresponds to the articular surface for the second sacral rib. The articular surface for the first sacral rib is larger than that for the second (Fig. 5B). The posteroventral margin of the ilium is undulate (Fig. 5A). The anterior process of the ischium fits with the most anterior wave of the posteroventral margin of the

ilium. The contact between pubis and ilium has been described by Andrews (1913) for *Metriorhynchus* and *Steneosaurus*. According to Claessens and Vickaryous (2012) this interpretation is incorrect, and there is no contact between the pubis and ilium in these crocodyliforms. However, due to the state of preservation, we can not identify an articular facet for the pubis on the anterior process of the ischium in any of the specimens of *Cricosaurus* here studied.

Ischium. Both ischia are incompletely preserved in MLP 72-IV-27-1. The left ischium is preserved from the neck to the proximal region, and the right one from the most proximal region of the ischiadic wing to the proximal region (Fig. 5C, D). The right ischium is completely preserved in MLP 73-II-27-6 and exposed in lateral view (Figs 5F, 7A). The ischia of *C. araucanensis* are roughly triangular and resemble those of other metriorhynchids (e.g., *Cricosaurus suevicus*, SMNS 9808; *Metriorhynchus superciliosus*, SMNS 10116 and *Torvoneustes carpenteri*, Wilkinson *et al.* 2008). The proximal end is divided into two processes separated by a notch. The anterior process is small and nearly circular in cross-section. This process is longer than the posterior one (Fig. 5C, D, F). The tip of the anterior process is a convex surface with a small articulation surface for the ilium. The posterior process is much larger than the anterior one and subquadrangular (Fig. 5C–D, F). This process has two articulation surfaces positioned in two planes. The articulation surface for the ilium is transverse to the major axis of the ischium. The articulation surface for the femur is oblique to the major axis of the ischium. Both articulation surfaces are slightly concave. In MLP 73-II-27-6, the ischiadic wing is flat with two regions clearly defined that form an angle of approximately 90° to each other (Fig. 5F). The anterior region is longer than the posterior one and corresponds to the surface for the union with the right ischium.

Pubis. The pubis is completely preserved only in MLP 73-II-27-6, but it is broken at the ends (Fig. 5G). The pubis shaft is rod-shaped, whereas the distal end is expanded. It is 73 mm in long and 38 mm wide at the distal end where there is a straight area that may represent the pubic symphysis (Fig. 5G).

Hind Limb. The hind limbs are incompletely preserved in MLP 72-IV-7-1. Both femora are preserved but only the right is complete. Zeugopodial elements and a metatarsal are partially preserved. The left femur is complete, and the right femur is partially preserved in MLP 73-II-27-6.

Femur. The femur has the sigmoidal shape typical of other metriorhynchids (Fig. 6; Fraas 1902, von Arthaber 1906, Andrews 1913, Wilkinson *et al.* 2008, Herrera *et al.* in press b, Young *et al.* in press). The femur is dorsoventrally compressed with the planes of both proxi-
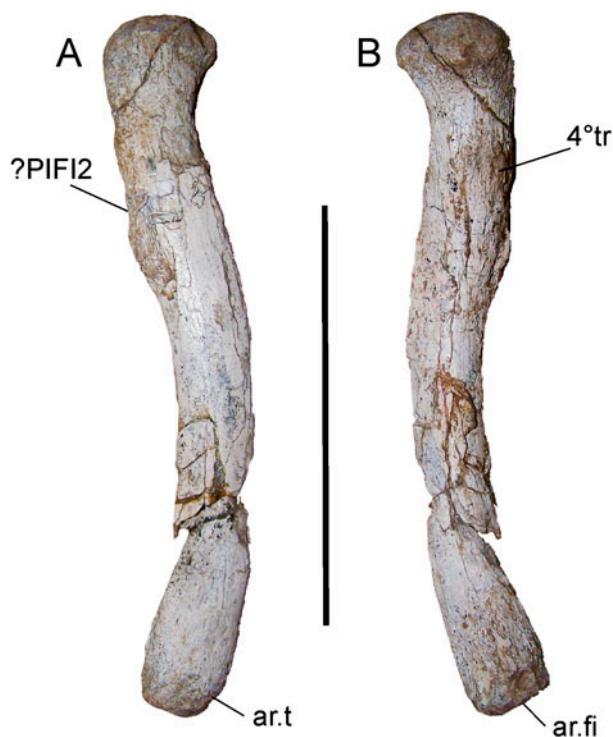
Fig. 6. Right femur of *Cricosaurus araucanensis* (MLP 72-IV-7-1). **A**, Dorsal view. **B**, Ventral view. Scale bar = 10 cm.

mal and distal ends parallel. In cross-section, the diaphysis is lenticular, whereas the epiphyses are circular. The right femur of MLP 72-IV-7-1 is 170 mm long with a proximal head width of 28 mm and a distal head width of 21 mm. The left femur of MLP 73-II-27-6 is 150 mm in total proximal-distal length. The femoral head is rounded without differentiated condyles as in *Torvoneustes carpenteri*, which has two condyles laterally protruding (Wilkinson *et al.* 2008). In proximal view, the dorsal margin of the femoral head is rounded; the ventral margin is triangular. The articular surface of the femoral head is triangular in Mr Leeds' specimen (Young *et al.* in press). The distal articular surfaces form a 45° angle (Fig. 6) as in *C. suevicus* (SMNS 9808) and the new Patagonian metriorhynchid (Herrera *et al.* in press b). The articular surface of the fibula is twice as long as the articular surface of the tibia. Both surfaces are flat and subquandrangular. Dorsally on the right femur of MLP 72-IV-7-1, there is a prominent structure with a rough surface on the proximal region and over the posterior margin (Fig. 6A). In extant crocodiles, this is the insertion area of M. puboischiofemoralis internus 2 (Romer 1923; PIFI2, Hutchinson and Gatesy 2000, Carrano and Hutchinson 2002, Otero *et al.* 2010). Posterior to this area, and over the posterior margin, there is a flat area that might correspond to the insertion area of M. ischiotrochantericus (ISTR). In extant crocodiles, the ISTR inserts in the proximal-posterior region of the femur (Otero *et al.* 2010). In medial view of the proximal-posterior region, there is a protrusive, very rough area (Fig. 6B), also evident in *Metriorhynchus superciliosus*

(SMNS 10116), *Metriorhynchus* sp. (GPIT/Re/0302) and the new Patagonian metriorhynchid (Herrera *et al.* in press b). In contrast, this very rough area is flat in *T. carpenteri* (Wilkinson *et al.* 2008). Although in metriorhynchids this protrusive and rough area does not form a low ridge, it corresponds to the osteological correlate for the attachment of the caudofemoralis muscles and was interpreted as a reduced fourth trochanter (Herrera 2012, Herrera *et al.* in press b). The absence of fourth trochanter *sensu stricto* has been considered a character shared by all metriorhynchids (e.g., Wilkinson *et al.* 2008, Young and Andrade 2009, Young *et al.* 2010, in press). However, these authors described a flattened rugose surface in the area where the fourth trochanter is located in other crocodyliforms.

Tibia. Only the proximal region of the left tibia is preserved in MLP 73-II-27-6. The tibia is long and slightly dorsoventrally compressed and has expanded proximal and distal ends (Fig. 7A). It is stouter than the fibula, which is a characteristic shared with *Gracilineustes leedsi* (=*Metriorhynchus laeve* of Andrews 1913), the new Patagonian metriorhynchid (Herrera *et al.* in press b) and *Cricosaurus suevicus* (SMNS 9808). The proximal end is more expanded than the proximal end of the fibula (Fig. 7A).

Fibula. The proximal region of the left fibula is preserved in MLP 73-II-27-6, whereas the distal end is preserved as an impression in the matrix (Fig. 7A). The fibula is long with the proximal and distal ends slightly expanded. The length inferred is 54 mm. The length of the fibula in MLP 73-II-27-6 is approximately one-third the length of the femur, as described by Andrews (1913) for *Metriorhynchus* and *Cricosaurus suevicus* (SMNS 9808, SMNS 90513).

Discussion

The postcranial remains of *Cricosaurus araucanensis* provide additional information on the skeletal architecture of metriorhynchids. Although the postcranial morphology is less informative of phylogeny than the skull [postcranial features represent only 15% of the characters used in phylogenetic analyses by Pol and Gasparini (2009) and 27% by Young *et al.* (in press)], they provide significant insights into the species' palaeobiology. Two traits are of particular interest: the closure pattern of the neurocentral suture and the morphology of the caudal vertebrae.

Neurocentral sutures and morphological maturity in *Cricosaurus araucanensis*

As demonstrated in extant crocodylians, neurocentral sutures in most caudal vertebrae are fully closed at hatching, whereas the remaining sutures close later in ontogeny (Brochu 1996). On this basis, Brochu (1996) proposed that in Crocodyliformes, the closure of the
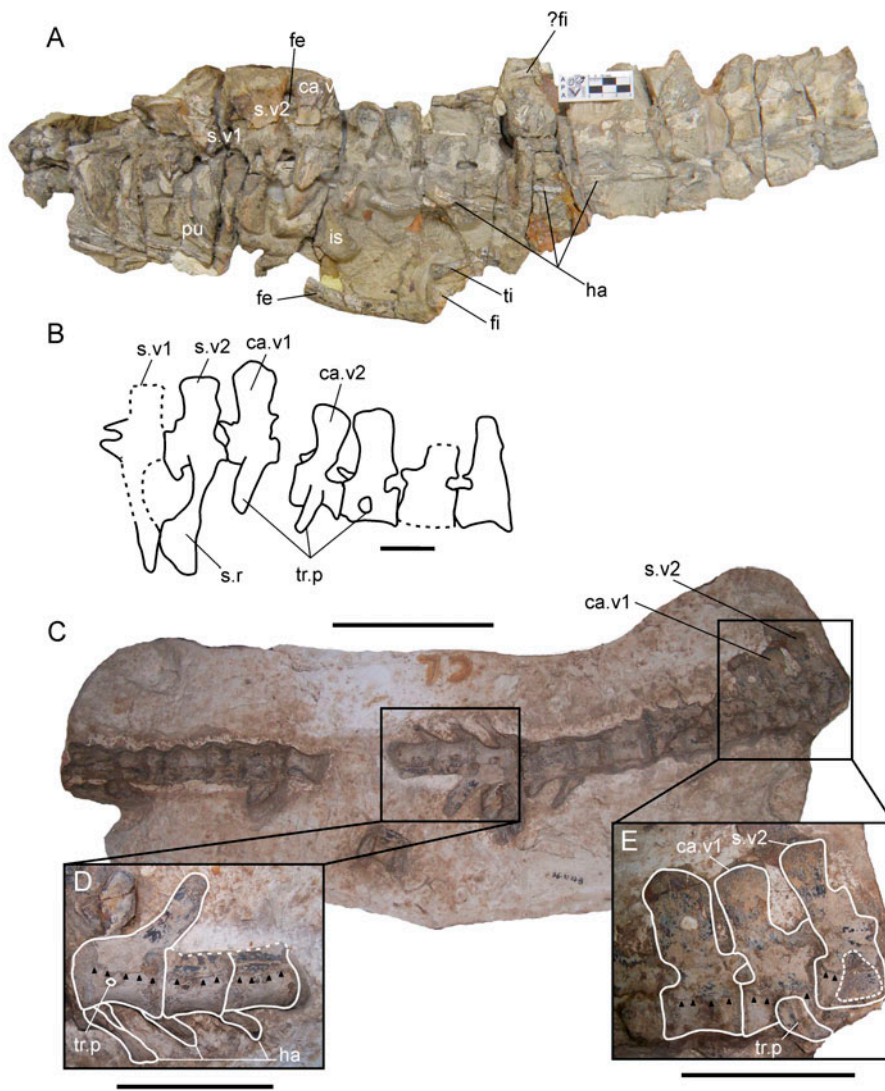
Fig. 7. **A**, **B**, *Cricosaurus araucanensis* MLP 73-II-27-6. **A**, Postcranial elements in left lateral view. **B**, Detail of sacral and most anterior caudal vertebral region. **C**–**E**, *Cricosaurus* sp. MLP 86-XI-10-8. **C**, Caudal vertebral region in left lateral view. **D**, Detail of haemal arches. Figure rotated 180° with respect to C. **E**, Detail of the second sacral vertebra and most anterior caudal vertebrae. Arrows indicate the neurocentral suture. Scale bars A, B = 3 cm, C = 10 cm, D, E = 5 cm.

neurocentral suture can be used as an indicator of relative maturity, providing a size-independent criterion of morphological maturity in extinct forms.

In contrast to squamates (Rieppel 1992a, b), the sequence of neurocentral suture closure is caudal to cranial in crocodylians. The neurocentral suture closure in *Alligator mississippiensis* occurs in very late postnatal ontogeny after they reach sexual maturity. Before sexual maturity, completely fused centra and neural arches are restricted to the caudal vertebral series, whereas presacral vertebrae commonly remain unfused throughout postnatal ontogeny, retaining open sutures in very mature individuals (Ikejiri 2012). Recent findings suggest that the crocodilian closure pattern is widespread among other archosaurs, although with certain variations (e.g., Irmis 2007, Renesto 2008, Evans *et al.* 2011). Within thalattosuchian crocodilyforms, the caudal-cranial sequence of neurocentral suture closure has been proposed for cf. *Pelagosaurus* sp. (Delfino and Dal Sasso 2006) and Mr Leeds' specimen (Young *et al.* in press).

The *Cricosaurus araucanensis* holotype reveals the same pattern of neurocentral closure as in extant crocodylians. The caudal, sacral and dorsal vertebrae have the neurocentral suture closed, whereas, in cervical vertebrae it remains open, indicating that the specimen is an adult and has a caudal-cranial sequence of neurocentral suture closure.

Specimens MLP 73-II-27-1 and MLP 86-XI-10-8 have open sutures in the dorsal vertebrae, and articulated sacral and first caudal vertebrae, respectively. Both specimens are smaller in overall size than the holotype of *C. araucanensis* (humerus length, 45 mm for MLP 72-IV-7-1 versus 31 mm for MLP 73-II-27-1; second sacral centum length, 33 mm for MLP 72-IV-7-1 versus 20 mm for MLP 86-XI-10-8). The open sutures and the small size of both specimens suggest that they were not fully mature individuals at the time of death. The pattern observed in MLP 86-XI-10-8 is quite interesting. In contrast to extant crocodylians, in which caudal neurocentral sutures are completely closed just after hatching (Brochu 1996, Ikejiri 2012), these sutures

remain completely open, indicating that neurocentral suture closure occurs later in postnatal ontogeny (Fig. 7D, E). Although an accurate measure of body length can not be determined, a comparison of the vertebral lengths with those of the *Cricosaurus araucanensis* holotype suggests that MLP 86-XI-10-8 was not a newborn.

Delayed timing of neurocentral closure, as observed in the caudal vertebrae, suggests the occurrence of skeletal paedomorphosis, which is a widespread heterochronic process among secondarily adapted aquatic reptiles. In the particular case of marine reptiles, Rieppel (1989) pointed out that skeletal paedomorphosis primarily affects the appendicular skeleton. In the case of metriorhynchids, deeply modified forelimbs transformed as paddles and poor ossification may have evolved by paedomorphosis (Herrera *et al.* 2009). However, new information indicates that delayed ossification occurs also in the vertebral column of metriorhynchids and probably also in basal thalattosuchians. This is not surprising, as delayed ossification appears to be a general phenomenon throughout the skeleton rather than restricted to limbs and girdles (Carroll 1997). Delayed ossification affecting the neurocentral sutures is well documented in basal pleurosaurs and sauropterygians, in which a loosely attached arch occurs throughout ontogeny (Brown 1981, Carroll and Gaskill 1985, Rieppel 1989).

Open sutures in dorsal and proximal caudal vertebrae of postnatal specimens of cf. *Pelagosaurus* (Delfino and Dal Sasso 2006, Delfino and Sánchez-Villagra 2010) suggest that this paedomorphic trait was common to thalattosuchians. Further exploration of a more extensive sample of thalattosuchians would be useful to test this hypothesis.

Morphology of caudal vertebrae

In extant crocodiles, the M. caudofemoralis longus extends from the third to 11th–15th caudal vertebrae (e.g., Romer 1923, Gatesy 1990, Otero *et al.* 2010). The point at which the caudal ribs disappear can be used as an indicator of the caudal extension of this muscle (Gatesy 1990). Schwarz-Wings *et al.* (2009) proposed for dyrosaurids that the decrease in width of the transverse processes and the height of the haemal arches indicate a sharp terminal decline of the cross-section of the M. caudofemoralis longus.

In *Cricosaurus* sp. (MLP 86-XI-10-8), the first 11 caudal vertebrae have transverse processes, whereas in *C. araucanensis* (MLP 73-II-27-6) all caudal vertebrae preserved (i.e., 12) have transverse processes. The transverse processes (=caudal rib) of the anteriormost caudal vertebrae are ventrally deflected, as in the sacral vertebrae. This feature is also present in *Metriorhynchus superciliosus* (SMNS 10116; von Arthaber 1906). According to Andrews, (1913) this feature is also present in Oxford Clay metriorhynchids, at least in the first

13 or 14 caudal vertebrae. The transverse processes in the first caudal vertebrae of *C. araucanensis* are borne entirely on the centrum and do not bear the neural arch. The inverse situation (i.e., the strong dorsally inclined angle of the transverse processes and the elevation of the transverse processes on the neural arch) has been described in some theropods (Persons and Currie 2011a). This morphology was interpreted as being related to an expanded hypaxial region, which the M. caudofemoralis could have filled at the expense of the epaxial region (Persons and Currie 2011a).

The transverse processes are reduced in width in comparison with the sacral ribs in MLP 73-II-27-6 and MLP 86-XI-10-8. The transverse processes are reduced to a small knob from fifth caudal vertebra backwards in MLP 86-XI-10-8. In *M. superciliosus* (SMNS 10116), the first 17 caudal vertebrae have transverse processes that decrease in size backwards. In *C. suevicus* (SMNS 9808), the first 11 caudal vertebrae have transverse processes, and from the fifth to 11th, the transverse processes decrease rapidly in size. This morphology (i.e., reduced and ventrally deflected transverse processes) would have restricted the expansion of the caudal hypaxial musculature (i.e., the M. caudofemoralis and M. ilio-ischiocaudalis) and increased the space for the epaxial musculature (i.e., the M. spinalis and M. longissimus). The reduction of caudofemoralis muscle in metriorhynchids has been previously proposed by others authors based on the reduced fourth trochanter (Hua 1994, Hua and Buffetaut 1997). The morphology described for the caudal vertebrae reinforces this hypothesis.

The notch described for the neural spine of the caudal vertebrae in *Cricosaurus araucanensis* and *C. suevicus* was related to an additional muscular insertion on the caudal vertebrae (Fraas 1902). In extant reptiles, the M. spinalis inserts onto the tips and lateral surfaces of the neural spines and M. longissimus inserts onto the dorsal surfaces of the transverse processes and on the lateral faces of the neural arches (Persons and Currie 2011a, b). The anterior process present in the neural spine of the caudal vertebrae in some *Cricosaurus* specimens could have been an insertion site for the M. spinalis. The relationship between the height of the neural spine and the haemal arches of dyrosaurids was related to the cross-section area of epaxial and hypaxial tail muscles (Schwarz-Wings *et al.* 2009). Unfortunately, due to preservation of Patagonian metriorhynchids, this relationship can not be determined along the tail. In extant reptiles, the epaxial musculature is involved in mediolateral and dorsoventral tail movements, and in maintaining tail stability (Persons and Currie 2011b). A putative increased epaxial musculature in *Cricosaurus araucanensis*, related to tail movements, is consistent with the swimming style and mode of propulsion by lateral undulation of the tail proposed for metriorhynchids (Massare 1988).

Acknowledgements

References

AMMON, L., 1905. Über Jurassische krokodile aus Bayern. *Geognostichen Jahresheften 18*, 55–71.

ANDREWS, C.W., 1913. *A descriptive catalogue of the marine reptiles of the Oxford Clay. Part II.* British Museum (Natural History), London, 206 pp.

ANDREWS, C.W., 1915. Note on a fore-paddle of *Metriorhynchus* from the Oxford Clay of Peterborough. *Geological Magazine 2*, 444–447.

BROCHU, C.A., 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology 16*, 49–62.

BROWN, D.S., 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum of Natural History (Geology) 35*, 253–347.

CARRANO, M.T. & HUTCHINSON, J.R., 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology 253*, 207–228.

CARROLL, R.L., 1997. Mesozoic marine reptiles as models of long-term, large-scale evolutionary phenomena. In *Ancient Marine Reptiles*. CALLAWAY, J. & NICHOLLS, E., eds, San Diego Academic Press, California, 467–489.

CARROLL, R.L. & GASKILL, P., 1985. The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Philosophical Transactions of the Royal Society of London B, Biological Sciences 309*, 343–393.

CAU, A. & FANTI, F., 2011. The oldest known metriorhynchid crocodylian from the Middle Jurassic of North-eastern Italy: *Neptunidraco ammoniticus* gen. et sp. nov. *Gondwana Research 19*, 550–565.

CLAESSENS, L.P.A.M. & VICKARYOUS, M.K., 2012. The evolution, development and skeletal identity of the crocodylian pelvis: revisiting a forgotten scientific debate. *Journal of Morphology 273*, 1185–1198.

DEBELMAS, J., 1952. Un crocodilien marin dans l'Hauterivien des environs de Comps (Var) *Dacosaurus maximus* Plieninger var. *gracilis* Quenstedt. *Travaux Laboratoire de Géologie l'université de Grenoble 29*, 101–116.

DELFINO, M. & DAL SASSO, C., 2006. Marine reptiles (Thalattosuchia) from the Early Jurassic of Lombardy (northern Italy). *Geobios 39*, 346–354.

DELFINO, M. & SÁNCHEZ-VILLAGRA, M.R., 2010. A survey of the rock record of reptilian ontogeny. *Seminars in Cell & Developmental Biology 21*, 432–440.

EVANS, D.C., BROWN, C.M., RYAN, M.J. & TSOGTBAATAR, K., 2011. Cranial ornamentation and ontogenetic status of *Homalocephale calathocercos* (Ornithischia: Pachycephalosauria) from the Nemegt Formation, Mongolia. *Journal of Vertebrate Paleontology 31*, 84–92.

FERNÁNDEZ, M. & GASPARINI, Z., 2000. Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. *Lethaia 33*, 269–276.

FERNÁNDEZ, M. & GASPARINI, Z., 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. *Naturwissenschaften 95*, 79–84.

FERNÁNDEZ, M.S. & HERRERA, Y., 2009. Paranasal sinus system of *Geosaurus araucanensis* and the homology of the antorbital fenestra of metriorhynchids (Thalattosuchia: Crocodylomorpha). *Journal of Vertebrate Paleontology 29*, 702–714.

FERNÁNDEZ, M.S., CARABAJAL, A.P., GASPARINI, Z. & CHONG DÍAZ, G., 2011. A metriorhynchid crocodyliform braincase from northern Chile. *Journal of Vertebrate Paleontology 31*, 369–377.

FRAAS, E., 1902. Die Neer-Crocodilier (Thalattosuchia) des Oberen ura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Palaeontographica 49*, 1–79.

GASPARINI, Z.B. de & DELLAPÉ, D., 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Tithoniano) de la Provincia de Neuquén (Argentina). *Actas 1° Congreso Geológico Chileno, Santiago, Chile*, C1–C21.

GASPARINI, Z. & FERNÁNDEZ, M., 2005. Jurassic marine reptiles of the Neuquén Basin: records, faunas and their palaeobiogeographic significance. In *The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics*. VEIGA, G.D., SPALLETTI, L.A., HOWELL, J.A. & SCHWARZ, E., eds, 279–294.

GASPARINI, Z. & FERNÁNDEZ, M., 2011. Reptiles marinos mesozoicos. In *Relatorio del XVIII Congreso Geológico Argentino, Neuquén*. LEANZA, H.A., ARREGUI, C., CARBONE, O., DANIELA, J.C. & VALLÉS, J.M., eds, Asociación Geológica Argentina, Buenos Aires, 529–538.

GATESY, S.M., 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology 16*, 170–186.

HERRERA, Y., 2012. *Análisis morfológico y paleobiológico de Cricosaurus araucanensis (Gasparini y Dellapé, 1976) (Crocodyliformes: Metriorhynchidae)*. PhD thesis, Universidad Nacional de La Plata, La Plata, 346 pp. (unpublished).

HERRERA, Y., FERNÁNDEZ, M.S. & VARELA, J.A., 2009. Morfología del miembro anterior de *Geosaurus araucanensis* Gasparini y Dellapé, 1976 (Crocodyliformes: Thalattosuchia). *Ameghiniana 46*, 657–667.

HERRERA, Y., FERNÁNDEZ, M.S. & GASPARINI, Z., in press a. The snout of *Cricosaurus araucanensis*: a case study in novel anatomy of the nasal region of metriorhynchids. *Lethaia*.

HERRERA, Y., GASPARINI, Z. & FERNÁNDEZ, M.S., in press b. A new Patagonian species of *Cricosaurus* (Crocodyliformes, Thalattosuchia): first evidence of *Cricosaurus* in Middle–Upper Tithonian lithographic limestones from Gondwana. *Palaeontology*.

HOFFSTETTER, R. & GASC, J.P., 1969. Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia. Morphology F, Volume 1*. GANS, C., BELLAIRS, A.D.A. & PARSONS, T.S., eds, Academic Press, London, 1–556.

HUA, S., 1994. Hydrodynamique et modalités d'allègement chez *Metriorhynchus superciliosus* (Crocodylia, Thalattosuchia: Implications paléoécologiques). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 193*, 1–19.

HUA, S. & BUFFETAUT, E., 1997. Crocodilia. In *Ancient Marine Reptiles*. CALLAWAY, J. & NICHOLLS, E., eds, San Diego Academic Press, California, 357–374.

HUA, S. & DE BUFFRÉNIL, V., 1996. Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology 16*, 703–717.

HUTCHINSON, J.R. & GATESY, S.M., 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology 26*, 734–751.

IKEJIRI, T., 2012. Histology-based morphology of the neurocentral synchondrosis in *Alligator mississippiensis* (Archosauria, Crocodylia). *The Anatomical Record 295*, 18–31.

IRMIS, R.B., 2007. Axial skeleton ontogeny in the parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology 27*, 350–361.

MASSARE, J.A., 1988. Swimming capabilities of mesozoic marine reptiles: implications for method of predation. *Paleobiology 14*, 187–205.

MÜLLER, G.B. & ALBERCH, P., 1990. Ontogeny of the limb skeleton in *Alligator mississippiensis*: developmental invariance and change in the evolution of Archosaur limbs. *Journal of Morphology 203*, 151–164.

OTERO, A., GALLINA, P.A. & HERRERA, Y., 2010. Pelvic musculature and function of *Caiman latirostris. Herpetological Journal 20*, 173–184.

PERSONS, W.S. & CURRIE, P.J., 2011a. The tail of *Tyrannosaurus*: reassessing the size and locomotive importance of the *M. caudofemoralis* in non-avian theropods. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology 294*, 119–131.

PERSONS, W.S. & CURRIE, P.J., 2011b. Dinosaur speed demon: The caudal musculature of *Carnotaurus sastrei* and implications for the evolution of South American abelisaurids. *Plos One 6*, e25763.

PIERCE, S.E., ANGIELCZYK, K.D. & RAYFIELD, E.J., 2009. Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation, and temporal patterns. *Palaeontology 52*, 1057–1097.

POL, D. & GASPARINI, Z., 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology 7*, 163–197.

RENESTO, R., 2008. Remains of a juvenile phytosaur from the Late Triassic of Northern Italy. *Rivista Italiana di Paleontologia e Stratigrafia 114*, 155–160.

RIEPPEL, O., 1989. *Helveticosaurus zollingeri* Peyer (Reptilia, Diapsida) skeletal paedomorphosis, functional anatomy and systematic affinities. *Palaeontographica A 208*, 123–152.

RIEPPEL, O., 1992a. Studies on skeleton formation in reptiles, III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). *Fieldiana (Zoology) new series 68*, 1–25.

RIEPPEL, O., 1992. Studies on skeleton formation in reptiles. I. The postembryonic development of the skeleton in *Cyrtodactylus pubisulcus* (Reptilia: Gekkonidae). *Journal of Zoology 227*, 87–100.

ROMER, A.S., 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bulletin of the American Museum of Natural History 48*, 533–552.

RUSCONI, C., 1948. Nuevo plesiosaurio, pez y langosta del mar jurásico de Mendoza. *Revista del Museo Historia Natural de Mendoza 2*, 3–12.

SCHWARZ-WINGS, D., FREY, E. & MARTIN, T., 2009. Reconstruction of the bracing system of the trunk and tail in Hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). *Journal of Vertebrate Paleontology 29*, 453–472.

VIGNAUD, P. & GASPARINI, Z.B., 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences, Paris 2*, 245–250.

VON ARTHABER, G., 1906. Beiträge zur Kenntis des Organisation und der Anpassungserscheinunugen des genus *Metriorhynchus. Beiträge zur Paläontologie Österreich-Ungarns und des Orients 19*, 287–320.

WILKINSON, L.E., YOUNG, M.T. & BENTON, M.J., 2008. A new metriorhynchid crocodile (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaeontology 51*, 1307–1333.

YOUNG, M.T. & ANDRADE, M.B., 2009. What is *Geosaurus*? Redescription of *G. giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society 157*, 551–585.

YOUNG, M.T., BRUSATTE, S.L., RUTA, M. & ANDRADE, M.B., 2010. The evolution of Metriorhynchidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity and biomechanics. *Zoological Journal of the Linnean Society 158*, 801–859.

YOUNG, M.T., BELL, M.A., ANDRADE, M.B. & BRUSATTE, S.L., 2011a. Body size estimation and evolution in metriorhynchid crocodylomorphs: implications for species diversification and niche partitioning. *Zoological Journal of the Linnean Society 163*, 1199–1216.

YOUNG, M.T., BELL, M.A. & BRUSATTE, S.L., 2011b. Craniofacial form and function in Metriorhynchidae (Crocodylomorpha: Thalattosuchia): modelling phenotypic evolution with maximum-likelihood methods. *Biology Letters 7*, 913–916.

YOUNG, M.T., AANDRADE, M.B., BRUSATTE, S.L., SAKAMOTO, M. & LISTON, J., in press. The oldest known metriorhynchid super-predator: a new genus and species from the Middle Jurassic of England, with implications for serration and mandibular evolution in predacious clades. *Journal of Systematic Palaeontology.*