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New Patagonian Cretaceous theropod sheds light about the early radiation of Coelurosauria

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Abstract: Here we describe a new theropod, *Bicentenaria argentina* nov. gen. et nov. sp., from the early Late Cretaceous of Patagonia. It is represented by more than a hundred bones belonging to different sized individuals, which were buried together in disarticulation after little transportation. The available association of skeletal elements suggests a gregarious behaviour for *Bicentenaria*, an ethological trait also recorded among other theropod clades. Increasing documentation of monospecific assemblages of different groups of theropods suggests that a gregarious behaviour may have constituted the ancestral condition for Theropoda, at least. *Bicentenaria* characterizes for the surangular bone with a high dorsal margin and a prominent lateral shelf, a retroarticular process that is low, wide and spoon-shaped, and quadrate bone with its lateral condyle larger than the medial one. Phylogenetic analysis found the Chinese *Tugulusaurus* and the Patagonian *Bicentenaria* as successive sister taxa of all other coelurosaurs, thus revealing the importance of the new taxon in the understanding of the early diversification of Coelurosauria. In particular, *Bicentenaria* amplifies the array of basal coelurosaurs that inhabited Gondwana during the Cretaceous, also including compsognathids, *Aniksosaurus* and *Santanaraptor*. Although still restricted to a handful of forms, available information indicates that Gondwana was a cradle for the evolution of different lineages of basal coelurosaurs, different from those documented in Upper Cretaceous beds in the northern landmasses. Analysis of body size distribution in averostran theropods results in the identification of two main episodes of drastic size reduction in the evolutionary history of Coelurosauria: one occurred at the initial radiation of the group (as represented by *Bicentenaria*, *Zuolong, Tugulusaurus*, compsognathids, and *Aniksosaurus*), and a second episode occurred at the early diverification of Paraves or avialans. Reduction in body size may have allowed adult coelurosaurians to exploit ecological niches not occupied before by larger basal averostrans.

Key words: Coelurosauria, gregarism, body size reduction, Cretaceous, South America.

Resumen: Nuevo terópodo del Cretácico de Patagonia brinda nuevas evidencias acerca de la radiación temprana de Coelurosauria. En la presente contribución se describe el nuevo terópodo *Bicentenaria argentina* nov. gen. et nov. sp., del Cretácico Tardío temprano de Patagonia. El nuevo taxón se encuentra representado por más de una centena de huesos pertenecientes a individuos de diferentes tamaños, los cuales fueron enterrados todos juntos en desarticulación, luego de un leve transporte. La asociación disponible de materiales sugiere hábitos gregarios para *Bicentenaria*, un rasgo etológico también registrado en otros clados de terópodos. La documentación recurrente de asociaciones monoespecíficas de diferentes grupos de terópodos sugiere que los hábitos gregarios pudieron haber constituido la condición ancestral para Theropoda. *Bicentenaria* se caracteriza por un hueso surangular con un margen dorsal prominente y con una repisa lateral bien desarrollada, un proceso retroarticular que es bajo, transversalmente amplio y en forma de cuchara, y un hueso cuadrado cuyo cóndilo lateral es de tamaño mucho mayor que el medial. El análisis filogenético recuperó al género chino *Tugulusaurus* y al patagónico *Bicentenaria* como grupos hermanos sucesivos de los restantes celurosaurios, revelando de este modo la importancia del nuevo taxón para el entendimiento de la radiación temprana de los Coelurosauria. En particular, *Bicentenaria* amplifica el elenco de celurosaurios basales que habitaron Gondwana durante el Cretácico, incluyendo entre otros a los compsognátidos, *Aniksosaurus* y *Santanaraptor*. A pesar de encontrarse restringida a un puñado de formas, la información disponible sugiere que Gondwana fue un importante centro para la evolución de diferentes linajes de celurosaurios basales, diferentes de aquellos representados en el Hemisferio Norte. Un

análisis de la distribución del tamaño corporal en los terópodos averostros permite identificar dos episodios principales de drástica reducción del tamaño en el curso de la historia evolutiva de los Coelurosauria. El primero de estos episodios ocurrió durante la radiación inicial del grupo (tal como es representado por *Bicentenaria*, *Zuolong, Tugulusaurus*, compsognátidos, y *Aniksosaurus*), y el segundo episodio tomó lugar en la temprana diversificación de Paraves o Avialae. La reducción en la talla corporal pudo haber permitido a los celurosaurios adultos explotar nichos no ocupados anteriormente por terópodos averostros basales de mayor tamaño.

Palabras clave: Coelurosauria, gregarismo, reducción de talla corporal, Cretácico, Sudamérica.

INTRODUCTION

Coelurosauria includes extant birds and all theropods sharing a more recent common ancestor with *Passer domesticus* than with *Allosaurus fragilis* (Holtz *et al.,* 2004). Coelurosaurs were highly diversified during Jurassic and Cretaceous times, including compsognathids, tyrannosauroids, ornithomimosaurians, oviraptorosaurians, therizinosauroids, alvarezsaurids, and dromaeosaurids, among the most notable groups. Most of these clades are well documented in the Northern Hemisphere, and although the record of Coelurosauria in the southern landmasses is still limited, discoveries produced in Patagonia in the last 15 years have favourably changed this situation (Novas, 2009). In particular, the fossil record of non-maniraptoran coelurosaurs in Gondwana is currently composed by *Mirischia asymmetrica* (Santana Formation, Aptian, Brazil; Naish *et al.,* 2004) and *Nqwebasaurus thwazi* (Kirkwood Formation, probably Valanginian; De Clerk *et al.,* 2000), both possible compsognathids, and the yet poorly understood *Aniksosaurus darwini* (Lower Bajo Barreal Formation, Cenomanian; Martínez & Novas, 2007) and *Santanaraptor placidus* (Santana Formation, Aptian, Brazil; Kellner, 1999).

Here we enlarge the list of Gondwanan coelurosaurs with the description of the new small-sized species *Bicentenaria argentina* nov. gen. et nov. sp. *Bicentenaria* is represented by several cranial and postcranial bones of multiple individuals that increase the taxonomic and morphological diversity of basal coelurosaurs in Gondwana. A comprehensive phylogenetic analysis of Coelurosauria recovers an unexpected high diversity of plesiomorphic lineages in the southern continents, and a two-step evolutionary trend towards the reduction of body size and mass among Coelurosauria, in the line leading to birds.

Institutional abbreviations. **AMNH**, American Museum of Natural History, New York; **MPCA**, Museo Provincial "Carlos Ameghino", Cipoletti, Río Negro; **USNM**, United States National Museum, Washington D.C.

MATERIALS AND METHODS

Collected material of *Bicentenaria argentina*

The skeletal remains of *Bicentenaria argentina* were collected by Mr. Raul Spedale in 1998 during an exceptional fall in the water level of the Ezequiel Ramos Mexía Reservoir (Fig. 1). All the bones were collected from a single quarry roughly 40 centimeters long, 30 centimeters wide, and 50 centimeters thick (R. Spedale, pers. comm.). The recovered bones are well preserved and lack signs of aerial exposure or scavenging before burial. Unfortunately, the bones suffered several breakages during the excavation process and no taphonomic information was collected during the process. Nevertheless, the bones were buried almost probably in disarticulation, as revealed by a block of sandstone still embedding a partial sacrum and fragments of the corresponding right iliac blade, that are chaotically attached with a fragment of left maxilla, four caudal vertebrae of different sections of the tail, as well as with the proximal end of a cranial dorsal rib. This kind of preservation indicates that bones of different individuals were transported and mixed up before their final burial. The collected bones include three femora of the left side with roughly the same size (approximately 31cm in length), thus indicating that the fossil assemblage is made up by, at least, three large different specimens. These large femora match with the size observed in several isolated dorsal, sacral and caudal vertebrae with a closed neurocentral suture. Thus, these large individuals would not be juveniles at the time of their death (Brochu, 1996; Irmis, 2007). Besides, the existence of a right distal femur with an identical morphology, but considerably smaller than the largest ones, indicates the presence of probably younger individuals in the bone assemblage. This statement is supported by the presence of a fragmentary maxilla bearing a tiny tooth with a crown height of 8 mm, obviously corresponding to a juvenile individual. In summary, the bone assemblage seems to be made up by different sized juvenile and adult specimens.

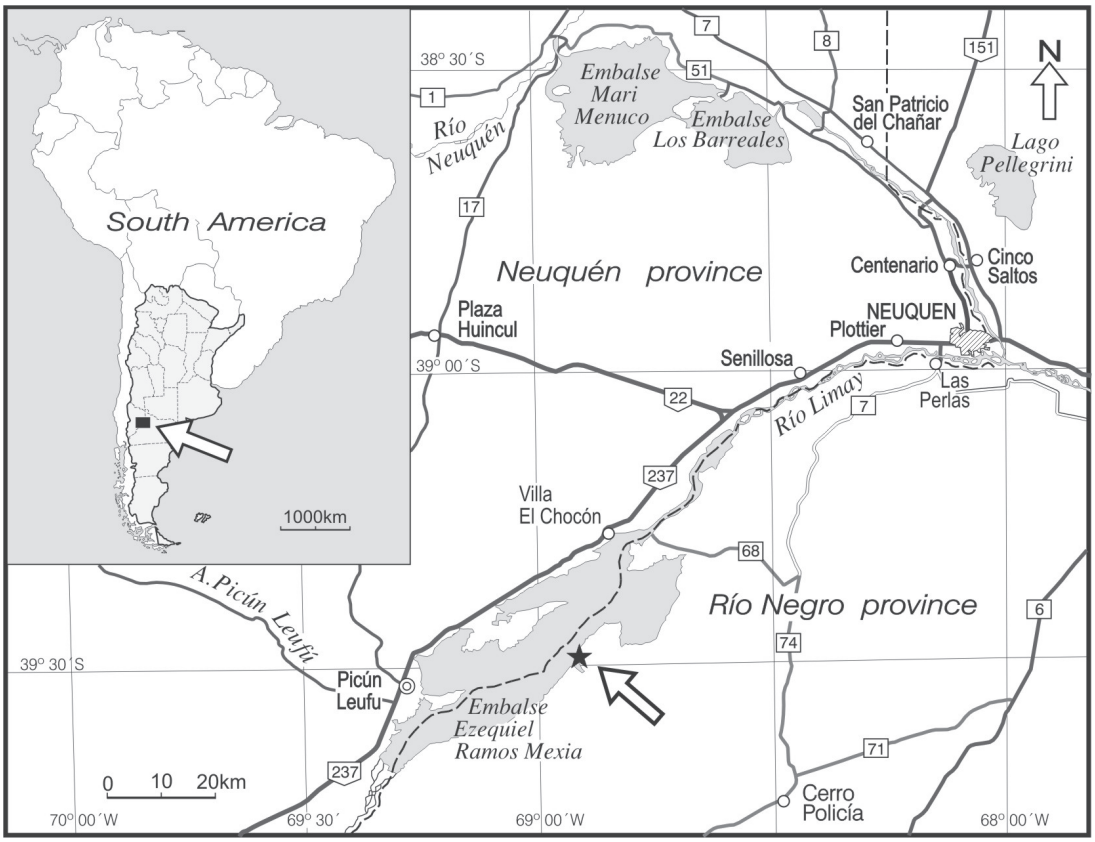


Fig. 1. Map showing the fossiliferous locality (star) where the holotype and paratypes of *Bicentenaria argentina* were found.

We interpret that both the holotype and paratype specimens belong to a single species for the following reasons: 1) duplicate hindlimb elements (e.g., femur, tibia, metatarsals, and pedal phalanges) possess an identical anatomy; 2) available bones exhibit theropod, tetanuran and coelurosaurian synapomorphies (these derived features are mentioned in the text below); and 3) there is no evidence of any other dinosaur taxon preserved in the quarry. Excepting for the fragmentary skull, the disarticulated nature of the assemblage avoids recognition of discrete specimens composed for more than a single bone.

Cladistic analysis

A phylogenetic numerical analysis was conducted to assess the phylogenetic relationships of *Bicentenaria argentina* among neotetanuran theropods. The data matrix was modified from that published by Zheng *et al.* (2009), in which the ingroup was focused on coelurosaurian theropods. The addition of ten operational taxonomic units (i.e., *Tugulusaurus faciles* Dong, 1973, *Santanaraptor placidus* Kellner, 1999, *Nqwebasaurus thwazi* De Clerk *et al.,* 2000, *Mirischia asymmetrica* Naish *et al.,* 2004, *Aniksosaurus darwini* Martínez & Novas, 2006, *Anchiornis huxleyi* Xu *et al.,* 2009a, *Mahakala omnogovae* Turner *et al.,* 2007, *Elaphrosaurus bambergi* Janensch, 1920, *Dilophosaurus wetherilli* Welles, 1954 and *Bicentenaria argentina* nov. gen. et nov. sp.) and three characters resulted in a modified data matrix composed of 363 characters and 100 taxa. The basal neotheropod *Dilophosaurus wetherilli* (Welles, 1954) was used to root the recovered most parsimonious trees (MPTs). The data matrix was analyzed under equally weighted parsimony using TNT 1.1 (Goloboff *et al.,*2008). A heuristic search of 100 replications of Wagner trees (with random addition sequence) followed by TBR branch-swapping algorithm (holding 10 trees per replicate) was performed. The best trees obtained at the end

of the replicates were subjected to a final round of TBR branch swapping. Zero length branches among any of the recovered MPTs were collapsed (i.e., rule 1 of Coddington & Scharff, 1994). All multistate characters were treated as unordered and no *a priori* character polarization was used (see Appendixes 1-2).

Analysis of body size evolution

This analysis was conducted through the scoring of femoral lengths as a continuous character across the theropods sampled in the previously analyzed data matrix [measurements taken mostly from Benson *et al.* (2011); estimations of femoral length were followed only if they were calculated after ilium or hindlimb bone lengths and taxa represented solely by juvenile specimens were considered as missing data] (see Appendix). Subsequently, the character was optimized in the topology of each recovered MPT following a maximum parsimony criterion through which the ancestral femoral length ranges were obtained.

SYSTEMATICS

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Coelurosauria Huene, 1920

Bicentenaria argentina nov. gen. et nov. sp.

Etymology. From bicentenary, due to the 200 years of the Revolution of May (25th May 1810), which lead to the first Argentinean autonomous government, thus constituting one of the most important chapters in the history of this South American country. Specific epithet honors Argentina, the country where the specimens were recovered.

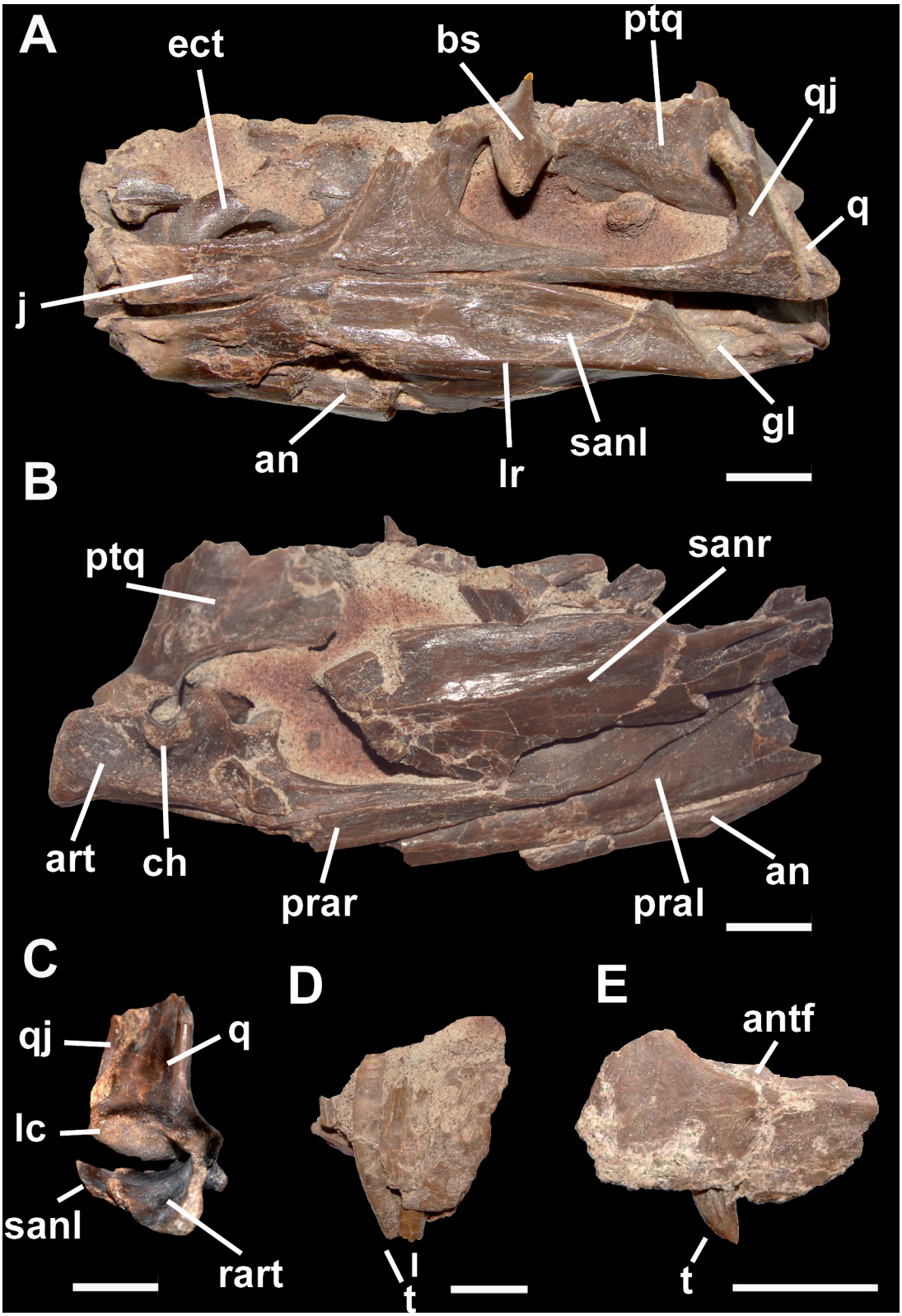
Holotype. MPCA 865, caudal half of skull in articulation with the lower jaws (Fig. 2).

Paratypes. MPCA 866, around 130 bones, including fragments of two articulated premaxillae with three pairs of teeth, an incomplete right maxilla with a single tooth, fragments of seventeen dorsal vertebrae, fourteen sacral vertebrae, twenty caudal vertebrae, fragments of two scapulae, caudodorsal corner of a right coracoid, proximal ends of three ulnae, distal end of radius, eight manual unguals, fragments of left ilium, proximal fragments of five pubic shafts, five incomplete femora, proximal thirds of two left tibiae and distal end of the right one, right astragalus, fragments of five metatarsals, fifteen non-ungual pedal phalanges, eight pedal unguals, and several isolated rib fragments.

Locality and horizon. Upper levels of the Candeleros Formation (Cenomanian, early Late Cretaceous; Leanza *et al.,* 2004), Río Limay Subgroup, Neuquén Group. The fossiliferous locality is placed at the east shore of Ezequiel Ramos Mexía Reservoir, Río Negro Province, Northern Patagonia, Argentina (Fig. 1). GPS coordinates of the fossil site are 39º 28' 9.82" S, 68º 54' 25.01" W. The rocks of the Candeleros Formation which yielded the remains of *Bicentenaria argentina* are made up by red medium sized sandstones and mudstones, with abundant dark-brownish paleosoils representing a fluvial environment under braided and meandering regimes, as well as in aeolian conditions (Leanza *et al.,* 2004; Garrido, 2011).

Diagnosis. *Bicentenaria argentina* was a small-sized theropod ca. 3 m long [estimated by extrapolating bone measurements from the reconstructed skeletons of *Compsognathus* and *Tanycolagreus*; Ostrom, 1978; Carpenter *et al.,* 2005)] and ca. 40 kg of body mass [following formula from Seebacher (2001)]. *Bicentenaria argentina* is diagnosed on the following autapomorphies: premaxillary teeth with mesial denticles only at the base of the crown; quadratojugal with a rostral process two times longer than the dorsal process; quadrate with lateral condyle much larger than the medial one; surangular with a raised dorsal margin trapezoidal-shaped in lateral profile; retroarticular process dorsoventrally depressed, transversely wide, and spoon-shaped; humerus with proximal end craniocaudally flattened, and distal end bearing a deep fossa on its cranial surface; and manual unguals of external digits bearing proximal dorsal lips.

Fig. 2. Selected cranial elements of *Bicentenaria argentina* nov. gen. et nov. sp. **A,** left lateral view of preserved caudal half of skull and jaws; **B**, right lateral view of preserved caudal half of skull and jaws; **C**, left quadrate and lower jaw in caudal view; **D**, fragmentary premaxillae with teeth in left lateral view; **E**, fragmentary left maxilla with tooth in lateral view. **Abbreviations: an**, angular; **antf**, antorbital fossa; **art**, articular; **bs**, basipterygoid process of basisphenoid; **ch**, notch for the chorda tympanica; **gl,** glenoid fossa; **j**, jugal; **lc**, lateral condyle of quadrate; **lr**, longitudinal ridge; **ect**, ectopterygoid; **prar**, right prearticular; **pral**, left prearticular; **ptq**, pterigoid ramus of quadrate; **q**, quadrate; **qj**, quadratojugal; **sanl**, left surangular; **sanr**, right surangular; **rart**, retroarticular process; **t**, tooth. Scale bars = 1 centimeter.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Description. The premaxillae of *Bicentenaria* bears at least four teeth, which are sub-circular in cross-section and mostly devoid of serrations at the distal and mesial margins of the crown. However, the second tooth of the right premaxilla possesses mesial denticles that are restricted to the basalmost portion of the crown. This morphology clearly departs from the "D"-shaped condition synapomorphic of tyrannosauroids (Rauhut *et al.*, 2009).

The preserved maxilla presents a nearly smooth external surface and a row of proportionally large neurovascular foramina, aligned parallel to the alveolar margin. The only available maxillary tooth is highly labiolingually compressed, and exhibits serrated mesial and distal carinae up to the tip of the crown. The distal serrations are coarser than the mesial ones, as it occurs in other coelurosaurs (e.g., *Zuolong, Ornitholestes, Velociraptor, Troodon*; Choiniere *et al.,* 2010; Currie *et al.,* 1990).

The jugal is incompletely preserved, lacking its rostral process; the caudal process is bifurcated into two long and acute prongs for articulation with the quadratojugal. The jugal bears a flat and lateroventrally oriented facet for the contact of the surangular when the jaws were closed.

The quadratojugal exhibits an acute and elongate rostral process for articulation with jugal. Its length exceeds the dorsoventral height of the ascending process of the quadratojugal. This condition differs from the shorter rostral process seen in most coelurosaurs, including tyrannosauroids (e.g., *Proceratosaurus, Tanycolagreus, Tarbosaurus*; Currie, 2003; Carpenter *et al.,* 2005; Rauhut *et al.,* 2009), ornithomimids (e.g., *Gallimimus*; Osmólska *et al.,* 1972), and compsognathids (e.g. *Compsognathus*; Ostrom, 1978). On the other hand, in *Sinraptor* and *Monolophosaurus*, this process is also rostrocaudally elongate, but constrasting with *Bicentenaria* in that in these two taxa the process is dorsoventrally thicker (Currie & Zhao, 1993). The rostral process appears to be dorsoventrally high, as occurs in several theropods, including *Proceratosaurus* and *Gallimimus* (Rauhut *et al.,* 2009; Osmólska *et al.,* 1972). In *Bicentenaria*, both rostral and ascending processes of the quadratojugal describe an angle lesser than 90 degrees. The ascending ramus of quadratojugal is rostrocaudally thin, a condition that constrasts with the robust one in other basal coelurosaurs, such as tyrannosauroids (e.g. *Tanycolagreus, Proceratosaurus*; Carpenter *et al.,* 2005; Rauhut *et al.,* 2009) and ornithomimids (e.g., *Gallimimus*; Osmólska *et al.,* 1972).

The quadrate exhibits a concave external edge and the quadrate foramen is small and proximally located, being very similar in proportion and morphology to that of *Allosaurus* (Madsen, 1976). The quadrate is a solid bone, lacking a caudal pneumatic diverticulum of the tympanic system, a condition exhibited by tyrannosaurids, ornithomimosaurs, troodontids, oviraptorids, and basal birds (Rauhut, 2003). The medial distal condyle of the quadrate is strongly reduced, being less than half the transverse width of the lateral condyle. Cranially, the quadrate exhibits a laminar and well-developed rostral process, a condition reminiscent to that present in *Tanycolagreus* (Carpenter *et al.,* 2005).

The ectopterygoid is incompletely preserved and partially obscured by other cranial bones. Its preserved portion suggests that it possessed a well-developed, hook-like lateral process. Medially, it articulates with the poorly preserved pterygoid.

The braincase of *Bicentenaria* is represented only by the left basipterygoid process of the basisphenoid. The lateral surface of the basipterygoid process is excavated by a very deep and wide pneumatic recess, resembling the condition present in *Stokesosaurus* (Chure & Madsen, 1998), for example. In tyrannosaurids and other coelurosaurs such recess on the basipterygoid process is much more reduced (Chure & Madsen, 1998; Rauhut *et al.,* 2009). The rostral and mid-portions of the mandibles are missing. The caudal half of both jaws is preserved, being somewhat distorted. The surangular shows on its rostral portion a deep notch, indicating the presence of a mandibular fenestra. The general contour of the bone, in lateral view, resembles that of *Allosaurus* (Madsen, 1976). However, its dorsal margin is more prominent, probably conforming an extended area for the insertion of the *M. adductor mandibular externus* (Currie & Zhao, 1993). The lateral surface of surangular shows a longitudinal shelf running below the glenoid cavity, as is also seen in other theropods (*Sinraptor, Allosaurus,* tyrannosaurids; Madsen, 1976; Currie & Zhao, 1993; Currie, 2003). On the lateral surface of the surangular there is a wide and straited area for the articulation with the angular (this latter bone is partially broken and displaced from its natural position). The caudal end of the surangular is triangular and with a prominent dorsal process that encloses the glenoid cavity from behind. The caudal extension of

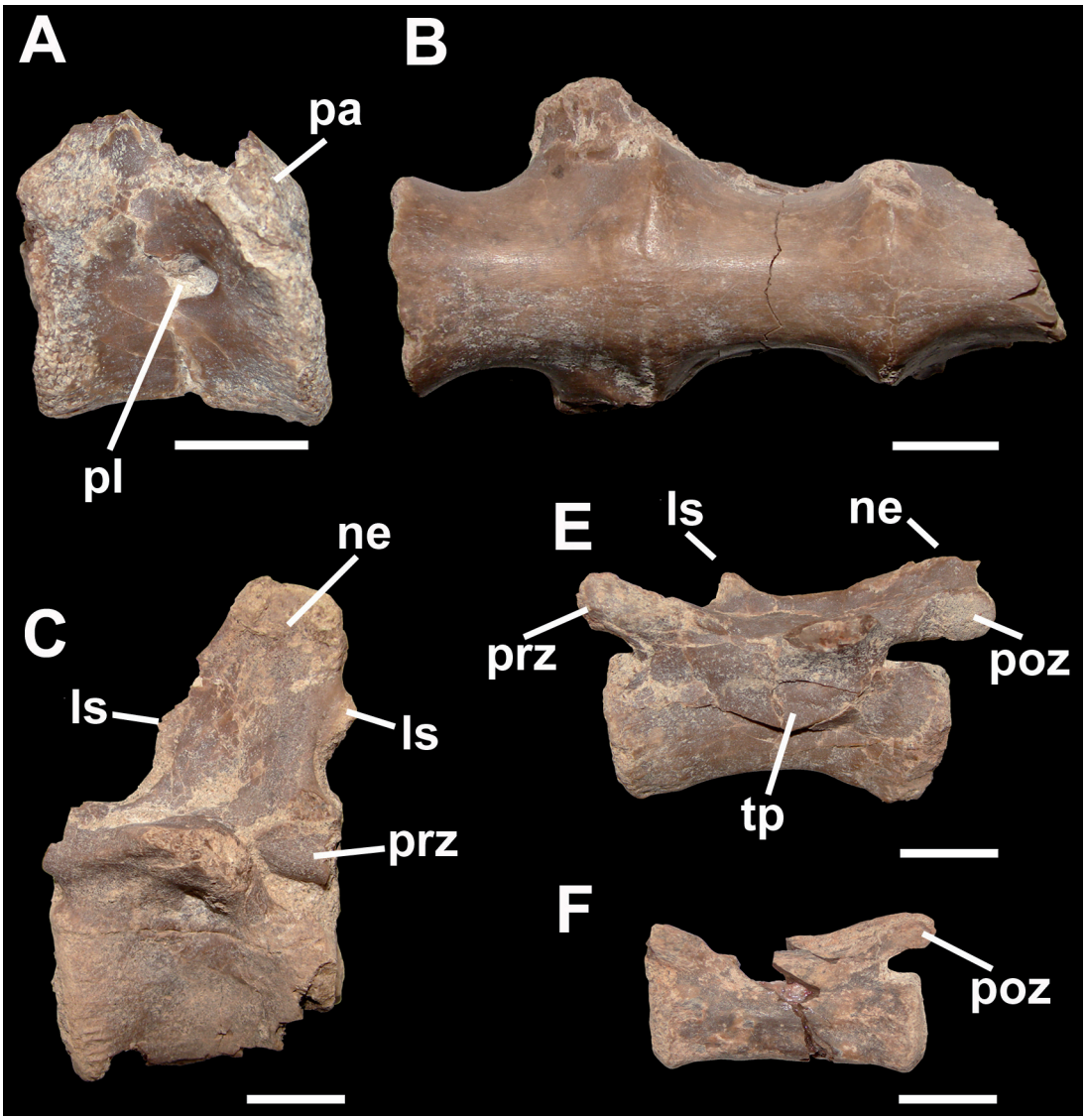


Fig. 3. Selected vertebral elements of *Bicentenaria argentina* nov. gen. et nov. sp. **A**, cranial dorsal centrum in right lateral view; **B**, partial sacrum in ventral view (cranial is towards the right); **C**, proximal caudal vertebra in left lateral view; **D**, distal caudal vertebra in left lateral view; **E**, distal caudal vertebra in left lateral view. **Abbreviations**: **ls**, ligament scar; **ne**, neural spine; **pa**, parapophysis; **pl**, pleurocoel; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Scale bar = 1 centimeter.

surangular behind the glenoid cavity resembles *Allosaurus*, being different from *Compsognathus* (Ostrom, 1978) in which the caudal end of the surangular extends further behind, and tyrannosaurids (Currie, 2003) in which the caudal end of the surangular is shorter and its caudal margin is subvertically oriented. In *Bicentenaria* the glenoid cavity is deeply excavated, apparently more than in *Sinraptor* and *Allosaurus*. The shape and size of the glenoid matches the morphology of the well-developed lateral articular condyle of the quadrate. The surangular portion of the glenoid is elliptical-shaped in dorsal view, with its largest axis rostromedially oriented. No signs of pneumaticity are detected in the articular, in contrast with the pneumatized condition seen in tyrannosauroids (Brusatte *et al.,* 2010).

The left angular preserves its rostral end, bearing a conspicuous ventral elliptical depression that may have served for ligament attach-

ment with the posteroventral process of dentary. The prearticular, instead, is a laminar bone that exhibits a laterally deflected lamina that wraps on the ventral margin of the angular.

The articular is large and robust and fits between the caudal ends of the surangular and prearticular. The retroarticular process of the articular is transversely wide, deeply concave, and mostly dorsally to caudodorsally oriented, conforming a spoon-shaped process similar to that in *Ornitholestes hermanni* (AMNH 619; Rauhut, 2003, fig. 21). The retroarticular process is separated from the glenoid fossa by a deep, transversely oriented ridge, as it is appreciated also in *Allosaurus* (USNM 4734) and *Ornitholestes* (AMNH 619). Medially, there is a prominent process dorsally notched, that served for the attachment of the chorda tympanica. This medially extended and dorsally notched process is also present in *Sinraptor* (Currie & Chao, 1993), *Allosaurus* (USNM 4734) and *Ornitholestes* (AMNH 619), but it is absent in abelisaurids (*Carnotaurus*, *Majungasaurus*; Bonaparte *et al.,* 1990; Sampson & Witmer, 2007) and paravians (e.g., *Deinonychus*; Ostrom, 1969). In other words, *Bicentenaria* seems to have retained a basal tetanuran morphology for the caudal end of the jaw.

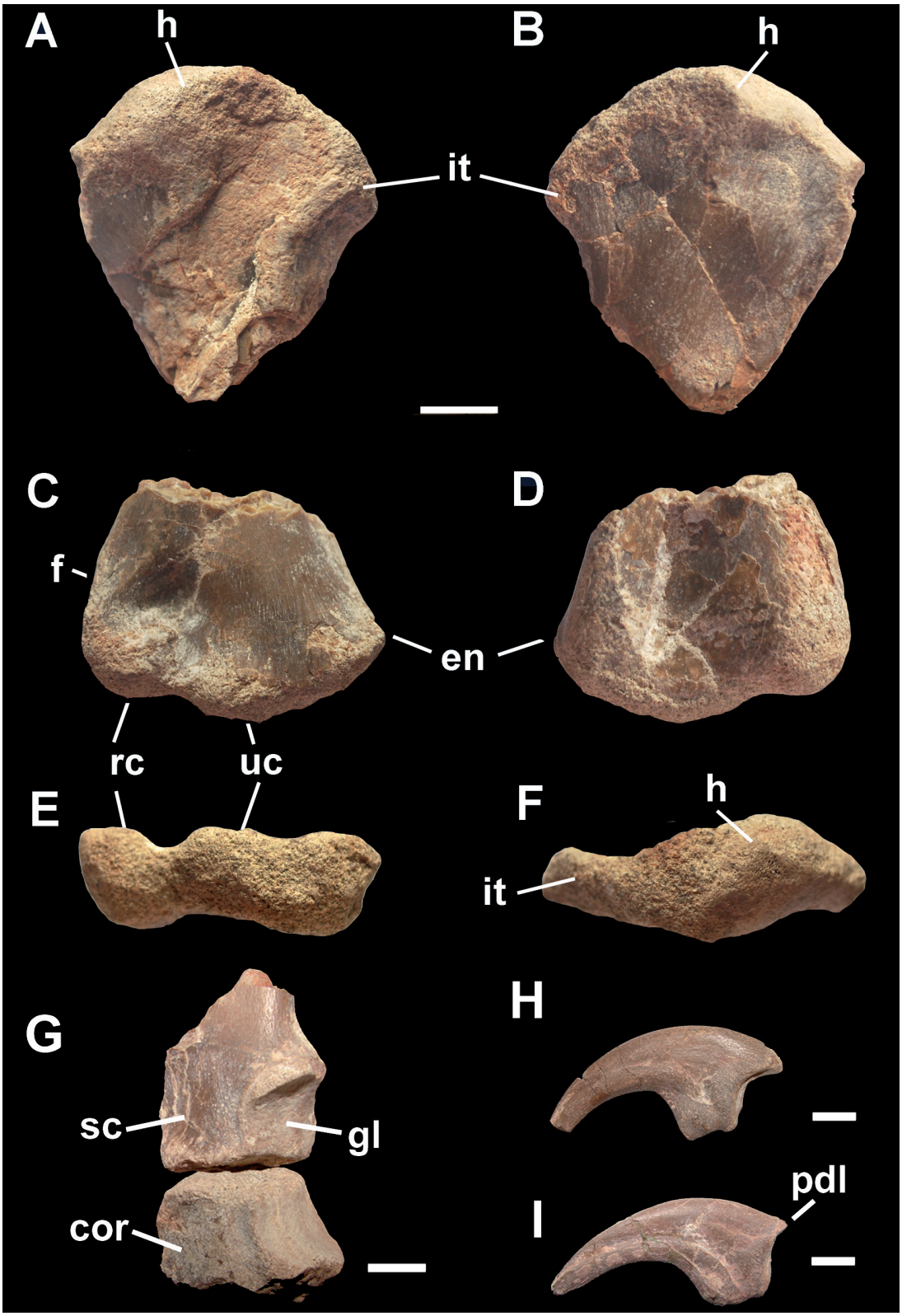
The vertebral column of *Bicentaria* is represented by several dorsal, sacral and caudal vertebrae belonging to different-sized individuals (Fig. 3). Two cranial dorsals (presumably dorsal vertebrae ?3rd and ?4th, based on general similarities with *Allosaurus*; Madsen, 1976), exhibit a sharp ventral keel and parapophyses located on the dorsal corner of centrum; a single pleurocoel perforates the centrum behind the parapophyses. The centrum of the presumed third dorsal has a slightly convex cranial articular surface and a deeply concave caudal surface. The centrum of the remaining dorsals is amphicoelous, and their ventral surfaces are flattened. Aside from the probable third dorsal vertebrae, the remaining available dorsals do not exhibit external pneumatic features. The broken portions of some centra reveal that the internal bone structure is of the camellate type (Benson *et al.,* 2012). The proximal third of an isolated rib resembles the shape of ribs corresponding to the 1st through 3rd dorsal ribs of *Allosaurus* (Madsen, 1976).

Portions of eight sacra are available, six of which are represented by two to four fused centra (Fig. 3). We assume that the sacrum of *Bicentenaria* was originally composed by five vertebrae, as is usual in other basal tetanurans and coelurosaurians (e.g., *Allosaurus, Tyrannosaurus*: Madsen, 1976; Brochu, 2002). Each sacral centrum is robust and ventrally rounded in transverse section; towards the caudal end of the sacrum the vertebrae become stouter. Sacrals are devoid of external pneumatic features.

Several caudal vertebrae corresponding to different portions of the tail are available (Fig. 3). A proximal caudal vertebra, resembling the caudal 4th of *Allosaurus* (Madsen, 1976), exhibits transverse processes that are ventrally excavated at their bases. The neural spine of this vertebra possesses ligament scars along both cranial and caudal margins, as it also occurs in *Allosaurus* (Madsen, 1976). The proximal caudal vertebrae bear tall and subdivided neural spines, resembling allosauroids (Madsen, 1976; Brusatte & Sereno, 2008) and some basal coelurosaurs (e.g. *Sinosauropteryx*; *Santanaraptor*; Currie & Chen, 2001; Kellner, 1999). The caudal vertebrae of *Bicentenaria* lack pleurocoels and exhibit a ventral sulcus bounded by two faint longitudinal ridges. Some isolated caudal vertebrae resemble caudals 19th through 20th of *Allosaurus* (Madsen, 1976). Most of the available distal caudals of *Bicentenaria* are damaged, and none of them preserves complete prezygapophyses. Thus, it is unknown if they possessed the elongate condition of most theropods.

The scapular girdle of *Bicentenaria* is represented by fragments of the proximal portions of the scapula and coracoid (Fig. 4). The glenoid fossa of the scapular girdle is large and wide, limited by a supraglenoid buttress. The proximal fragment of a left humerus and the distal extremes of both left and right humeri are preserved (Fig. 4). The proximal end is craniocaudally flattened, different from the cranially excavated condition of most theropods (e.g., *Coelophysis, Allosaurus, Deinonychus*; Madsen, 1976; Ostrom, 1969). The internal tuberosity is

Fig. 4. Selected scapular girdle and forelimb elements of *Bicentenaria argentina* nov. gen. et nov. sp. Right humerus. **A,** cranial view of proximal end; **B**, caudal view of proximal end; **C**, cranial view of distal end; **D**, caudal view of distal end; **E**, distal view; **F**, proximal view; **G**, fragmentary left scapula and coracoid in lateral view; **H**, manual ungual of digit I or II; **I**, manual ungual probably of digit III. **Abbreviations**: **cor**, coracoid; **en**, entepicondyle; **f**, fossa; **gl**, glenoid cavity; **h**, humeral head; **it**, internal tuberosity; **pdl**, proximodorsal lip; **rc**, radial condyle; **sc**, scapula; **uc**, ulnar condyle. Scale bar = 1 centimeter.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subtriangular in cranial aspect. The proximal articular head is kidney-shaped, being caudally convex and cranially concave. The slender morphology of the preserved portion of the proximal humerus contrasts with the robustness of the scapular girdle. Notably, the cranial surface of the distal humerus bears a deep and rounded fossa above the radial condyle. The distal articular condyles of the humerus are poorly defined, but the entepicondyle is prominent. The ulna bears a poorly developed olecranon process. The manual unguals are trenchant and transversely compressed; the larger ones are interpreted as belonging to digit first (Fig. 4). Some smaller unguals possess a proximodorsal lip and a prominent ventral flexor tubercle, which are here recognized as corresponding to the third manual digit. Proximal dorsal lips are absent in manual unguals of compsognathids and *Ornitholestes*, but they are present in some derived coelurosaurs such as oviraptorosaurs and paravians (Novas *et al.,* 2005), as well as in some basal taxa, including *Tanycolagreus* and *Guanlong* (Carpenter *et al.,* 2005; Xu *et al.,* 2006). However, due to the restricted distribution of this feature among coelurosaurs, we assume that the presence of dorsal lips in some of the manual unguals of *Bicentenaria* may constitute an autapomorphic trait of this taxon.

The ilium of *Bicentenaria* exhibits a prominent but faintly laterally projected supraacetabular crest (Fig. 5). The brevis fossa is transversely narrow. The brevis shelf is strongly developed and projects ventromedially as in *Allosaurus* (Madsen, 1976), but differs from *Aniksosaurus* in which this shelf is flaring outwards (Martinez & Novas 2006). A large portion of a right pubic shaft is available, which preserves the base of the pubic tubercle (i.e., the ambiens process) and resembles the condition observed in many other theropods (e.g., *Sinraptor*, *Allosaurus*, *Gallimimus*, *Aerosteon*; Osmólska *et al.,* 1972; Madsen, 1976; Currie & Zhao, 1993; Sereno *et al.,* 2008). The medial flange of the pubic shaft (the pubic apron) originates as a low but sharp ridge on the caudo-medial margin of pubis, at level of the ambiens process. This flange becomes much more prominent cranially and distally, resembling the condition of *Allosaurus* (Madsen, 1976). Although the proximal end of the preserved pubis is incomplete, the similarities with *Allosaurus* suggest that the obturator foramen of *Bicentenaria* was ventrally open.

The femur of *Bicentenaria* is long and slender (a composite restoration indicates a maximum length of approximately 31 cm), differing from the robust condition of basal tetanurans (e.g., *Allosaurus*; Madsen, 1976) and *Aniksosaurus* (Martínez & Novas, 2006). The femur of *Bicentenaria* (Fig. 5) has a craniomedially-oriented head, bearing a deep posteromedial sulcus for the passage of the *Lig. capitis femoris*. The anterior trochanter is damaged in all available femora, but a wing-shaped condition is inferred based on the craniocaudally expanded condition of its base. The anterior trochanter is separated from the femoral head by a deep cleft. A strongly developed bulge, presumably homologous to the trochanteric shelf of more basal dinosaurs (Novas, 1996), is present laterodistally to the anterior trochanter. The fourth trochanter is reduced to a proximodistally extended ridge, but its corresponding medial scar for the attachment of the *M. caudifemoralis brevis* is deep. The distal femur presents a well-developed mediodistal crest, bounding a deep longitudinal medial depression, as occurs in most basal neotheropods (e.g. "*Syntarsus*" *kayentakatae*; *Ceratosaurus*; *Allosaurus*; Rowe, 1989; Gilmore, 1920; Madsen 1976) and some basal coelurosaurs (e.g., *Tyrannosaurus*; Brochu, 2002). Distally, the femur exhibits a markedly deep extensor groove. The tibia exhibits a cnemial crest that is proximodistally short and slightly projected cranially, as it occurs in other coelurosaurians (Rauhut, 2003). The lateral condyle of proximal tibia is prominent, but it is craniocaudally shorter than in *Allosaurus* (Madsen, 1976). The distal end of tibia presents a square-shaped internal malleolus. The facet for the reception of the ascending process of the astragalus is almost inexistent, as in most coelurosaurs (Rauhut, 2003, 2005).

The astragalus (Fig. 6) exhibits a large and rounded medial condyle, which is separated from the lateral one by a median constriction of the astragalar body. The ascending process is restricted to the lateral half of the astragalar body, resembling the condition of non-coelurosaurian theropods as well as basal coelurosars, such as *Tugulusaurus* (Rauhut & Xu, 2005). By contrast, more derived coelurosaurians exhibit an ascending process transversely expanded for most of the transverse width of the astragalus (Long & Welles, 1974; Rauhut, 2003). The preserved pedal bones of *Bicentenaria* are gracile and metatarsals III and IV, at least, lack a ginglymous distal end. The first metatarsal is reduced to a splint-like bone. The pedal ungual phalanges are acute and poorly curved, with subtriangular proximal ends (Fig. 5).

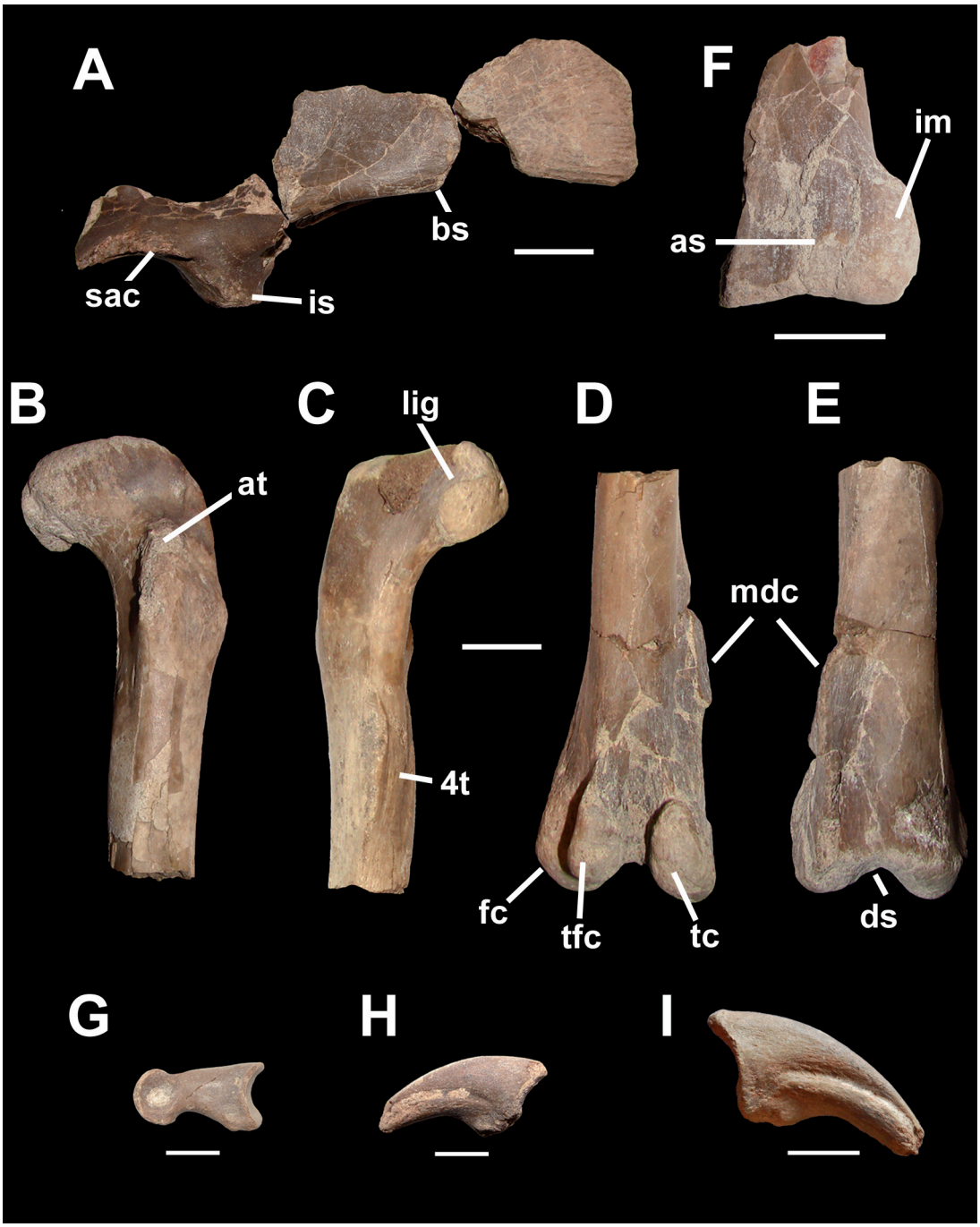

Fig. 5. Selected pelvic girdle and hindlimb elements of *Bicentenaria argentina* nov. gen. et nov. sp. **A**, left ilium in lateral view; **B,C**, proximal end of left femur in **B**, cranial and **C**, caudal views; **D, E**, distal end of left femur in **D**, caudal and **E**, cranial views; **F**, distal end of right tibia in cranial view; **G**, non-ungual pedal phalanx in lateral view; **H**, pedal ungual phalanx of digit VI in lateral view; **I**, pedal ungual phalanx of digits II or III in lateral view. **Abbreviations: as**, articular surface for the ascending astragalar process; **at**, anterior trochanter; **bs**, brevis shelf; **ds**, distal sulcus; **4t**, fourth trochanter; **im**, inner malleolus; **is**, ischiac pedicle; **lig**, ligament sulcus; **mdc**, mediodistal crest; **sac**, supracetabular crest; **tc**, tibial condyle; **tfc**, tibiofibular condyle. Scale bar: **A-F** = 2 centimeters; **G-I** = 1 centimeter.

DISCUSSION

Bicentenaria argentina comes from the Candeleros Formation which yielded other theropod dinosaurs such as the carcharodontosaurid *Giganotosaurus carolini* (Coria & Salgado 1995), the abelisaurid *Ekrixinatosaurus novasi* (Calvo *et al.,* 2004), and the unenlagiid *Buiteraptor gonzalezorum* (Makovicky *et al.,* 2005). *Bicentenaria* clearly differs from the first two taxa in being a much smaller animal of gracile construction, devoid of the synapomorphies characterizing carcharodontontosaurids and abelisaurids. Besides, *Bicentenaria* lacks the highly derived, avian-like features, present in the paravian coelurosaur *Buitreraptor*.

In South America, another sedimentary unit that yielded a similar dinosaur fauna of Cenomanian age is the Lower Bajo Barreal Formation, cropping out in central Patagonia (Novas, 2009). The Lower Bajo Barreal Formation yielded the remains of the basal coelurosaur *Aniksosaurus darwini* (Martínez & Novas, 2006), with a body size somewhat smaller than its roughly coeval *Bicentenaria*. Nevertheless, *Aniksosaurus* differs from the latter one in having limb bones proportionally more robust, especially regarding the humerus and femur. The ilium of *Aniksosaurus* clearly differs from *Bicentenaria* in having a greatly expanded and flaring outwards brevis shelf (Martínez & Novas, 2006). The femur of *Aniksosaurus* differs from that of *Bicentenaria* in lacking a well-developed mediodistal crest, and a deep posteromedial sulcus for the passage of the *Lig. capitis femoris*. The tibia of *Aniksosaurus* plesiomorphically retained a transverse ridge for the articulation with the ascending process of the astragalus, a condition that is absent in *Bicentenaria*. Moreover, *Aniksosaurus* exhibits some features that may support sister-group relationships with the clade made up by Ornithomimosauria plus Maniraptoriformes (e.g., caudally divergent postacetabular iliac blades; undivided neural spines of caudal vertebrae). In other words, *Bicentenaria* and *Aniksosaurus* are not closely related each other, but constitute representatives of different lineages of basal coelurosaurians that inhabited Patagonia during Cenomanian times.

Another South American theropod that deserves some comparisons with *Bicentenaria* is the Aptian *Santanaraptor*, from the Santana Formation of NE Brazil (Kellner, 1999). At first glance, both taxa resemble in the long and slender proportions of the femur, in the common presence of a deep posteromedial sulcus for the passage of the *Lig. capitis femoris*, and that the proximal caudals presents tall and subdivided neural spines. However, several differences allow distinguish *Bicentenaria* from the Brazilian form. For example, available bones of *Santanaraptor* are considerable smaller and more gracile than those of *Bicentenaria*; the femur of *Santanaraptor* is devoid of fourth trochanter and the mediodistal crest is absent (Kellner, 1999). In *Santanaraptor* the distal end of tibia is much more compressed craniocaudally than in *Bicentenaria*, and the internal malleolus of tibia lacks the square-shaped contour in cranial view described for *Bicentenaria*. In *Santanaraptor* the astragalus exhibits some traits that are more derived than in *Bicentenaria*: the ascending process is dorsoventrally extended and transversely wide, and the caudal process of the astragalar body is much less developed than in the Patagonian form.

Based on the comparisons made above, *Bicentenaria* results clearly distinguishable from other known basal coelurosaurs from the Cretaceous of South America. With the aim to assess the phylogenetic position of *Bicentenaria* among basal coelurosaurs, we performed a phylogenetic cladistic analysis (see Materials and Methods), the results of which were 1388 most parsimonious trees of 2886 steps, with a consistency index of 0.321 and a retention index of 0.753. Optimal trees were found 50 times of the total of 100 replications. The strict consensus tree depicts a large polytomy close to the base of Coelurosauria, but the main lineages within this clade are relatively well-resolved. However, the lack of resolution close to the base of Coelurosauria is mostly a consequence of a single wild-card taxon, the enigmatic South American coelurosaur *Santanaraptor*. This taxon is found alternatively as a very basal tyrannosauroid or as a basal maniraptoriform. After an *a posteriori* pruning of *Santanaraptor*, the strict reduced consensus depicts a well-resolved overall topology, but some polytomies are still present in nodes deeply nested within Compsognathidae and at the base of Maniraptoriformes among basal coelurosaurs (Fig. 7). *Bicentenaria argentina* was found as a very basal coelurosaur, placed between the archaic allosauroids and the lineage leading to the avian radiation. The Chinese theropod *Tugulusaurus* was found as the most basal coelurosaur, a result that is congruent with the hypothesis proposed by Rauhut & Xu (2005). The basal position of *Tugulusaurus* within Coelurosauria is supported by the retention of a

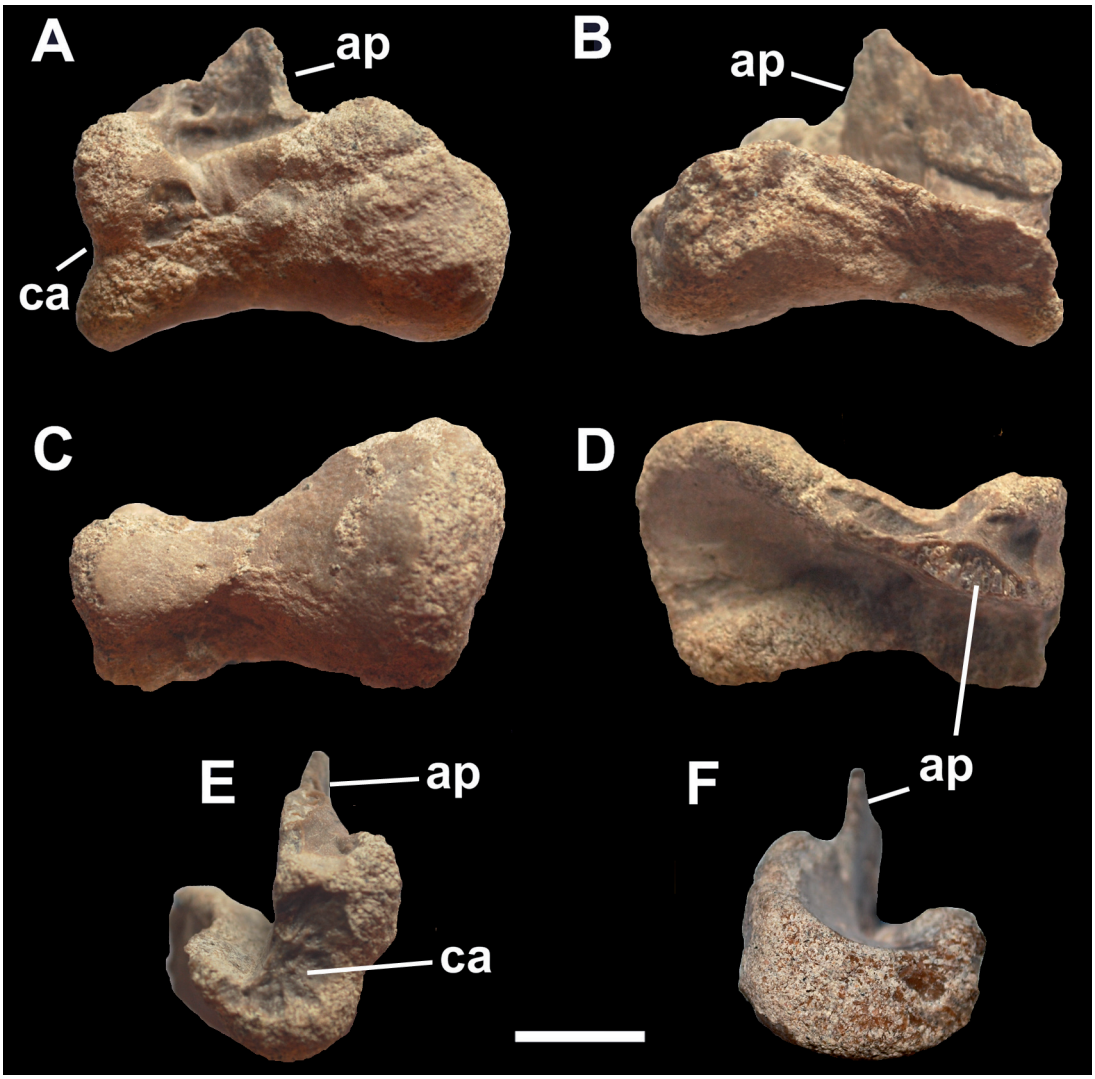

Fig. 6. Right astragalus *Bicentenaria argentina* nov. gen. et nov. sp. **A,** cranial view; **B**, caudal view; **C**, distal view; **D**, proximal view; **E**, lateral view; **F**, medial view. Abbreviations: **ap**, ascending process; **ca**, articular surface for calcaneum. Scale bar = 1 centimeter.

symplesiomorphic distal end of tibia with a well-rimmed facet for the reception of the ascending process of astragalus, contrasting with the condition observed in *Bicentenaria* and all other coelurosaurs, in which this facet is absent (except *Aniksosaurus*). The coelurosaurs more derived than *Tugulusaurus*, including *Bicentenaria*, share apomorphic maxillary tooth crowns with increased density of denticles along the mesial margin, pubis with a transversely compressed distal end, and a distal end of the tibia without well-defined borders of the facet for the reception of the ascending process of the astragalus (the condition of the first two characters is unknown in *Tugulusaurus*). However, *Bicentenaria* lacks the synapomorphies present in more derived coelurosaurians, supporting the basal position hypothesized for the new Patagonian taxon. The synapomorphies that are shared by the coelurosaurs more derived than *Bicentenaria* include: quadratojugal with a rostral process shorter than the dorsal one, caudal vertebrae with undivided neural spines, distal end of femur without a mediodistal crest (apomorphically reversed in tyrannosaurids), and astragalus with a transversely broad and tall ascending process.

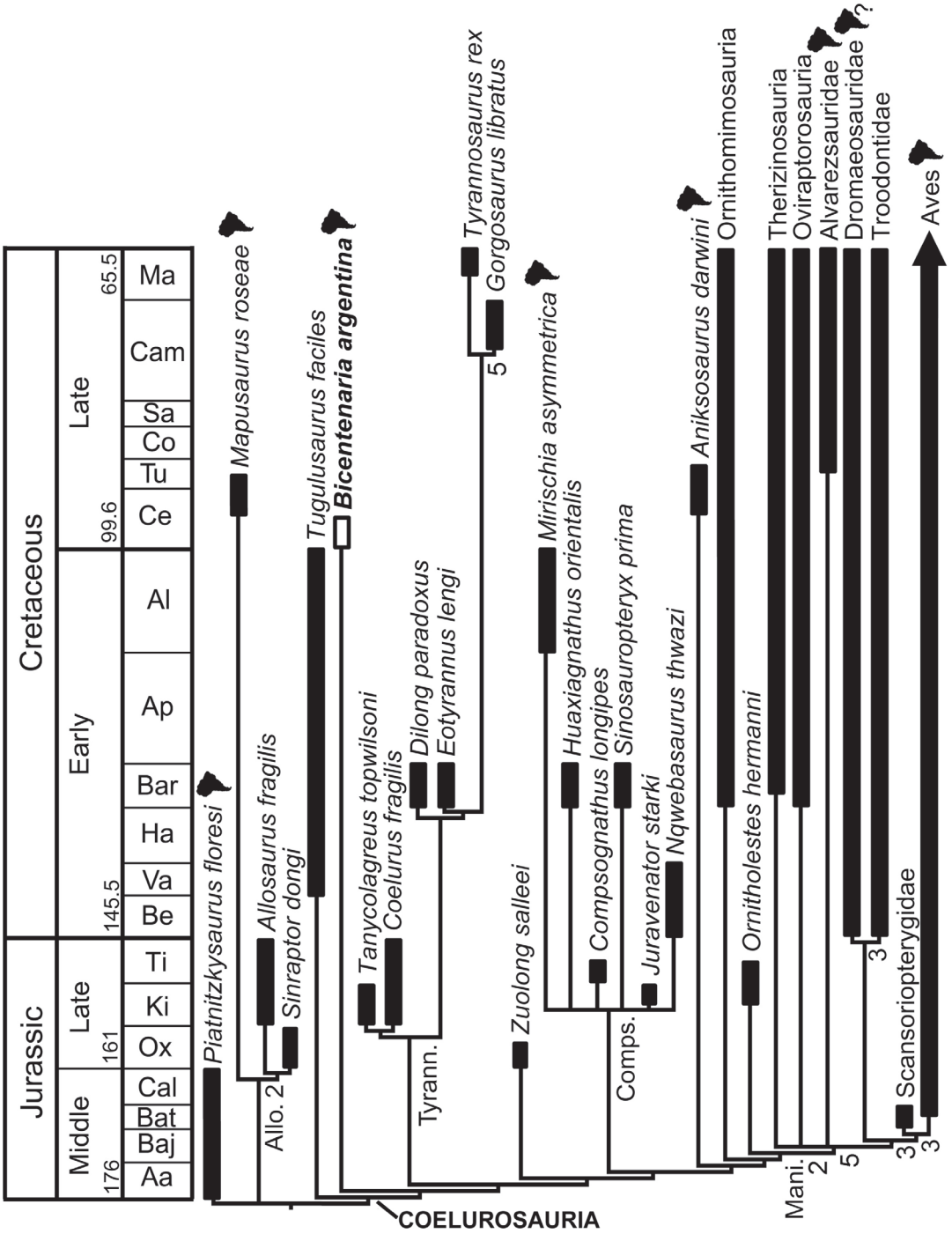

Fig. 7. Simplified strict reduced consensus cladogram after the *a posteriori* pruning of *Santanaraptor* indicating the phylogenetic relationships of *Bicentenaria argentina*. The numbers below the nodes are Bremer values greater than 1.

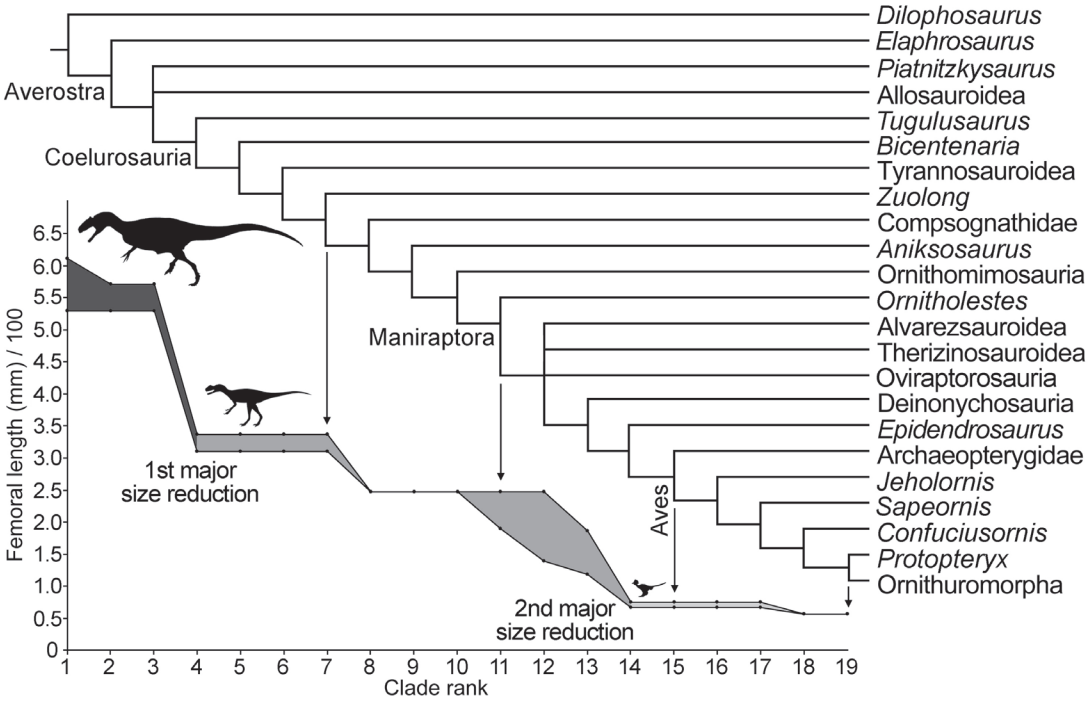

Fig. 8. Body size evolution through basal therpopod phylogeny after the optimization of femoral length as a continuous character in each MPT recovered. The graphic at the bottom shows the ancestral reconstruction of femoral length (in mm) / 100 against clade rank for each stem node represented in the theropod phylogeny (above).

In the present analysis, the Brazilian *Mirischia* (Naish *et al.,* 2004) and the South African *Nqwebasaurus* (De Clerk *et al.,* 2000) are nested within Compsognathidae, indicating a cosmopolitan distribution for this family during, at least, the Early Cretaceous. The problematic Brazilian *Santanaraptor* (Kellner, 1999) is here recovered as an indeterminate basal coelurosaur, while the South American *Aniksosaurus* is found as the sister-taxon of the clade including Ornithomimosauria and Maniraptoriformes. Accordingly, the results of our phylogenetic analysis indicate the presence of, at least, four different lineages of basal Gondwanan coelurosaurs, with their ghost lineages extending back to the Middle and Late Jurassic. Thus, a previously unexpected high taxonomic diversity of basal coelurosaurs appears to have inhabited Gondwana during the Cretaceous. Particularly, in the case of *Bicentenaria argentina* and *Aniksosaurus darwini*, we hypothesize extensive ghost lineages of about 70 millions of years. These extensive ghost lineages are in agreement with the remarkable anatomical specializations recognized for each of these almost coeval species.

Bicentenaria exhibits a size approaching 3 m long and elongate and gracile hindlimb bones, an overall morphology reminiscent to that of some basals coelurosaurs, such as *Tanycolagreus, Coelurus, Ornitholestes, Aniksosaurus,* and *Santanaraptor*, among other taxa. The largest femora of *Bicentenaria* (approximate length 31 cm) indicate that this taxon achieved a body length of about 3 meters and a body mass of 40 kg [calculated by extrapolating measurements of the basal coelurosaurs *Compsognathus* and *Tanycolagreus*, and employing equation applied by Seebacher (2001)]. The presence of closed neurocentral sutures in the vertebrae belonging to the large-sized individuals suggests that the available larger individuals of *Bicentenaria* were not juveniles, at least (Brochu, 1996; Irmis, 2007). The body length of *Bicentenaria* resembles that observed in other basal coelurosaurs, such as *Tanycolagreus* (femur length of 35.6 cm; Carpenter *et al.*, 2005a), *Zuolong* (femur length of 33.6 cm; Choiniere *et al.,* 2010), and *Aniksosaurus* (femur length of 24.7 cm; Martínez & Novas, 2006). The body size of all these basal coelurosaurs is considerably smaller than those of non-coelurosaurian averostrans, such as ceratosaurians, spinosauroids, and allosauroids. In

this regard, the whole clade Coelurosauria was characterized by a size-decrease trend (Carrano, 2006). With the aim to explore size-trend evolution in Coelurosauria, we optimized femoral length as a proxi of body size, and this trait was considered as a continuous character in our strict reduced consensus tree (see Materials and Methods). As a result, two main episodes of drastic size reduction are identified in the evolutionary history of the group (Fig. 8). In basal averostrans (i.e., ceratosaurians, spinosauroids, and allosauroids) it was reconstructed an ancestral femoral length of 57.0-52.9 cm which conspicuously drop downs to a femoral length of 33.6-31.0 cm in basal coelurosaurs (e.g., *Bicentenaria*, *Zuolong, Aniksosaurus*), conforming a first major reduction in the body size (Fig. 8). The reduction in body size of coelurosaurs would have allowed adult forms to exploit ecological niches not occupied by larger basal averostrans. A first step of miniaturization in the coelurosaurian lineage would have resulted in lower generational times and higher rates of evolutionary change. This hypothesis would explain, at least in part, the extraordinary radiation observed among coelurosaurs during the Middle and Late Jurassic.

The ancestral body size of the coelurosaurs faintly decreased gradually towards the avian lineage up to a femoral length of 24.7-1.39 cm in the Therizinosauroidea + Alverezsauridae + Oviraptorosauria + Paraves clade. By coupling the previous results with those recovered by Turner *et al.,* (2007), it becomes apparent that a second drastic decrease in body size took place at the Paraves-Avialae transition (Fig. 8), reaching in Avialae an ancestral femoral length of 0.75-0.67 cm. The remarkable body size reduction observed at the base of Coelurosauria represents an evolutionary event preceeding body size miniaturization reported for derived paravians (Turner *et al.,* 2007), involving a reduction of about 30 times with respect to more basal tetanuran taxa. Accordingly, the miniaturization of body size that benefited birds to develop flying capabilities (Novas & Puerta, 1997; Turner *et al.,* 2007) seems to have occurred in an apparent two-step pattern of size reduction in theropod evolution: a first one at the base of Coelurosauria, and a second one at the base of Avialae or its most immediate sister-taxa (i.e., Paraves; Turner *et al.,* 2007).

The fact that *Bicentenaria* is known from several specimens corresponding to different ontogenetic stages, and that they were found together in a reduced fossil spot, leads to the interpretation that this taxon had gregarious behaviour, at least at the time of their death. The discovery of multiple individuals in a single monospecific quarry (interpreted as indicative of gregarious habits) have been usually documented among non-avian theropods (Horner, 1997), being present in at least seven non-avian theropod taxa: coelophysoids (Colbert, 1990), ceratosaurians (Xu *et al.,* 2009), carcharodontosaurids (Coria & Currie, 2006), *Aniksosaurus* (Martínez & Novas, 2006), tyrannosauroids (Currie, 2000; Eberth & McCrea, 2002), ornithomimosaurids (Kobayashi & Lü, 2003), troodontids (Varricchio, 1995), and dromaeosaurids (Roach & Brinkman, 2007). Thus, based on available evidence, a gregarious behaviour seems to represent an ancestral ethological condition for Theropoda, if not Dinosauria as a whole.

CONCLUSIONS

The discovery of *Bicentenaria argentina* increases the taxonomic diversity and morphological disparity of Gondwanan coelurosaurs, indicating that this supercontinent was a cradle for the evolutionary radiation of basal members of the clade. The transition between archaic theropods (i.e., basal averostrans) and the avian lineage (i.e., Coelurosauria) is spotted as one of the most interesting episodes of dinosaur macroevolution (Brusatte & Sereno, 2008; Holtz, 2004) and the description of *Bicentenaria* adds more information about such evolutionary transition. In particular, the new discovery lends support to the hypothesis that a notable reduction in body size occurred early in the evolution of Coelurosauria, thus preceeding the remarkable miniaturization documented among paravian coelurosaurs. Size reduction may have played an important role in the evolutionary diversification of coelurosaurs as a whole.

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Appendix 1

List of characters that have been added to the original data matrix of Zheng *et al.* (2009). The enumeration given below continues that of Zheng *et al.* (2009):

361) Rostral process of quadratojugal: equal or longer (0); shorter (1) than the dorsal process of the quadratojugal.

362) Pubis distal end: transversely broad, expanded from the transverse width of the shaft (0); transversely flattened (1). (Benson *et al.,* 2010)

363) Facet for the reception of the ascending process of the astragalus in the distal end of the tibia: medially bounded by a sharp step (0); bounded medially by a very slight edge or without well-defined borders (1).

Appendix 2

Scorings of the operational taxonomic units included in the present phylogenetic analysis:

Dilophosaurus wetherilli
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Mapusaurus
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Gorgosaurus libratus

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Huaxiagnathus orientalis

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Struthiomimus altus

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Gallimimus bullatus

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Falcarius utahensis

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Alxasaurus elesitaiensis

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Nothronychus mckinleyi

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?????????????0???101?0????0?0?00?????????????????????????000????001?0?????????????????1????11???1????00????????0????????0??????
Erliansaurus bellamanus

???0?????????????0????
?????????????????00?10????0?00010?????1???1?????????????????????0??0?000?000?????????????????????0?????????????????11?????????????????????
?????????????????????????????????0?10010?001110000101000110000 1??????01?????????????????0100????????1?00???00??0?1??????0??????1
Nanshiungosaurus brevispinus

???0001?00??0???0????????
?????????????????????????????????????1?0???0???20020?0?0102???2?????????????????
?????????????????????1?010???10011?????????????????????????0???0??1???1?????????????????0??????
Neimongosaurus yangi

???21????0?????????????0?000?1?1??10011?0101?0?0?1??2?01000210
?1????????000100000?????????????1??21100??2?????????????????????00?00000????0??000000?20100??????0?1???0?0????11?121????0?????????
????????0??????0111110000???010?1?????????????????????????????????010000?00??0000????????0??001110100?????0?01????000????
Segnosaurus galbiensis

???2??10?0000?000???0100001?????????????????????????????0????????
??????????0?10?1?00????????0???100211001?200210?0?1020?0????????00??0?00?0000?21?0??00????1??0?0????1110121111?????????????
????????00?????01??????021?0?0??0?????????????????????????????1000100??0?010011???01??????001??11?01?0??????01?????0?0???
Erlikosaurus andrewsi

?0110??02?1?1?0???010011100??10001?100000100011000?0??00100?111122001000000200 01?00100001?????????????????????????????????????
????????????????????0???0?00?021????00??01?00?0?000111?1?11?000100 1?0010
0100001000000000 1?????????????0???0?0?001100001?????????0??1111100???1?????0100???01??
Therizinosaurus cheloniformis

???
??????????001000?0?00??001000?0???0???????0?0????11?????????????????????
????????????????????????????02??0?00??0?011??000101?0???1?10???11???0???0?10????????????
Patagonykus puertai

???111????????1??2?????
???????????0020??30210?110??110????????1??????0?????10?00?11?1?00???10011?0??0?????01??0???1???0??????010?????????????????????
????????????????????1?1?????????00?0???????0?????00?1?????????????11??1????0?????????????????????1???????1?????????00??01
Mononykus olecranus

??????00???????112???100?????????????????????????2???0???????01?1?11010011????1??2?????
?1???1000?000200030210?1122?1100??1????1??000????????3??0?011010011101121100002 0?00001??00???1??0?0????01??000?????0??????
????????????????????0?111?00?00000000?010001000?????00?1?????????111??1??00000000?????0??00???001100?1????1?00?????010???1
Shuvuuia deserti

?011010000000?112010000?00??00?111??000010000101010010010???1?110001000000021000?021??000??0111111011101?0??1?201??201200
0100?1000?00020?03021??1122011000?1?1011?2000?00021032?0??110100111011211000020100?1100000110000001000 1?1??0?100110??0010
01001011 0?00??0?0??????001?00000??0???001?000??0?000110???0????1??111?000?0010011000?00002?0011000121111 01?0?0?0100?11
Protarchaeopteryx robusta

????????????????????0???0??000????????02022??0002????00?1?????????????????01????10
?????0???0???1?????00??10100000002?1?????????2200?1?1????00?1???0?????????????0???000?000???10??????0????00??1?101??0?0?????1?
0?0?????????????010?11?0000?001111000??010??10?010001000000000010 11?1?1?000000??00000??0000100?000000011010?1????????0???
Elmisaurus rarus

???
????????????????????????0??01?1???100010??01????0?????????????????????????????????????
??0??????000010000?0??00?????????01?0?0000010??11??????1??0??00??0??1???1?????1?????
Caenagnathus collinsi

???20110?00100?011????3???
??00??0??????0????0?????????????????????

????????1?10??0????????????0???0???

Rinchenia mongoliensis

?01?0????0??????????0111?1????1011?10013??00???000?0??????00??1?221120?01100??111?1?3??????1?????????1???1???1???0???????1?
????????111?1??00000???1?0??00?10??1??0??????????????????????????0????0????0???????0??10??001????00???0?????????10101???01?
01110?010?10??????????????????1?????????????????????????????0??????1???????????????????????????0?????1???1?????11100?11???

Citipati osmolskae

?011001001001??2210001111110001011?1001321000110000011001100011022112 0?0110010111?1?3??????101100110010111001??20???00210
0111?011111?010000100?1100000111002110 0?110220?0??1010010?1101000000100?000001000000010010011 0?000000000??0???010101101010
01110101001??????10????010?0010110100101000000000000000100??????1??101?0000000101100100000 1??00000100?10?01?1110?0?10??

Ingenia yanshini

?01?0?????????????????1111110001 0?1?1??132??0?1???0?0??0011?????1221120?01100?0111?1?3??????????0??1??1???1???2???01????210
0???0011111111?000000??1000001010021 1??11?0220000 11010?110110100000?100100000000000?1100?0?11??000?0?0000?0??101010110?01?
01110?010?10??????????0010?001011010010100000010000000110000001011?101?00?????001000100000000000000101?101011011000 11???

Khaan mckennai

?0110??????????????00111?110?01011?1001321000110?000??00110??????21120?01?00?0111??????????10110??1??1011110??????1??00210
?111001??111110000?00?1100000111002110?1110220001?101??1??110100?0??100100000000000000100100110?000???000??0??1010101101010
011101010?10?????001110010?0010110100101000000000000001100000010 11?101100000000 01000100000000000000100?10101?0?1010110??

Heyuannia huangi

??11????????????????????????????????0??????????????0????????????????1120?011?0??1?????3??????1???????????????0?2???????????0
?111?????11??10?00?10??1110?01010021???1??0220??011?1??1??1?010000?0?0????0000000?001??01??1????00???0????0??1????????????
????????0?1??????00?110010?00?01?0100001000000 1?0?00?01???00000011?1?1?0?0001000???010?0?00?0000001?1??0?01?0????01????

Sinovenator changii

?0???1002?00001112000010 1?11100???1??????000011???011?10100??????000?001??????0000021??01?????11?1110001101000010 00110????
1?????????010111?0?????????000???21??0111002000111011100?11110000???0010001001??000?????0?1??000011?0??0??001100?10?000??
010?1?1100??0?00001111??00100?????????????????0?????000000???2011011?101?1???0011??0??1000102?00??000??1?0??110???00???1?

Mei long

?0?????????????????11010?????00?01?000022100001?10?010??100??????0001 0010??1?0000?021??01?0011011110011?1010?01???01101 2?1
11011????101?11?10?0?1?10000000???2111?1???020??11101110?0111100?0101101?0001?11011?0?0000???00000 0????0????0?110011???001?
0100101??????????1111??0001 0011110?0??0?????0??????00000????????1??1?11100?1?1??000?11??1?21?000000?01?010110???0?00???

Byronosaurus jaffei

?????101???101?1100110101011?00??????20220?????????????1?100??????0000001??11????00021??01?0?0???????010110????????0??0
2???1????0?0??0????????1??????????0????0????100???0?00?100
?101100??0100???10?00110???11?????????????????????0??11?????
0??????????

Sinornithoides youngi

?0??0??????????????1?000??1???0????0020?2???????1?0???????????????00??0010???????0001101 01??????11?1001??????????0011?1210
2101??????01?11??0?00??10000000????????????0?200?????1?1???1 1110?????1????0001?11001?0??010????0000???00????3011001 1011??1?
0100??1?000?1?0?011???0?00??0111101001010001000000000000???0???11?111110001111000010????21000000000 1?010110???0?0?111

IGM100 44 unnamed troodontid

??????012???1??0????????????????1??11???????1?0??????0??????????????????????????????
?????????????????????????10000000???01?1?001???00??????0?0??1???????3??????????????
???????1???0??????????????????????????1?0101000?000????00000?????????????1???0?1111????0?????????0???0?????0?0?????????????

Troodon formosus

???1?1112?1101000001???0?010100??????20220000210?00?1?01100????0?10??001??????????01101 0100???1111100101101111?1000?1020??
11???????????????010????0????????????1????????????????1??0?011?100??????0100001210?01????0?0????0??01000???0?30??????0?1????
????10?000???1?10??111????????????1?01?0??????????????????????????????????????11?10101 1110??????0?101??0??000??0?????10???01?????

Saurornithoides mongoliensis

?01??1?1??1101???0?110001?10000????????2????????????????????1?010?100?0010??1????0001101010????????1???0??0?????100??1????
0??002000?0101?10??11110??????????00??211?01??????0??1?0?????00??00?30?00011011001
00000??1?0???1?010??1??0???????????????????????????????????????0011??1???1??01011110????100??0???0????0??01?????000??10??11

Saurornithoides junior

?01101?12??110100?001?000??100?000????2022000?21??0????11100??????100?001???1????0001101 0100??????????????????1?1000?102
0???01?????????????????00??00???1100???0?30?100101?0
0100000101 0000?110?0?????0???1?????????????*??1?????????????0??01?1???0?0??1?????*

Unenlagia

???1111?01????0???????0
??????????0?0??1?01????????????01221110?1110201 01???111201 1?01??0????????????????????0???????11???????????0?0???????????????
????????????????????101??0??0?11?????????????????????1?0????02???011?????????????1??????1221????0?00??????????1???????????1?

Buitreraptor gonzalezorum

?0110?????????????????00001011??00??????????100?10??0011?0?????????00??001??????????021??100?00101 1110011 1?010???1000 1012?0
21???????01101111010?1?100?0??????11?101??122??1?111?110???11?0??0??1?011?011210000????????1??00?0????000????0????????10010
01?0?01?0??????0?0?111?00?10011120?????????????????????????0?101?1?????1?0???0?2??????1201 1021??000?0??1??1?1?0??0?000??1

Rahonavis ostromi

???011111?0?1?11?011012?0
2?????????0?????11??000????????0112110 0111102?001?101??00111?10000??1??100011010000????????1??????0??????0?0????????????????
????????????????????1111??3?0???130?????????????????????????0211?011?101?01?10021?????11?11?1100??01???????1?11?????00???1

Bambiraptor feinbergi

?0110?????0?0?1??1??00?0?01110000??10?01??10?1????0?01?0?????????00??010??1??0000?0101 1100?????0?120011??10??0???0011??110
?????0011001011110?001?1010000010?21?0011100 20001?1021100?1?110000??10010001101?0?000?00?0?1??0000 0????000?0000000?10130 01?
?100101?10?0111000 11011000?00111201011010001000000101100101020110 1101?10000 1001100?001200101100000100001011110???000011?

Tianyuraptor ostromi

??11???????????????????0????1110?????????????0??1??????????????????????????????????0?0?01010??0???0?????????0?0?0?1??01?0111?
??????1??00?011110?001?10100001112?1??0?110?2?0?111021?0??1?110??????????00?11????000??0???1??00?0????00???000???????300?0
??00?0??????010??0?111?000?0011110100?0100?10?01011110 0102020010 11?10100???????100001??0?0110000???000?0111??????0???1?

Sinornithosaurus millenii

?011??????0?????????00???11100????10001?1100?1???0?01???????????00?00100??1????0101011100????????1??1???????0???00?1??1??
?????0111?01031110?00???0?0000010?211?0??10?2?0?111022?0????1???????1?01000112110?0?000?1001??0000???0?00?0001001101300?0
?100101?1?00110?0??????0001001112 1?0010110000100011110000 1?211111??1?10000120 1?0000012??112?0000010001 10101?0????0??011

Microraptor zhaoianus

1?1??????????????????00??0??010?0?1????0?0100000?????001?1??01?1000?01???0110?11?
2111?01?100?1?1?10100?110100001101211 0?011002?0?111022100?11111??00?1001?10112110??00??010?11?000????0??00?00?100?1???????
??00??1?1?0???0??0?1111000100111211 0??0110000100011110010002111110?1?10000120111000 0020?1121000000 10001?0101?0???000???1

NGMC91
?011????????????????200????11??00?????001???0??????????????????????0000100??1??0?0?010??10??0??????????????????????01???1??
??1?????10??031?10?00??1?100001?????????????????????????????1???0????????????11????0???10????000????10????0001001101 3?01?
1100??1?1?0?1?0?00?????0?0?001112110??011000?1000110100100??????1??1?1??001201110000??????21?0000100011010??0??????0???

Tsaagan mangas
?01100100100001201120000101010000 1?100012110110001000??00001?0???00000100?1111000101010100 0????0??
2??0??00??00?0?
0000???0?0??00010013?000100000 1?1???0?0?0??
0???1?????0???????0??

Adasaurus mongoliensis
??1100?????????????????????????0?????001???????????0????0????????????????0?????0?0?0????????01???0?2?01?1?????011000????1??
??????????0??1?1???????????????00221100111 0???0????021?0??1???00?????????001100?0010?????0?1??000???????0?000????????????0?
??????1????0?????01111??00?0??????????????????????????????02???011?1011000101110????12???01?00??01??????1???0????0?0?1?

Velociraptor mongoliensis
?011001001000012011200001011100001110001211 1?10001000100001110101000000100111100001010111000011000120011111011111000110111 0
21110011100111111010011100000010022110011100200011112110011110000000100101011010010000 00?0011000000000000000000100130000
1000001010010100001101000010011110100101000100000000110010202001011?001100000111000001200101100000100001010110000?000011

Saurornitholestes langstoni
????????????????????????01110????????????111???????????????11????0???010?????00???010111000?11000120011111011011100?1011??
11??????????01?1???????10??000100221?0?11???0???00?0????00?000?0???0000??????013????
?0??00??10?1?1000011????00100?????1????????????????11001??0????????????????????1??00?1??010??0?????0??0?0?01?0???0??????

Deinonychus antirrhopus
?0110????1???????11?0000?0111000011100012??????0?1????0?00?11010?000?0100111?1000?010111000?1100012001?111011????00110110?
21?10???1?010111101001110000001002211001110020001110?010011111000000100100011010000000?00?00110000 0?0?000?0000??00?00013000?
000????000?1?1100010 01?????0111101001010001000000001100102000010110001100010111000000 12?00001000001000010101100000000011

Achillobator giganticus
?????????????????????????01110??000101??????0?01200?111100?????????011??
1?????????0101?????????????00?010220?0111100100?011010?00?11110?0????00?000?101????0???????1???0????????0?000??????013????
?????????????10??00000??00??0???1???????????0?????01?0????0000100100?1??????11??????1000000?0??????????0??1?????0????1?

Dromaeosaurus albertensis
?0??0010000000000010??0?0?0???0??0111 0????1111????10001?1001100???000001001111100 0?00010100
0???1??????00???
???00?0?0000???0?00?000?00????0??00?001001010 0000??0111???????????
????????0??01?????000????00??

Utahraptor ostrommaysi
?????????????????????0?0??????????00???01???101??0????00??101111 1?0??????0?1011??
????????????01????????????????????2?????11001??0???0??????1???000????00?0??????????????????????0????????0???????0?0???????
?????????????0?????000???001?00??????????????????10???0???????????0??????????0??????

Atrociraptor marshalli
? 1 1 1 0 ? 0 ? 1 ? ? ? ?
1 ? ? ? ? 0 1 0 0 0 1 1 1 ? 0 0 ? -
???0??????0????0??00??00??00?3??????0?????010?011
0???

Epidendrosaurus ningchengensis
?0????????????????????????????????????10000?1?00??????????0????????2??00000?002000??????????????????????00?010?00???01?01011
????1??????1011?10?00??10100000011?1???1??020?0?0?1?02?0??1?0100?0??0?????000010?000?0110?1??100????00?0?0??0???????????1?
?????01???10????00?1111????0021020 10??0100010000000000000????011?1?1?01102000 01100???0001100000000 10?11101?0??1?000???

Archaeopteryx lithographica
101?0010??000??112011010??11100?011?00002100010?0000?0??100111?1000000100000 2?0000020??00000?111??100?0??010?0???002101211
1000?????0010111100 00?11000000101121?0001?00200012101110 1?111100000?1001001 0?0010?000000100110000 0?0?0000102001011101000 10
0100101?0??00?0001?11110?3?012113011 0?0100010001000010010202010011?1011011120010000010000121000000000110101?00000000?11

Wellnhoferia grandis
?0????????????????110?0??00??010????????000202200 20?????????????????0????02?00231
??00??????0101111 0?0????0?0000001??1?????1??0??0?1?1?11?01?1?0100?0????01001???010?000??010????00?0???1000?0200101?1???????
0?00????0???0?0?0??11?1?0310?21130?10?011001000100001001020 2???011?1?110111200?000001??0012100000000 1?0101???????0??1?

Jeholornis prima
10??????????????????1?????0??????????0??????0?????????????????????????120?010??00200?1?1?2??0???0??????????????1???1????02???211
?1?????1?1?0103?110?00??1100000001221??0???10??0?????21?0??????1?000??1?01011??0010?000?0010????1000???00?0102?0?0?1????0?10
?1???01?01?0????01?1111?031012113011??011000?110011000000002???01??1?1?0111200010 0101??0?1110000000000?10101?0??1??00?11

Sapeornis chaoyangensis
?011????????????????11011?????00001?000002??0011???00?????????????000?010??00?00000??3??????0????????0?00?010?2???0??????21
?1001????10001111 0?00??1120000?011?1??01??100?0?1?10211 01??010000???0??1110000???000?0010?1???000???1010?0??0?0?1101?0010
0?0??01?0??0?????1?111?00310121131 11?1011100?111001 1100?1?02???011?1?110111????1??101?00?01?000000000110?0110??1?00?11?

Confuciusornis sanctus
10110???????????????11000?0???00001???0??2??0?01??0?0???01???????000010000?10?0001?1?3??????0???1??1????01110?2???0??????2?
?111?110100013111400011111000010112101????100?0012103210111??10??11?1121111010010?000000100110?000???001??0??0011?????0010
0000?01?0?10?????11111?000101211211101010000010101011001000 2???011?1?1101112000101101??0011?000000000?10?01?0??100?2?11

Protopteryx fengningensis
10??????????????????110????????????????0?????????????01?????????????000??1???????0?0??2???0??0?????????0?????1??2???????????2?
?111?11?11??031?10000??1120000001??????????????0?1?1???????????1???1????????1110010?0?0??0101????00?????0????2?01?111???00?1
0?00?01?0???????01?????1?3?012113111??011000?1100101100 01???????11?1?1?0111200?0??10??????1??00000000110?01?0????0???1?

Yanornis martini
?01??????????????????111?0??????0??????0????????????0?1?0????????????000?011??00????00020??0000????11???????????0?2?????????????
?111?1???0?0031?10?00??1120?00?????????????00???121?32?01???0100?1??11??112?00010?000??010????00?????101?1?200001?1???0011
0?00??1?00?00?0001111??1???012113111??0110?0011?0?1111101??????01??1?1101??20000???0???????1??00000000110?0??0??10?????1

Hagryphus giganteus
???
??????????????????????10000001???0???????????????????????????????????
???????????????????????????????????0?011100000001 0001?00100???????????????????????0?11??????????????????0??0?0??????????????

Alvarezsaurus calvoi
???1???100???????????2?1??2?12??
??????????0?0?0??????????????1???00111?0??2????????????????????1?00???0?01??10000000???0????????1???0???????????0???????????????
?????????????????111110??0??????????????????????????????0?1????0???????????1?????000?0???????0??1000???0?????11??1????000???1

Microvenator celer
??21?10?0?????????????????????011?0?110001111100???0???1002??
????????????1000??01000??????0??1002??1011?????0?????10110?0101100?001001 0?????0??0???0??1??0?0???00?0?0?????????????
????????00????????0?111??????011110??0?????????????????0?0????0????011?????????????????????0????00000?1????0?????????0??1??1
Avimimus portentosus
?01?0??1000 1?00??0??1?1?????????1???1?????00?11??0?0010011 0??????2?1???00?0??0110???3???????0110111110101?0?00??100????????
?????????????11?000100???110?????00?211?01??0?2000???0101000001100?0???100111100 20??00??0???01?0??00000?00??0?????0????????1?
????1011???0?????001?????????111??1??????0?????????????????00??011?101?0???00000????1000002?0000?0?????????10??011?0?11
Caudipteryx
00110?????????????0?110?010000011?0001321000 1?00?00?????????????21010?00?????10031?3?????00????0?100????????0???01????210
?111000??00101000 1?00??1000000010020???11?02200?111?10?10?11?01??0????0100000200000000010?110?000???0?00?0??1000100100011
0100111?0010?????001110?10?0001110100?0100000010?0001101?0000101 1?101100000000???0100000100000000001101 01?0??000011?1
Oviraptor philoceratops
?0110??????????1??00????111?0?011???0132??0?1?0???0?100????1????1120?01100?01?1?1?3??????0??1???1??????1?0?????????????
???1?????11?1?0?000001?110?0001???21?00???00100100?????00?0000??????01?1?010??1?
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Conchoraptor gracilis
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Chirostenotes pergracilis
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Incisivosaurus gauthieri
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IGM100 42 unnamed oviraptorid
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?1???01?111111000 0?0??1000000110021 10?1110220??1?1010?1??1?01000????????000010000000100?001?0??00?0?0?00?0??1010101101010
01110101??10?????001010010?001011?100?010001?000000000010000001011?10110???000001100 10?000100010001 00?101011110101 1???
Mahakala
??????100??00000011?????????????????????????1000?????000000000110 1?????????????????????2???1????1?100?200????????????000??010?1
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????1??1?0????????0????????????1?1???10??00?00??????0?010???????10??01?01???1111?????????100??0??????010??????001????
Anchiornis
0 0 1 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 0 1 0 ? ? 1 1 1 ? 0 0 ? ? ? ? ? 0 ? 2 ? 0 0 0 ? ? 1 ? ? ? ? 1 ? 1 ? 1 ? ? ? ? ? ? ? ? ? ? - 0 0 0 ? ? 0 1 ? ? 1 ? ? ? ? ? 0 0 2 0 - - 0 1 ? ? 0 ? 1 0 1 ? ? -
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0110101?0??00000001?

Appendix 3.

Table of femoral lengths and respective sources of information employed to analyse body length evolution in non-avian theropods. The femoral length was divided by 100 because TNT 1.1 cannot deal with three digits values. The juvenile individuals are depicted with an asterisk and they were not considered in the analysis. Estimated measurements are depicted between brackets. Abbreviation: Fem, femoral.

Taxa	Fem length (mm)/100	References
Achillobator	5.50	Turner *et al.* (2007); Benson *et al.* (2011)
Anchiornis	0.66	Xu *et al.* (2009a)
Adasaurus	2.73	Turner *et al.* (2007); Benson *et al.* (2011)
Allosaurus	10.01	Carrano (2005)
Alvarezsaurus	[0.70]	-
Alxasaurus	5.55	Russel & Dong (1993a)
Aniksosaurus	2.47	Martínez & Novas (2006)
Anserimimus	4.33	Carrano (2005)
Archaeopteryx	0.61	Elzanowski (2001)
Archaeornithomimus	4.02	Carrano (2005)
Atrociraptor	?	-
Avimimus	1.86	Carrano (2005)
Bambiraptor	1.19	Burnham *et al.* (2000)
Beipiaosaurus	2.65	Xu *et al.* (1999); Xu *et al.* (2009b)
Bicentenaria	[3.10]	MPCN-PV 0056
Buitreraptor	1.45	Makovicky *et al.* (2005)
Byronosaurus	?	-
Caenagnathus	?	-
Caudipteryx	1.45-1.52	Zhou & Wang (2000); Zhou *et al.* (2000)
Chirostenotes	?	-

Citipati	[3.50]	Benson *et al.* (2011)
Coelurus	2.10	Carpenter *et al.* (2005a)
Compsognathus	0.67	Ostrom (1978)
Conchoraptor	?	-
Confuciusornis	0.42-0.47	Chiappe *et al.* (1999); Zhou & Zhang (2002)
Deinocheirus	?	-
Deinonychus	4.40	Turner *et al.* (2007); Benson *et al.* (2011)
Dilong	1.81*	Benson *et al.* (2011)
Dilophosaurus	6.10	Benson *et al.* (2011)
Dromaeosaurus	?	-
Elaphrosaurus	5.29	Carrano (2005)
Elmisaurus	?	-
Epidendrosaurus	0.16	Zhang *et al.* (2008)
Erliansaurus	4.12	Xu *et al.* (2002); Benson *et al.* (2011)
Erlikosaurus	?	-
Falcarius	3.40	Zanno (2010); Benson *et al.* (2011)
Gallimimus	6.80	Osmólska *et al.* (1972)
Garudimimus	3.71*	Kobayashi & Barsbold (2005)
Gorgosaurus	10.40	Erickson *et al.* (2004)
Guanlong	4.12	Benson *et al.* (2011)
Hagryphus	?	-
Harpymimus	4.50	Benson *et al.* (2011)
Heyuannia	2.27	measured from Lü (2002)
Huaxiagnathus	1.83	measured from Hwang *et al.* (2004)
IGM_100_42	?	-
IGM_100_44	?	-
Incisivosaurus	?	-
Ingenia	2.28	Holtz (1994)
Jeholornis	0.75	Zhou & Zhang (2002)
Juravenator	0.52*	Chiappe & Göhlich (2010)
Khaan	1.42	Benson *et al.* (2011)
Mahakala	0.79	Turner *et al.* (2011)
Mapusaurus	13.00	Coria & Currie (2006)
Mei	0.81	Xu & Norell (2004)
Microraptor	0.75-0.97	Xu *et al.*, (2003); Turner *et al.* (2007)
Microvenator	1.24*	Makovicky & Sues (1998)
Mirischia	?	-
Mononykus	1.39	Perle *et al.* (1994)
Nanshiungosaurus	?	-
Neimongosaurus	3.66	Zhang *et al.* (2001)
NGMC91	?	-
Nothronychus	6.96	Zanno *et al.* (2009)
Nqwebasaurus	[1.18]	de Klerk *et al.* (2000)
Ornitholestes	2.15	Carpenter *et al.* (2005a)
Ornithomimus	6.32	Benson *et al.* (2011)
Oviraptor	2.62	Carrano (2005)
Patagonykus	[2.85]	Benson *et al.* (2011)
Pelecanimimus	?	-
Piatnitzkysaurus	5.70	Benson *et al.* (2011)
Protarchaeopteryx	1.22	Ji *et al.* (1998)
Protopteryx	?	-
Rahonavis	0.88	Forster *et al.* (1998)
Rinchenia	[2.17]	Benson *et al.* (2011)
Santanaraptor	1.89	MN 4802-V
Sapeornis	0.80	Zhou & Zhang (2002)
Saurornithoides	2.00	Turner *et al.* (2007); Benson *et al.* (2011)
Saurornitholestes	2.25	Turner *et al.* (2007); Benson *et al.* (2011)
Segnosaurus	8.40	Carrano (2005)
Shenzhousaurus	1.91	Benson *et al.* (2011)
Shuvuuia	?	-
Sinornithoides	1.40	Russel & Dong (1993b)
Sinornithosaurus	1.48	Xu *et al.* (1999)
Sinosauropteryx	0.86	Chen *et al.* (1998)
Sinovenator	1.18	Xu *et al.* (2002)
Sinraptor	8.76	Currie & Zhao (1993)
Struthiomimus	5.13	Russell (1972)
Tanycolagreus	3.56	Carpenter *et al.* (2005a)
Therizinosaurus	?	-
Tianyuraptor	2.05	measured from Zheng *et al.* (2009)
Troodon	3.17	Carrano (2005)
Tsaagan	?	-
Tugulusaurus	2.15	Rauhut & Xu (2005)
Tyrannosaurus	13.43	Brochu (2002)
Unenlagia	3.80	Novas *et al.* (2009)
Utah_taxon	?	-
Utahraptor	?	-
Velociraptor	2.38	Norell & Makovicky (1999)
Wellnhoferia	0.67	Elzanowski (2001)
Yanornis	0.56	measured from Zhou & Zhang (2001)
Zuolong	3.36	Choiniere *et al.* (2010)