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## COMMENTS ON THE TAXONOMIC DIVERSITY AND PALEOBIOGEOGRAPHY OF THE EARLIEST KNOWN DINOSAUR ASSEMBLAGES (LATE CARNIAN–EARLIEST NORIAN)

*Comentarios sobre la diversidad taxonómica y paleobiogeografía de las asociaciones de dinosaurios más antiguas (Carniano tardío-Noriano más temprano).*

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**Abstract.** The beginning of dinosaur evolution is currently known based on a handful of upper Carnian–lowermost Norian (232–225 Mya) localities situated in a paleolatitudinal belt of approximately 40–50° S in Argentina, Brazil, Zimbabwe and India. The taxonomic diversity of the oldest known dinosaur-bearing assemblages, included within the *Hyperodapedon* Assemblage Zone, is reviewed here. The Brazilian “*Teyuwasu barberenarai*” is reinterpreted as a *nomen dubium* representing an indeterminate dinosauriform, the record of *cf. Saturnalia* from Zimbabwe is considered a basal saurischian and only one of the Indian specimens described by Huene can be unambiguously assigned to Dinosauria. The highest early dinosaur species richness sampled is concentrated in southwestern Pangean assemblages (Argentina and Brazil), with 10 to 11 different described species. By contrast, only one or two species can be currently recognized from the approximately coeval beds of south–central Pangea (Zimbabwe and India), which are much less well sampled. The oldest known dinosaur assemblages appear to have been mostly restricted to subtropical to cool temperate arid areas based on recent paleoclimatological reconstructions. This observation agrees with the hypothesis that the absence of dinosaurs in the upper levels of the Ischigualasto Formation of Argentina is related to an increase in humidity in the basin. Accordingly, climatic factors, with humidity as probably the most important, may have controlled the paleobiogeographic distribution of the oldest known dinosaur assemblages. The achievement of a worldwide dinosaur distribution during the latest Triassic may have occurred after a global climate change, such as the end of the “Carnian Pluvial Event”, and/or the invasion of more tropical humid climates by dinosaurs.

**Key Words.** Archosauria, Dinosauria, Triassic, Paleobiogeography, Macroevolution.

**Resumen.** La temprana evolución de los dinosaurios es conocida actualmente gracias a un número reducido de localidades del Carniano superior-Noriano más inferior (232-225 Ma) de Argentina, Brasil, Zimbabwe e India, situadas en un cinturón paleolatitudinal alrededor de los 40-50° S. La diversidad taxonómica de las asociaciones portadoras de dinosaurios más antiguas conocidas, incluidas en la Biozona de *Hyperodapedon*, es aquí revisada. “*Teyuwasu barberenarai*” de Brasil es reinterpretado como un *nomen dubium* de un dinosauriformes indeterminado, el registro de *cf. Saturnalia* de Zimbabwe es propuesto como un sauriskuio basal y solo uno de los especímenes provenientes de India, descrito por Huene, puede ser asignado de manera no ambigua a Dinosauria. La diversidad taxonómica más rica de dinosaurios está concentrada en asociaciones del suroeste de Pangea, con 10 a 11 especies diferentes (Argentina y Brasil). En contraste, sólo una o dos especies pueden ser reconocidas actualmente en los niveles aproximadamente coetáneos del centro-sur de Pangea (Zimbabwe e India), los cuales se encuentran considerablemente menos muestreados. Basados en reconstrucciones paleoclimáticas recientes, las asociaciones de dinosaurios más antiguas conocidas parecen haber estado mayormente restringidas a áreas áridas subtropicales a templadas frías. Esta observación concuerda con la hipótesis de que la ausencia de dinosaurios en los niveles superiores de la Formación Ischigualasto pudo haber estado relacionada con un incremento en la humedad de la cuenca. En consecuencia, los factores climáticos, probablemente con la humedad como el más importante, pudieron haber controlado la distribución paleobiogeográfica de las asociaciones de dinosaurios más antiguas conocidas. El logro de una distribución mundial por parte de los dinosaurios durante el Triásico más tardío pudo haber ocurrido después de un cambio climático global, tal como el fin del “Evento Pluvial Carniano”, y/o la incursión de los dinosaurios en climas tropicales húmedos.

**Palabras clave.** Archosauria, Dinosauria, Triásico, Paleobiogeografía, Macroevolución.

## INTRODUCTION

Dinosaurs were one of the most important tetrapod groups of Mesozoic terrestrial ecosystems. The oldest representatives of the clade come from Upper Triassic beds of Argentina (Ischigualasto Formation), Brazil (Santa Maria Formation), Zimbabwe (Pebbly Akose Formation), and India (lower Maleri Formation) (Huene, 1940; Colbert, 1958, 1970; Reig, 1963; Casamiquela, 1967; Bonaparte, 1976; Chatterjee, 1987; Sereno and Novas, 1992; Rogers *et al.*, 1993; Sereno *et al.*, 1993; Raath, 1996; Langer *et al.*, 1999, 2010; Langer, 2005a; Furin *et al.*, 2006; Martínez and Alcober, 2009; Alcober and Martínez, 2010; Brusatte *et al.*, 2010; Ezcurra, 2010a; Cabreira *et al.*, 2011; Martínez *et al.*, 2011). These beds are inferred to be late Carnian to earliest Norian in age because of vertebrate biostratigraphical correlations with the Ischigualasto Formation, which is constrained to approximately 232–225 Mya on the basis of radioisotopic data (Rogers *et al.*, 1993; Langer, 2005a; Furin *et al.*, 2006; Martínez *et al.*, 2011). Almost complete skeletons of early dinosaurs have been discovered in Argentina (e.g. *Eoraptor*, *Herrerasaurus*, *Eodromaeus*; Sereno and Novas, 1992; Sereno *et al.*, 1993; Martínez *et al.*, 2011) and more recently from Brazil (e.g. *Saturnalia*, *Pampadromaeus*; Langer *et al.*, 1999; Cabreira *et al.*, 2011), providing a wealth of anatomical information on the early evolution of the group. However, early dinosaur remains from the Pebbly Arkose and lower Maleri formations are currently scarce, although these formations have been much less extensively sampled (Huene, 1940; Colbert, 1958; Chatterjee, 1987; Raath, 1996; Langer *et al.*, 2010; Novas *et al.*, 2011).

Conversely, mid-late Norian dinosaur-bearing beds are more common worldwide than those from the Carnian-earliest Norian,

and a larger Norian dinosaur sample is currently available (Brusatte *et al.*, 2010; Langer *et al.*, 2010; Ezcurra, 2010a). The latter is particularly evident for Norian outcrops of Europe [e.g. Trossingen Formation (=Knollenmergel *sensu* Beutler, 2005), Löwenstein Formation (=Stubensandstein *sensu* Beutler, 2005); Fraas, 1913; Huene, 1934; Rauhut and Hungerbühler, 2000; Galton, 2001], Argentina (e.g. Los Colorados and Laguna Colorado formations; Bonaparte, 1972; Casamiquela, 1977), South Africa (e.g. lower Elliot Formation; Huxley, 1866; Haughton, 1924; Kitching and Raath, 1984; Olsen and Galton, 1984; Galton and Van Heerden, 1998; Galton *et al.*, 2005; Butler *et al.*, 2007; Yates, 2003, 2007a, b; Yates and Kitching, 2003) and the USA (e.g. Chinle Formation; Colbert, 1950, 1989; Long and Murry, 1995; Hunt *et al.*, 1998; Irmis, 2005; Parker and Irmis, 2005; Irmis *et al.*, 2007; Nesbitt *et al.*, 2007, 2009; Sues *et al.*, 2011), which have provided abundant remains of basal sauropodomorphs (with the exception of North America) and basal neotheropods (with the exception of South Africa).

The new discoveries and continuous work of multiple authors have considerably improved the knowledge of the origin and early evolutionary radiation of dinosaurs in the last two decades. In particular, Brusatte *et al.* (2010) and Langer *et al.* (2010) conducted extensive reviews of the current understanding of this issue, and a recently published volume focused on this topic also provided a wealth of new information (Butler *et al.*, 2011). The present contribution will focus on a review of the taxonomic diversity of the oldest known dinosaur assemblages, including a reappraisal of the taxonomy and systematics of some of their specimens. The latter contributes to a more complete understanding of the macroevolutionary patterns that occurred in the first

ca. 7 million years (late Carnian–earliest Norian: Martínez *et al.*, 2011) of dinosaur evolution.

**Institutional abbreviations.** BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; G/K, Geological Survey of India, collection G/K; GR, Ghost Ranch Ruth May Museum of Paleontology, New Mexico, USA; ISI, Geological Studies Unit of the Indian Statistical Institute, Calcutta, India; MACN-Pv, Museo Argentino de Ciencias Naturales, Paleontología de Vertebrados, Buenos Aires, Argentina; MB, Humboldt Museum für Naturkunde, Berlin, Germany; MCP, Museo de Ciencias e Tecnología, Porto Alegre, Brazil; NHMUK, Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; PVL, Fundación “Miguel Lillo”, San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; PEFO, Petrified Forest National Park, Arizona, USA; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UFRGS, Universidad Federal de Río Grande do Sul, Porto Alegre, Brazil; UFSM, Universidad Federal de Santa María, Santa María, Brazil; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe.

## DISCUSSION

**The earliest dinosaur records: late Carnian–earliest Norian assemblages (*Hyporedapedon* Assemblage Zone)**

### South America

The South American record provides unquestionably the best sample of the oldest

known dinosaur-bearing assemblages currently available worldwide. Indeed, at an alpha-taxonomic level, the record of South American Triassic dinosaurs (15 species) represents 60% of the total of southern Pangea (25 species) and 37.5% of the worldwide (ca. 40 species) Late Triassic species richness. The main dinosaur-bearing depocenters of South America are the Ischigualasto-Villa Unión Basin in northwestern Argentina and the Paraná Basin in southern Brazil (Reig, 1963; Colbert, 1970; Sereno and Novas, 1992; Langer *et al.*, 1999). Both basins yielded late Carnian–earliest Norian dinosaur remains that are among the oldest specimens known so far.

*Ischigualasto-Villa Unión Basin: Ischigualasto Formation.* The lower levels of the Ischigualasto Formation have been dated to  $231.4 \pm 0.3$  Mya (late Carnian: Rogers *et al.*, 1993; Furin *et al.*, 2006; Rene *et al.*, 2010) (from a bentonite ash sampled approximately 20 m above the base of the formation within an approximately 700 m thick section: Martínez *et al.*, 2011). A second radioisotopic age yielded a date of  $225.9 \pm 0.9$  Mya (earliest Norian) for the upper third of the Ischigualasto Formation (Martínez *et al.*, 2011) (from feldspars sampled approximately 630 m from the base of the formation within an approximately 700 m thick section: Martínez *et al.*, 2011). A third radioisotopic date of  $218 \pm 1.7$  Mya (middle Norian) was preliminary reported by Shipman (2004) (from a single sample within a bed 26 m below the contact between the Ischigualasto and Los Colorados formation within a section at the eastern extremity of the Ischigualasto Formation that is poorly correlated to the rest of the formation: Currie *et al.*, 2009). However, Martínez *et al.* (2011) considered this dating unreliable because of the uncertainty in the stratigraphic location and the fact that the methodology used to derive it

has yet to be published in detail. Accordingly, if the rate of sedimentary deposition of the unit was roughly constant, most of the lower half of the Ischigualasto Formation should be upper Carnian and the upper half should be lowermost Norian in age (Furin *et al.*, 2006; Martínez *et al.*, 2011). As a result, the Carnian-Norian boundary should be located close to the middle of the Ischigualasto Formation, within the Valle de la Luna Member (Irmis *et al.*, 2011; Martínez *et al.*, 2011).

The lower levels of the Ischigualasto Formation (0–300 m) belong to the *Hyperodapedon* Assemblage Zone (AZ) (Chatterjee, 1980; Benton, 1983a; Rogers *et al.*, 1993; Langer, 2005a, b; Langer *et al.*, 2007a; equivalent to the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone of Martínez *et al.*, 2011), which can be roughly constrained to the late Carnian (Martínez *et al.*, 2011). Lucas (1998, 2010) and Lucas *et al.* (2007) proposed an Adamanian age for the Ischigualasto Formation, correlating the South American assemblage with the Adamanian fauna of the North American Blue Mesa Member of the Chinle Formation. However, Irmis *et al.* (2010, 2011) pointed out that radioisotopic dates indicate that the North American Adamanian fauna is younger than the Ischigualasto Formation. This result falsifies global correlations of the Ischigualasto Formation employing an Adamanian age and raises strong concerns as to the use of “land vertebrate faunachrons” for such long-range biostratigraphic correlations (Irmis *et al.*, 2010). Thus, there is no current evidence that *Hyperodapedon*-bearing formations, including the Ischigualasto, Santa María, Pebbly Arkose, lower Maleri and Lossiemouth Sandstone formations, are of substantially different ages (*contra* Lucas, 2010). Accordingly, the global correlations proposed by Langer (2005a, b) employing

the *Hyperodapedon* AZ are followed here.

The La Peña, Cancha de Bochas and parts of the Valle de la Luna members of the Ischigualasto Formation have yielded a diverse sample of early dinosaurs (see Martínez *et al.*, 2011), that currently minimally includes six different species: two herrerasaurians (*Herrerasaurus ischigualastensis* Reig, 1963; Sereno and Novas, 1992; *Sanjuansaurus gordilloi* Alcober and Martínez, 2010), three basal sauropodomorphs (*Eoraptor lunensis* Sereno *et al.*, 1993; *Panphagia protos* Martínez and Alcober, 2009; *Chromogisaurus novasi* Ezcurra, 2010a; note that *Eoraptor lunensis* has been more commonly interpreted as a basal saurischian or a basal theropod: Sereno *et al.*, 1993; Ezcurra, 2006, 2010a; Langer and Benton, 2006; Irmis *et al.*, 2007; Nesbitt *et al.*, 2009a), and the probable basal theropod *Eodromaeus murphi* Martínez *et al.*, 2011 (Figure 1). Among these taxa, *Herrerasaurus ischigualastensis* was the most abundant predator within the tetrapod assemblage of the lower Ischigualasto Formation (Martínez *et al.*, 2011). A seventh dinosaur species from the lower Ischigualasto Formation may be represented by a putative ornithischian preliminarily reported on the basis of an isolated cervical vertebra (Haro and Salinas, 2006). Nevertheless, this report requires a more comprehensive study before it can be confirmed. Dinosaur remains are currently absent from the upper half of the Ischigualasto Formation, which corresponds to the *Exaeretodon* and *Jachaleria* biozones (upper two-thirds of the Valle de la Luna and Quebrada de la Sal members) (Martínez *et al.*, 2011).

The ornithischian *Pisanosaurus mertii* (*P. mertii*: Casamiquela, 1967) comes from the Hoyada del Cerro Las Lajas, southeast to Los Palacios, in an area of the Ischigualasto Formation that crops out in La Rioja Province (Casamiquela, 1967; Bonaparte,



1976, 1997). Bonaparte (1976, 1997) indicated that the holotype and only known specimen of *Pisanosaurus mertii* came from the middle levels of the Ischigualasto Formation. However, Martínez *et al.* (2011) noted that the stratigraphic correlation between the locality in which *Pisanosaurus mertii* was found and the area of the Ischigualasto Formation that crops out in the San Juan Province is poorly constrained. Furthermore, in addition to *Pisanosaurus mertii*, only the holotype of the ornithosuchid *Venaticosuchus rusconii* and a basal crocodylomorph specimen were collected in this locality (Bonaparte, 1971, 1978, 1982; Ezcurra *et al.*, 2008), whereas no rhynchosaur, cynodont or saurischian specimen was found (J. Bonaparte, pers. comm. 2011). Due to the absence of the latter taxa it is impossible to assess lateral correlations between the San Juan and La Rioja outcrops of the Ischigualasto Formation on the basis of biostratigraphy (Ezcurra, 2012). As a result, the *Pisanosaurus*-bearing locality is considered to occupy an indeterminate stratigraphic position within the Ischigualasto Formation (Martínez *et al.*, 2011), at least until

more precise geological or biostratigraphical information from the Hoyada del Cerro las Lajas locality is available. Thus, the referral of *Pisanosaurus mertii* to the *Hyperodapedon* AZ should be considered ambiguous based on the currently available evidence.

*Paraná Basin: Santa Maria Formation.* The *Hyperodapedon* AZ is also documented in the upper levels of the Santa Maria Formation of the Brazilian Paraná Basin (Langer *et al.*, 2007a), and, as a consequence, this section has been interpreted as coeval with the lower Ischigualasto Formation (Langer, 2005b). The Santa Maria Formation has yielded the remains of four different species of dinosaurs: the herrerasaurid *Staurikosaurus pricei* Colbert, 1970, the basal sauropodomorphs *Saturnalia tupiniquim* Langer *et al.*, 1999 (based on at least three individuals: Langer *et al.*, 1999, 2007b; Langer, 2003), *Pampadromaeus barberenai* Cabreira *et al.*, 2011, and a still undescribed fragmentary postcranium (UFSM 11330) of a sauropodomorph more derived and larger than *Saturnalia* (Da-Rosa *et al.*, 2006). As a result, the sauropodomorphs constitute the most abundant group within the sampled dino-



**Figure 1** - Drawing showing two individuals of the early dinosaur *Eoraptor lunensis* at the shore of a pool in a river during the deposition of the first half of the Ischigualasto Formation, NW Argentina (ca. 230 Mya). Artwork by Emilio López-Rolandi.

saur specimens from the Santa Maria Formation, contrasting with the situation in the coeval beds of the Ischigualasto Formation, in which the herrerasaurid *Herrerasaurus* is the most common dinosaur.

A highly problematic taxon that has not been properly described and reviewed is the putative basal dinosaur *Teyuwasu barberenai* (Figure 2), also known from the *Hyporodapedon* AZ of the Santa Maria Formation. Kischlat (1999) named *Teyuwasu barberenai* on the basis of a right femur (BSPG AS XXV 53) (Figure 2A–F) and tibia (BSPG AS XXV 54) (Figure 2G–L) that had previously been assigned by Huene (1938, 1942) to the “rauisuchian” *Hoplitosuchus rauti*. Kischlat (1999) interpreted *Teyuwasu* as a robust dinosaur, but no characters were clearly indicated in support of this referral. Nevertheless, this author (Kischlat, 1999: 58) did describe some putative dinosaurian features of *Teyuwasu*, such as a “tibia with a cnemial crest and a helicoidal rounded distal articular surface, which is so developed as to encompass the ascending process of the astragalus”. More recent authors have considered *Teyuwasu barberenai* as an indeterminate putative early dinosaur (Langer, 2004; Langer *et al.*, 2010).

The preserved bones of *Teyuwasu barberenai* have suffered strong taphonomic alteration, and as a result they are poorly preserved (Figure 2). Thus, the interpretation of the morphology of these bones should be considered tentative. The femur is preserved in three portions that have been attached with plaster with no direct contact between them (BSPG AS XXV 53) (Figure 2A–D). The perimeters of the separate fragments of shaft match one another, and, as a result, it appears that no or only a small portion of the femoral diaphysis is missing. The femur appears to have belonged to a robust animal, but the taphonomic

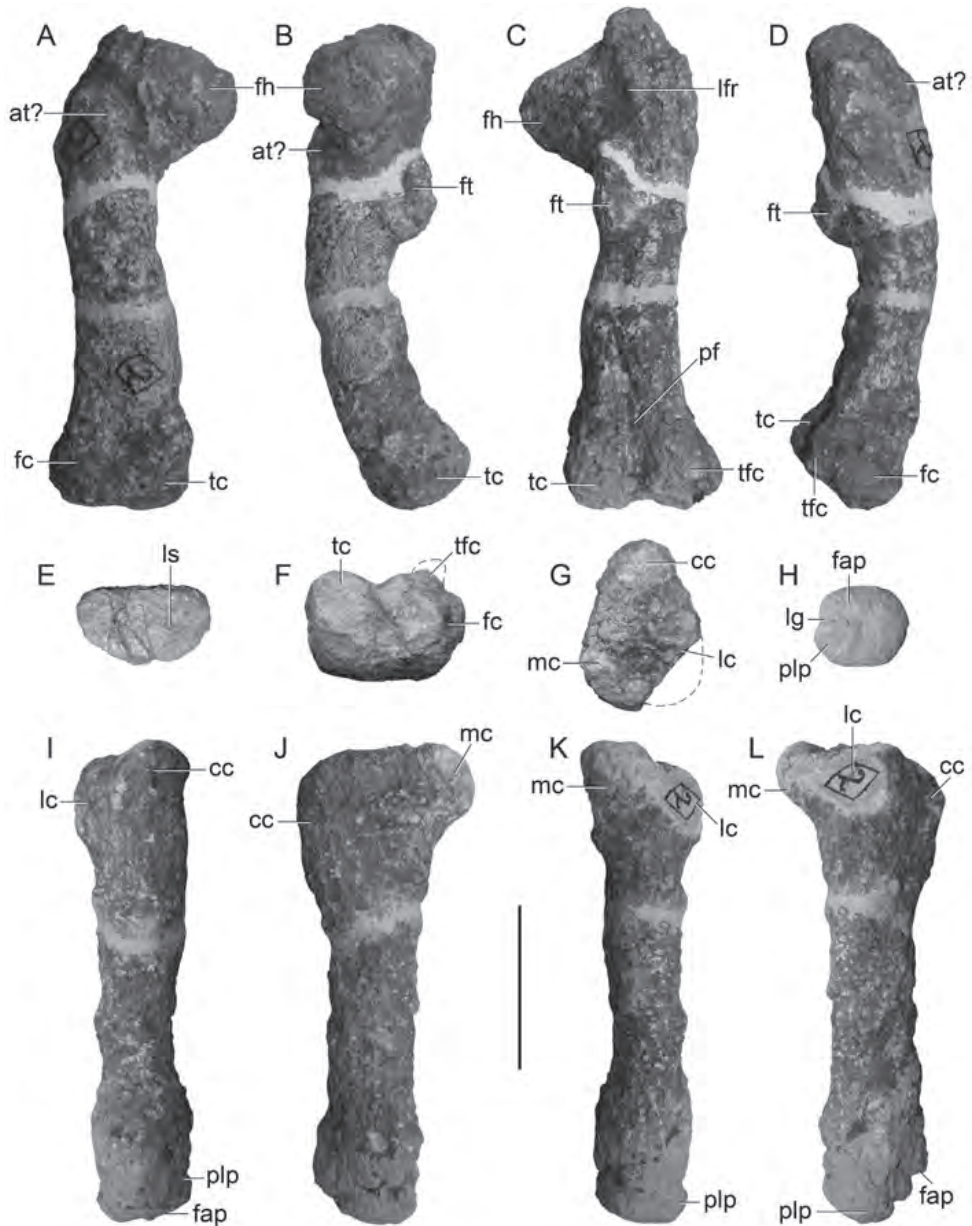
alterations have probably exaggerated this robustness (BSPG AS XXV 53). BSPG AS XXV 53 measures 27.6 cm in length as preserved. The femoral head is anteromedially directed and appears to be strongly inturned (Figure 2A–C). However, it is evident from the proximal surface of the femur that the medial half of the femoral head is displaced ventrally with respect to the rest of the bone due to two longitudinal fractures (Figure 2C: lfr), that appears to correspond to the proximodistally directed parallel ridges described by Kischlat (1999). As a result, the femoral head appears to be more ventrally located than in life, and the degree to which it is inturned has probably also been exaggerated. The absence of a posterior notch between the femoral head and shaft and the apparently proximally located fourth trochanter, with a proximal border above the ventral margin of the femoral head, bolster this interpretation. The femoral head is rounded in posterior view, resembling the condition in *Staurikosaurus pricei* (Bittencourt and Kellner, 2009), *Alwalkeria maleriensis* (ISI R306), *Tawa hallae* (Nesbitt *et al.*, 2009a), and some sauropodomorphs such as *Efraasia* (SMNS 12220, 14881), *Eucnemesaurus* (Yates, 2007a), *Riojasaurus* (PVL 3808) and *Lessemsaurus* (Pol and Powell, 2007). By contrast, a femoral head that is square in outline is observed in *Herrerasaurus ischigualastensis* (Novas, 1993; PVL 2566), *Chindesaurus bryansmalli* (cast of PEFO 10395; GR 226), *Saturnalia tupiniqium* (Langer, 2003), neotheropods (e.g. *Liliensternus liliensterni*: MB R. 2175; *Coelophysus rhodesiensis*: cast of QG1; *Dilophosaurus wetherilli*: UCMP 37302), and ornithischians (e.g. *Eocursor*: Butler, 2010; *Stormbergia*: Butler, 2005; *Scutellosaurus*: UCMP 130580). The proximal surface of the femoral head possesses a partially preserved shallow longitudinal sulcus (Figure 2E: ls), as also

occurs in silesaurids and basal dinosaurs (Ezcurra, 2006; Nesbitt, 2011). The poor preservation of the proximal surface of the bone prevents an assessment as to whether it was straight or curved. The posterior tuberosity of the femoral head is strongly reduced, resembling the condition of basal dinosaurs (Novas, 1996) and the basal silesaurid *Asilisaurus kongwe* (Nesbitt, 2011). The anterior surface of the shaft of BSPG AS XXV 53, at the level of the ventral margin of the femoral head, possesses a low proximodistally extending structure that probably represents the anterior trochanter (Figure 2A, B, D: at?), which resembles that of other basal saurischians, such as *Herrerasaurus ischigualastensis* (Novas, 1993) and *Saturnalia tupiniquim* (Langer, 2003). The trochanteric shelf seems to be absent, as occurs in *Eucoelophysis baldwini* (Ezcurra, 2006), *Eoraptor lunensis* (PVSJ 512), *Guaibasaurus candelariensis* (MCP 2355-PV; UFRGS PV 0725T), *Staurikosaurus pricei* (Bittencourt and Kellner, 2009), most sauropodomorphs (e.g. *Plateosaurus*, *Riojasaurus*; Bonaparte, 1972; Moser, 2003), “gracile” forms of basal neotheropods (Raath, 1977, 1990), and ornithischians (e.g. *Eocursor*: Butler, 2010; *Stormbergia*: Butler, 2005; *Scutellosaurus*: UCMP 130580). The fourth trochanter is well developed posteriorly, transversely thick and apparently located well proximally in the shaft (Figure 2B–D), but the latter appears to be a post-mortem artefact (see above). The fourth trochanter appears to be symmetric in medial or lateral view, contrasting with most basal saurischian and sauropodomorph dinosaurs (e.g. *Herrerasaurus ischigualastensis*: Novas, 1993; *Saturnalia tupiniquim*: Langer, 2003). However, this condition cannot be assessed confidently because of the poor preservation of the bone and should be considered tentative. The distal end of the femur is transversely wider than ante-

roposteriorly deep. Only the base of the tibiofibular crest is preserved, but it appears to have extended more posteriorly than the tibial condyle (Figure 2F). The tibial condyle has a straight medial margin and a rounded posterior margin. The fibular condyle is strongly convex in distal view. The popliteal fossa is moderately deep and the anterior extensor groove is absent.

The tibia of *Teyuwasu barberenai* is also a very robust bone, with a total length of 26.4 cm (BSPG AS XXV 54) (Figure 2I–L). Thus, it is considerably longer than the tibiae of the known specimens of *Saturnalia tupiniquim* (Langer, 2003) and *Eoraptor lunensis* (PVSJ 512) (ca. 15 cm), and slightly longer than that of *Staurikosaurus pricei* (24.6 cm: Colbert, 1970). However, it is smaller than several specimens of *Herrerasaurus ischigualastensis* (PVL 2566: Reig, 1963; Novas, 1993) as well as the still undescribed sauropodomorph from Alemoa reported by Da-Rosa *et al.* (2006). The cnemial crest is low and not laterally curved (Figure 2G), contrasting with the condition widely observed in basal dinosaurs (Irmis *et al.*, 2007; Nesbitt, 2011). Although only a portion of the base of the lateral condyle is preserved, the medial condyle would have been considerably more posteriorly extended because the posterior tip of the base of the lateral condyle is positioned considerably more anteriorly than the posterior end of the former condyle (Figure 2G). This feature resembles the morphology observed in the basal dinosauriform *Marasuchus lilloensis* (Serenó and Arcucci, 1994), ornithischians (e.g. *Pisanosaurus mertii*: PVL 2577; *Eocursor parvus*: Butler, 2010), *Sanjuanasaurus gordilloi* (PVSJ 605), some specimens of *Herrerasaurus ischigualastensis* (MACN-Pv 18060, holotype of “*Ischisaurus cattoi*”: Ezcurra, 2012; PVL 2558) and sauropodomorphs (e.g. *Saturnalia tupiniquim*: Langer,





**Figure 2** - Indeterminate dinosauriform "*Teyuwasu barberenai*". Right femur (BSPG AS XXV 53) in anterior (A), medial (B), posterior (C), lateral (D), proximal (E) and distal (F) views, and right tibia (BSPG AS XXV 54) in proximal (G), distal (H), anterior (I), medial (J), posterior (K) and lateral (L) views. Scale bar equals 10 cm. **Abbreviations.** at?, probable anterior trochanter; cc, cnemial crest; fap, facet for the reception of the ascending process of the astragalus; fc, fibular condyle; fh, femoral head; ft, fourth trochanter; lc, lateral condyle; lfr, longitudinal fracture; lg, longitudinal groove; ls, longitudinal sulcus; mc, medial condyle; pf, popliteal fossa; plp, posterolateral process; tc, tibial condyle; tfc, tibiofibular crest.

2003; *Panphagia protos*: PVL 874; *Chromogisaurus novasi*: Ezcurra, 2010a). The medial condyle is distinctly posteriorly projected with respect to the shaft in lateral and medial views. The tibial shaft is straight in lateral and anterior views. The distal end of the tibia has an oval outline, being transversely wider than anteroposteriorly deep and lacking a posteromedial ridge (Figure 2H), as also occurs in basal dinosauromorphs (e.g. *Marasuchus lilloensis*: Sereno and Arcucci, 1994; *Silesaurus opolensis*: Dzik, 2003) and herrerasaurids (Novas, 1989). By contrast, in ornithischians (e.g. *Pisanosaurus mertii*: PVL 2577; *Eocursor parvus*: Butler, 2010), sauropodomorphs (e.g. *Saturnalia tupiniquim*: Langer, 2003; *Panphagia protos*: Martínez and Alcober, 2009; *Chromogisaurus novasi*: Ezcurra, 2010a) and neotheropods (e.g. *Liliensternus liliensterni*: MB R. 2175; *Zupaysaurus rougieri*: Ezcurra and Novas, 2007) the tibia possesses a distinct posteromedial corner in distal view as a result of the presence of such a longitudinal ridge. The facet for the reception of the ascending process of the astragalus is horizontally oriented (Figure 2I: fap) and anteroposteriorly shallower than half of the depth of the distal end of the bone (Figure 2H). The posterolateral process of the distal end of the tibia possesses a convex posterior surface and is slightly more laterally extended than the facet for the reception of the ascending process of the astragalus, resembling the condition of several basal dinosauriforms (e.g. *Pseudolagosuchus major*: PULR 053; some specimens of *Herrerasaurus ischigualastensis*: PVSJ 373). The posterolateral process and the facet for the reception of the ascending process of the astragalus are separated by a lateral groove (Figure 2H: lg).

The only dinosaurian synapomorphy potentially present in the holotype of *Teyuwa-*

*su barberenai* is a strongly inturned femoral head (Benton, 1990; Ezcurra, 2006; Irmis *et al.*, 2007; Brusatte *et al.*, 2010; Langer *et al.*, 2010). However, as noted above, this character may well be an artefact related to the strong taphonomic alterations suffered by the bones. Accordingly, the assignment of *Teyuwasu barberenai* to Dinosauria should be considered ambiguous. Nevertheless, *Teyuwasu barberenai* can be assigned confidently to the clade that includes silesaurids and dinosaurs based on the presence of a femur with a longitudinal proximal groove, and a reduced posterior tuberosity on the femoral head, and the tibia with a posterolateral process exceeding laterally the facet for the reception of the ascending process of the astragalus and with a longitudinal lateral groove separating the posterolateral process and the facet for the reception of the ascending process of the astragalus (Novas, 1989, 1996; Ezcurra, 2006; Langer and Benton, 2006; Irmis *et al.*, 2007; Nesbitt, 2011; considering *Pseudolagosuchus major* to be a silesaurid dinosauriform as recovered by Nesbitt *et al.*, 2010). In addition, the probable presence of an anterior trochanter on the femur and a tibia with asymmetric posterior condyles of the proximal end are additional synapomorphies that support Dinosauromorpha or more inclusive clades (Ezcurra, 2006; Nesbitt *et al.*, 2009b). The lack of clear autapomorphies or a unique combination of characters, in combination with the extremely poor state of preservation of the holotype, means that *Teyuwasu* and *Teyuwasu barberenai* must be considered as *nomina dubia* that represent an indeterminate dinosauriform with an apparent robust morphology.

## Africa

*Cabora Bassa Basin: Pebbly Arkose Formation.* The late Carnian–earliest Norian dinosaur record in Africa is currently much more restricted than in South America (Langer, 2005a; Langer *et al.*, 2010). The oldest known dinosaur specimen from this continent was reported by Raath (1996), as part of a poorly sampled Triassic tetrapod assemblage from the Pebbly Arkose Formation (Cabora Bassa Basin), lower Zambezi Valley of Zimbabwe. This fauna is dominated by individuals of the rhynchosaur *Hyperodapedon*, and likely pertains to the *Hyperodapedon* AZ (Raath *et al.*, 1992; Langer, 2005b; Langer *et al.*, 2010). Raath (1996) described a fragment of dinosaur femoral shaft from these beds that probably represents the oldest dinosaur record outside of South America and India. This specimen was originally interpreted as a “prosauropod” (Raath, 1996), but, more recently, Langer *et al.* (1999: 515) considered that “the morphology of the femoral fragment of the unnamed Zimbabwean sauropodomorph is almost indistinguishable from that of *Saturnalia*, and it would not be surprising if they belonged to the same taxon.” This specimen is considered here to belong to a saurischian because of the presence of an asymmetric fourth trochanter, which is not pendant as occurs in ornithischians. However, the Zimbabwean material closely resembles the morphology present in a range of basal saurischians, including *Saturnalia tupiniquim* but also *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei*, and no synapomorphies can be identified that allow assignment to a more precise phylogenetic referral. Thus, this specimen is here re-interpreted as representing an indeterminate saurischian dinosaur.

## India

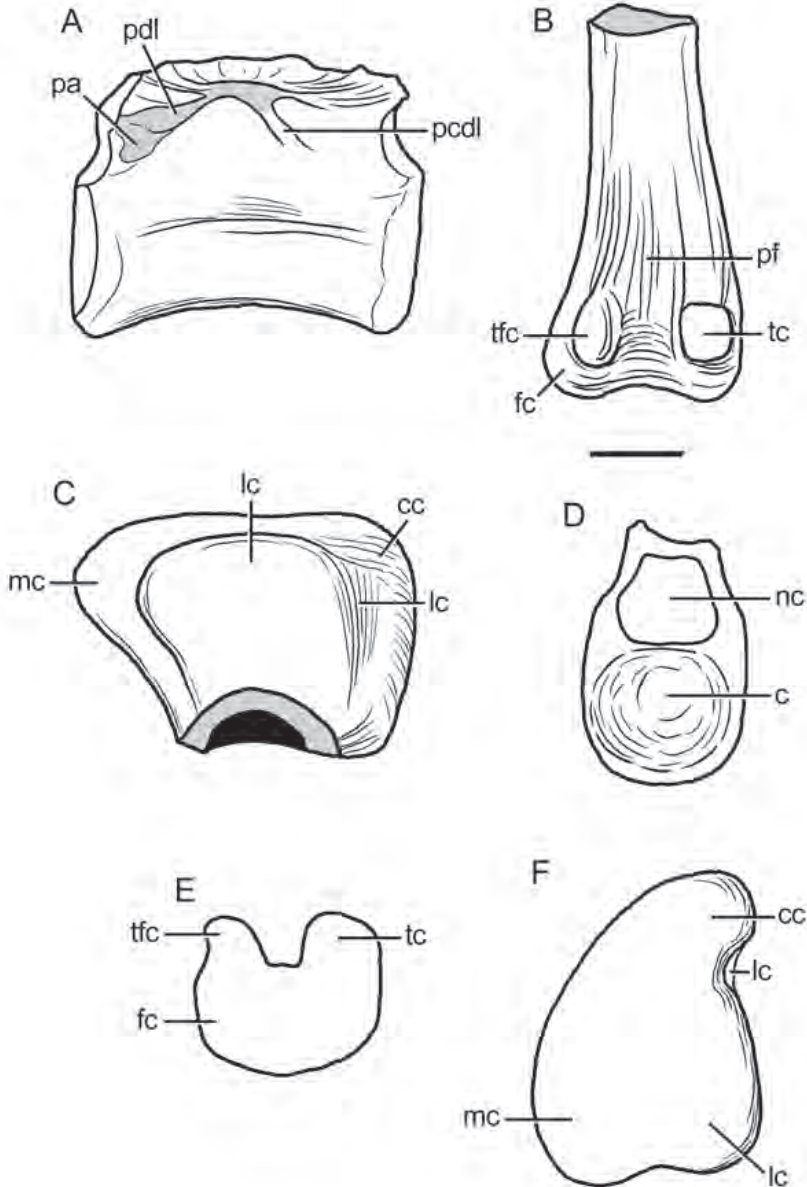
*Gondwana formations: lower Maleri Formation.* The lower Maleri Formation has been correlated with the South American *Hyperodapedon* AZ (late Carnian–earliest Norian) based on the presence of a faunal assemblage dominated by individuals of the rhynchosaur *Hyperodapedon* (= *Paradapedon*) *huxleyi* and the cynodont *Exaeretodon* (Langer, 2005a; see Benton, 1983b). Among the diverse tetrapod fauna recovered from this unit, the only named dinosaur species is *Alwalkeria maleriensis*, which is known by a single specimen that includes a right femur and astragalus (Chatterjee, 1987; Remes and Rauhut, 2005). *Alwalkeria maleriensis* can be considered as a valid species of saurischian, with an unusual femoral morphology and a more conservative astragalar morphology (Novas *et al.*, 2011). Before the description of *Alwalkeria*, Huene (1940) reported the first dinosaur remains collected from the Maleri beds of India (Figure 3). Huene (1940) described five isolated postcranial bones from the *Hyperodapedon*-bearing levels of the Maleri Formation, including the distal half of a femur (K. 33/608a) (Figure 3B, E), the proximal end of a tibia (K. 33/621a) (Figure 3C, F), and three incomplete dorsal vertebrae (K. 33/606b, 621b, G. 281/1a) (Figure 3A, D). Huene (1940) assigned the smaller dinosaur bones, represented by the femur, tibia and one of the dorsal vertebrae, to an indeterminate coelurosaur theropod, whereas the two larger dorsal vertebrae were considered to represent a prosauropod (cf. *Massospondylus* sp.) based on their similarity in size and shape to prosauropod vertebrae (Huene, 1940: 38). In particular, Huene (1940: 37) proposed that the small coelurosaur vertebra and femur “could well go together” (Figure 3A-B, D-E) and suggested their assignment to the family “Podokesauridae” (with a taxonomic con-

tent similar to that currently understand as *Coelophysoidea*) based on their overall resemblance to specimens of "*Coelophysis longicollis*" (= *Coelophysis bauri*). The proximal tibia (Figure 3C, F) was interpreted by Huene (1940) as belonging to a different taxon of coelurosaur because of its larger size. Subsequently, Colbert (1958) reviewed the tetrapods collected from the Maleri Formation and also highlighted the similarities between the putative coelurosaur remains described by Huene (1940) and those of the genus *Coelophysis*, also suggesting that they represented members of "*Podokesauridae*". Colbert (1958) did not support the interpretation of Huene (1940) that the proximal end of the tibia belonged to a second coelurosaur form, and instead interpreted the putative podokesaurid remains as probably representing a single species. However, Colbert (1958) disagreed with the taxonomic assignment provided by Huene (1940) for the two larger vertebrae and stated that these vertebrae belonged to phytosaurs because they matched almost exactly in size, shape and general morphology with comparable elements of North American parasuchians. Subsequent authors followed the taxonomic revision conducted by Colbert (1958) (e.g. Roy Chowdhury, 1965). However, Chatterjee (1987) did not discuss the dinosaur remains described by Huene (1940) and they have also been ignored by more recent reviews of early dinosaur evolution (e.g. Brusatte *et al.*, 2010; Langer *et al.*, 2010; Novas *et al.*, 2011; but see Kutty *et al.*, 2007).

Major advances in the understanding of early dinosaur anatomy and systematics subsequent to the work of Colbert (1958) invite a re-evaluation of these specimens here. Huene (1940: 37) indicated that the smaller dorsal vertebra (K. 33/606b) and the distal femur (K. 33/608a) were found in the

same locality and "could well go together". However, it is not clear exactly what Huene meant by this statement, whether the specimens would belong to a single individual, or to a single species. Nevertheless, the ratio of the centrum width to the distal femoral width ranges between 0.78–0.83 (based on the anterior and posterior surfaces of the centrum, respectively), which is considerably higher than ratios found in other basal dinosaur specimens, such as in the holotype and a referred specimen of *Herrerasaurus ischigualastensis* (PVL 2566: 0.55–0.67; PVSJ 373: 0.37–0.53; considering the first to tenth dorsal vertebrae measured by Novas, 1993) and the holotype of *Coelophysis rhodesiensis* (NHMUK R9584 cast of QG 1: 0.50–0.54; considering the anterior–middle dorsal vertebrae measured by Raath, 1977). Accordingly, the smaller dorsal vertebra and the distal femur cannot be confirmed as belonging to the same individual and should be considered independently.

The smaller vertebra (K. 33/606b; Figure 3A, D) appears to be an anterior or middle dorsal because the parapophyses (represented by the base of the left parapophysis; Huene, 1940: plate 10, 5a) are still placed on the anteroventral corner of the neural arch pedicle, resembling the condition observed in dorsal vertebrae 1–10 of *Herrerasaurus ischigualastensis* (Novas, 1993). The centrum is amphicoelous and considerably elongated, being around twice as long as high, as also occurs in several archosauromorphs (e.g. *Malerisaurus langstoni*: Chatterjee, 1986; *Effigia okeeffeae*: Nesbitt, 2007; *Coelophysis rhodesiensis*: Raath, 1977). The neural arch possesses well-developed paradiapophyseal and posterior centrodiapophyseal laminae, as also occurs in the dorsal vertebrae of a wide array of archosauromorphs (e.g. *Tanystropheus conspicuus*: Wild, 1973; *Erythrosuchus africanus*: Gower,



**Figure 3** - Putative dinosaur specimens described by Huene (1940) and reviewed by Colbert (1956) from the Maleri beds of central India. (A, D) Archosauromorph partial dorsal vertebra in left lateral (A) and posterior (B) views; (B, E) archosaur distal left femur in posterior (B) and distal (E) views; and (C, F) dinosaur proximal right tibia in lateral (C) and proximal (F) views. Scale bar equals 1 cm. Drawings modified from Huene (1940: plate 10).

**Abbreviations:** c, centrum; cc, cnemial crest; fc, fibular condyle; lc, lateral condyle and anterior sulcus; mc, medial condyle; nc, neural canal; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pdl, paradiapophyseal lamina; pf, popliteal fossa; tc, tibiofibular crest; tfc, tibiofibular crest.



2001, 2003; *Hypselorhachis mirabilis*: Butler *et al.*, 2009; *Effigia okeeffeae*: Nesbitt, 2007; *Silesaurus opolensis*: Piechowski and Dzik, 2010; *Herrerasaurus ischigualastensis*: Novas, 1993; *Coelophysis rhodesiensis*: Raath, 1977). K. 33/606b does not exhibit any synapomorphy of Dinosauria, but the presence of well-developed neural arch laminae is a feature only recognized in basal archosauromorphs among Triassic tetrapods. Accordingly, this specimen should be considered as an indeterminate archosauromorph.

The distal femur (K. 33/608a; Figure 3B, E) possesses a slightly transversely expanded distal end with respect to the shaft. The popliteal fossa is deep and extends proximally slightly beyond the distal condyles of the femur. The anterior margin of the femur is strongly convex in distal view, lacking an extensor fossa. By contrast, *Alwalkeria maleriensis* seems to possess a medially displaced anterior extensor groove (ISI R306). Although the anterior surface of the distal femur of *Alwalkeria maleriensis* is damaged, the morphology and position of the probable extensor groove closely resembles that of basal neotheropods (e.g. *Coelophysis rhodesiensis*: NHMUK R9585, cast), suggesting that it is a natural feature. The tibial condyle is strongly posteriorly developed and has a square outline in distal view. The tibiofibular crest does not project beyond the posterior level of the tibial condyle and curves slightly laterally. The fibular condyle possesses a rounded lateral margin in distal view. K. 33/608a can be included within Archosauria because of the presence of strongly posteriorly projecting distal condyles, resembling the condition of phytosaurus (e.g. *Pseudopalatus*: Nesbitt, 2011) but see Nesbitt, 2011 for an alternative position of phytosaurs outside Archosauria, most pseudosuchians (e.g. *Riojasuchus tenuiseps*, *Hesperosuchus agilis*,

*Postosuchus kirkpatricki*: Nesbitt, 2011) and ornithomirans (e.g. *Dimorphodon macronyx*: NHMUK 41212-13; *Lagerpeton chanarensis*: PVL 4619; *Marasuchus lilloensis*: PVL 3871; *Silesaurus opolensis*: Dzik, 2003; *Pisanosaurus mertii*: PVL 2577; *Herrerasaurus ischigualastensis*: Novas, 1993; *Saturnalia tupiniquim*: Langer, 2003; *Liliensernus lilienserni*: MB R. 2175). By contrast, the distal femoral condyles of non-archosaur archosauromorphs are poorly posteriorly projected, such as in *Tanystropheus conspicuus* (Wild, 1973), *Malerisaurus langstoni* (Chatterjee, 1986), *Erythrosuchus africanus* (Gower, 2003), *Euparkeria capensis* (Ewer, 1965), *Doswellia kaltenbachi* (Dilkes and Sues, 2009), *Vancleavea campi* (Nesbitt *et al.*, 2009c) and *Chanaresuchus bonapartei* (PVL 6244). In addition, the overall morphology of K. 33/608a is very similar to that of *Silesaurus* (*S. opolensis*: Dzik, 2003) and almost identical to that observed in basal saurischian dinosaurs (e.g. tibial condyle with a square outline, rounded fibular condyle, concave lateral margin of the tibiofibular crest), including *Herrerasaurus ischigualastensis* (PVSJ 373; Novas, 1993) and *Saturnalia tupiniquim* (Langer, 2003). However, K. 33/608a more closely resembles basal saurischians than *Silesaurus* based on the proportionally narrower femur in distal view. K. 33/608a lacks neotheropod features, such as a mediodistal crest or an infrapopliteal ridge. Accordingly, this specimen is considered here as an indeterminate archosaur cf. Saurischia. If K. 33/608a actually represents a saurischian dinosaur, it would constitute a second dinosaur taxon from the lower Maleri Formation, distinct from *Alwalkeria maleriensis*.

The proximal tibia (K. 33/621a; Figure 3C, F) possesses a distinct cnemial crest that curves laterally, as usually occurs in dinosaurs (e.g. *Herrerasaurus ischigualastensis*: Novas, 1993; *Panphagia protos*: PVSJ 874;

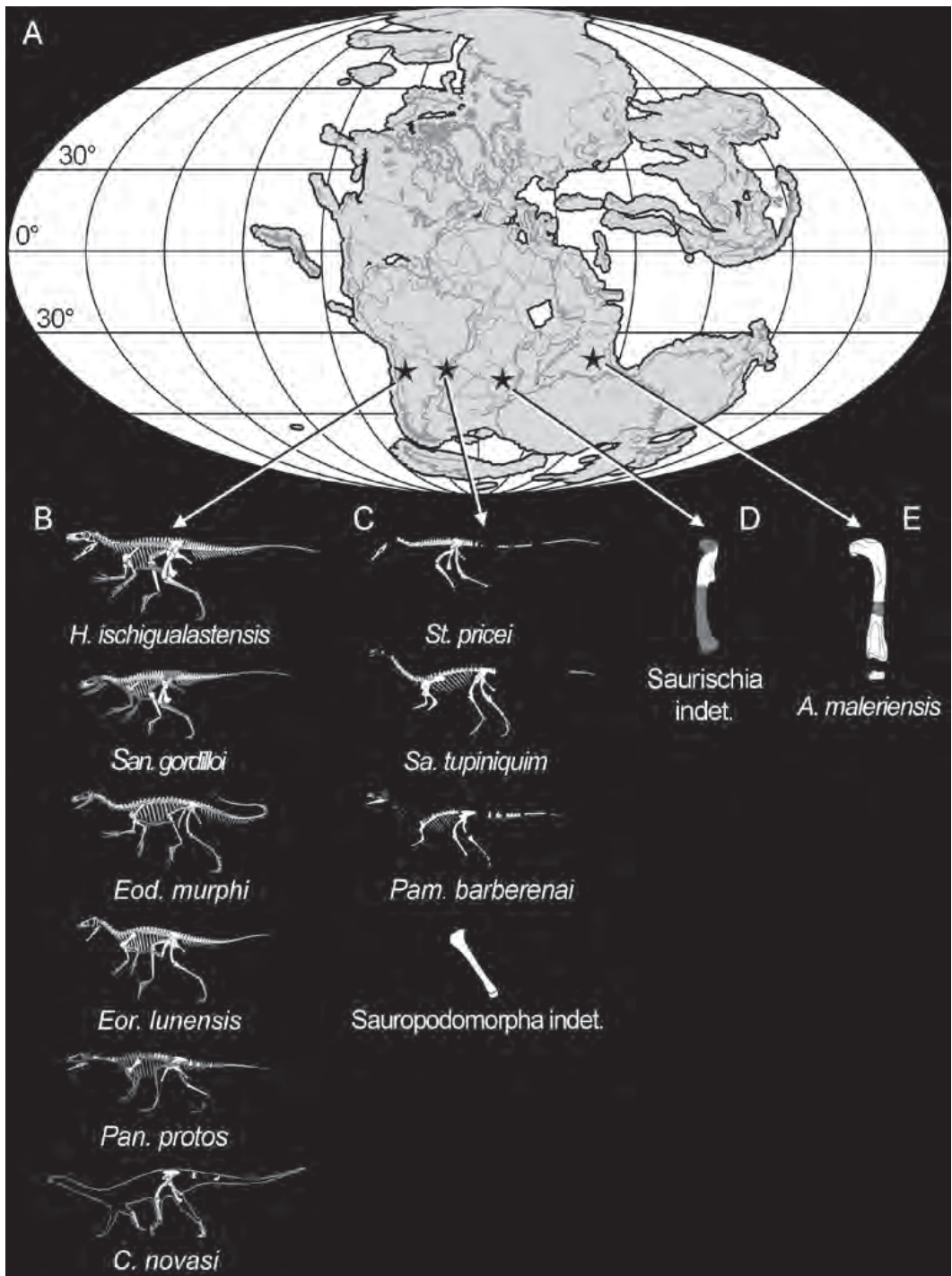
*Saturnalia tupiniqium*: Langer, 2003; *Pisanosaurus mertii*: PVL 2577; *Eocursor parvus*: Butler, 2010; *Liliensternus liliensterni*: MB R. 2175). The lateral surface of the cnemial crest seems to lack the longitudinal lip that it is observed in some basal dinosaurs, such as *Pisanosaurus mertii* (PVL 2577), *Panphagia protos* (PVSJ 874) and *Liliensternus liliensterni* (MB R. 2175). The lateral condyle is only differentiated from the cnemial crest by the longitudinal depression that received the anterior border of the proximal end of the fibula. The medial condyle is slightly more posteriorly extended than the lateral condyle, resembling the condition of *Panphagia protos* (PVSJ 874), but contrasting with the more asymmetric proximal condyles present in *Marasuchus lilloensis* (Sereno and Arcucci, 1994), ornithischians (e.g. *Pisanosaurus mertii*: PVL 2577; *Eocursor parvus*: Butler, 2010), sauropodomorphs (e.g. *Saturnalia tupiniqium*: Langer, 2003; *Panphagia protos*: PVL 874; *Chromogisaurus novasi*: Ezcurra, 2010a), *Sanjuansaurus gordilloi* (PVSJ 605) and some referred specimens of *Herrerasaurus ischigualastensis* (PVL 2588 and probably MACN-Pv 18060, holotype of “*Ischisaurus cattoi*”: Ezcurra, 2012). The lateral and medial condyles are separated by a wide posterior groove, contrasting with basal ornithischians (e.g. *Pisanosaurus*: PVL 2577; *Eocursor parvus*: Butler, 2010) and some neotheropods (e.g. *Gojirasaurus quaxi*: Carpenter, 1997) that possess a deep posterior notch separating both condyles. A gentle concavity in the proximal surface of the bone separates the cnemial crest from the posterior condyles in medial view. K. 33/621a can be assigned to Dinosauria because of the presence of a laterally curved cnemial crest, which has been recovered as a dinosaur synapomorphy by recent phylogenetic analyses (Irmis *et al.*, 2007; Nesbitt, 2011). Within Dinosauria, K. 33/621a does not match the morphology ob-

served in the proximal end of the tibia of basal ornithischians, in which the cnemial crest is very well developed, the lateral condyle is considerably more projected posteriorly than the medial condyle and both condyles are separated by a deep posterior notch (e.g. *Pisanosaurus mertii*: PVL 2577; *Eocursor parvus*: Butler, 2010). Accordingly, K. 33/621a most likely represents a basal saurischian dinosaur. Unfortunately, there are no overlapping bones between K. 33/621a and the holotype of *Alwalkeria maleriensis* that allow an assessment of whether they represent distinct taxa.

The criticisms made by Colbert (1958) of the putative dinosaurian affinities of the large vertebral centra described by Huene (1940) (K. 33/606b; G. 281/1a) are followed here. These specimens do not exhibit any sauropodomorph or dinosaurian synapomorphies. As a result, the proximal tibia K. 33/621a is the only specimen described by Huene (1940) that can be unambiguously referred to Dinosauria. Due to the absence of overlapping elements between *Alwalkeria maleriensis* and 33/621a, the minimal sampled dinosaur taxonomic diversity of the lower Maleri Formation is currently restricted to a single species.

## DISCUSSION

The taxonomic review conducted here of some of the oldest known dinosaur specimens collected from the *Hyperodapedon* Assemblage Zone bolsters previous observations that the richest sampled dinosaur taxonomic diversity is concentrated in southwestern Pangean assemblages, with 10 to 11 different species (Argentina and Brazil) (Figure 4A-C). By contrast, only one or two species can be currently recognized from approximately coeval beds of south-



**Figure 4** - (A) Paleobiogeographical distribution of the oldest known dinosaur assemblages indicated with black stars during the late Carnian–earliest Norian (*Hyperodapedon* AZ) (paleomap for 230 Mya downloaded from the *Paleobiology Database*). Named dinosaur species currently known from the *Hyperodapedon* AZ of the (B) Ischigualasto Formation, (C) Santa Maria Formation, (D) Pebbly Arkose Formation and (E) lower Maleri Formation. *Herrerasaurus ischigualastensis* modified from Sereno and Novas (1992); *Sanjuansaurus gordilloi* modified from Alcober and Martínez (2010); *Eodromaeus murphi* modified from Martínez *et al.* (2011); *Eoraptor lunensis* modified from Sereno *et al.* (1993); *Panphagia protos* modified from Martínez and Alcober (2009); *Chromogisaurus novasi* modified from Ezcurra (2010a); *Staurikosaurus pricei* modified from Bittencourt and Kellner (2009); *Saturnalia tupiniquim* modified from Langer and Benton (2006); *Pampadromaeus barberanai* modified from Cabreira *et al.* (2011); *Alwalkeria maleriensis* and *Saurischia* indet. modified from Langer (2004).

central Pangea (Zimbabwe and India) (Figure 4A, D-E), although those units have been much less well sampled than those of Brazil and Argentina. The oldest known dinosaur-bearing assemblages are currently restricted to outcrops from southern Pangea during the late Carnian–earliest Norian, in a paleolatitudinal belt of approximately 40–50° S (Ezcurra, 2010b) (Figure 4A). This paleolatitudinal belt appears to have included mostly subtropical to cool temperate arid areas during the Late Triassic, according to recent paleoclimatological reconstructions (Sellwood and Valdes, 2006). In agreement with this observation, Martínez *et al.* (2011) suggested that the absence of dinosaurs in the upper levels of the Ischigualasto Formation could be related to an increase in humidity through time in the Ischigualasto-Villa Unión Basin. These combined lines of evidence favour the idea that climatic factors, with humidity as probably the most important, may have controlled the distribution of the oldest known dinosaur assemblages. The climatological conditions under which the sediments of the Indian lower Maleri Formation were deposited are not completely clear, but it may have had a more humid climate than in northwestern Argentina, southern Brazil or Zimbabwe (Sellwood and Valdes, 2006: Figure 2b, c). By contrast, in humid tropical to warm temperate areas of Laurasia, between 0–30° N, the currently available tetrapod assemblages have yielded only

non-dinosaur dinosauriforms (e.g. *Silesaurus opolensis*: Dzik, 2003; *Saltopus elginensis*: Benton and Walker, 2011; *Diodorus scytobrachion*: Kammerer *et al.*, 2012). This latter observation may indicate a disjunct distribution between dinosaurs and non-dinosaur dinosauriforms during the late Carnian–earliest Norian. Nevertheless, it should be pointed out that these hypotheses could be easily rejected if dinosaurs are discovered in beds of that age outside of the 40–50° S paleolatitudinal belt. The presence of dinosaurs in younger Triassic beds (middle Norian–Rhaetian) of North America and Europe has been explained through a south to north dispersal event (Nesbitt *et al.*, 2009a; Irmis, 2011). Thus, the achievement of a worldwide dinosaur distribution during the latest Triassic may have occurred after a global climate change (e.g. the end of the “Carnian Pluvial Event”; Simms and Ruffell, 1989; see Roghi *et al.*, 2010) and/or the invasion of more tropical humid climates by dinosaurs.

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