

New dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmaram formations of Central India

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ABSTRACT: The beginning of dinosaur evolution is currently known based on a handful of highly informative Gondwanan outcrops of Ischigualastian age (late Carnian–early Norian). The richest Triassic dinosaur records of the southern continents are those of South America and South Africa, with taxonomically diverse faunas, whereas faunas from India and central Africa are more poorly known. Here, the known diversity of Gondwanan Triassic dinosaurs is increased with new specimens from central India, which allow a more comprehensive characterisation of these dinosaur assemblages. Five dinosauriform specimens are reported from the probable late Norian–earliest Rhaetian Upper Maleri Formation, including two new sauropodomorph species, the non-plateosaurian *Nambalia roychowdhurii* and the plateosaurian *Jaklapallisaurus asymmetrica*, a guai-basaurid and two basal dinosauriforms. The Lower Dharmaram Formation, probably latest Norian–Rhaetian in age, includes basal sauropodomorph and neotheropod remains, providing the second record of a Triassic Gondwanan neotheropod. The currently available evidence suggests that the oldest known Gondwanan dinosaur assemblages (Ischigualastian) were not homogeneous, but more diverse in South America than in India. In addition, the Upper Maleri and Lower Dharmaram dinosaur assemblages resemble purported coeval South American and European beds in the presence of basal sauropodomorphs. Accordingly, the current available evidence of the Triassic beds of the Pranhita–Godavari Basin suggests that dinosaurs increased in diversity and abundance during the late Norian to Rhaetian in this region of Gondwana.



KEY WORDS: Archosauria, Gondwana, macroevolution, phylogeny, Sauropodomorpha

Dinosaurs were one of the most important groups of tetrapods within Mesozoic terrestrial ecosystems. The oldest representatives of the clade come from Late Triassic Gondwanan beds of Argentina (Ischigualasto Formation), Brazil (Santa Maria Formation), Zimbabwe (Pebbly Arkose Formation) and India (Lower Maleri Formation) (Colbert 1970; Chatterjee 1987; Sereno & Novas 1992; Sereno *et al.* 1993; Raath 1996; Langer *et al.* 1999, 2010; Langer 2005). These beds are inferred to be late Carnian to earliest Norian in age because of vertebrate biostratigraphical correlations with the lower levels of the Ischigualasto Formation, which are dated to about 231 Mya by radioisotopic methods (Rogers *et al.* 1993; Langer 2005; Furin *et al.* 2006). Almost complete skeletons of early dinosaurs have been exhumed from Argentina (e.g. *Eoraptor*, *Herrerasaurus*; Sereno & Novas 1992; Sereno *et al.* 1993) and more recently from Brazil (e.g. *Saturnalia*, *Guaibasaurus*; Langer *et al.* 1999; Bonaparte *et al.* 2007), providing a wealth of anatomical information that informs understanding of the early evolution of the group. However, early dinosaur remains from the Pebbly Arkose and Lower Maleri formations are currently scarce (Chatterjee 1987; Raath 1996; Langer *et al.* 2010).

Conversely, Norian dinosaur-bearing beds are more common worldwide than those from the Carnian, and a larger dinosaur sample is currently available (Langer *et al.* 2010; Brusatte *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 (=Middle Stubensandstein *sensu* Beutler 2005); Fraas 1913; von Huene 1934; Rauhut & Hungerbühler 2000; Galton 2001a), Argentina (e.g. Los Colorados and Laguna Colorada formations; Bonaparte 1972; Casamiquela 1977) and the USA (e.g. Chinle Formation; Irmis 2005; Parker & Irmis 2005; Irmis *et al.* 2007a; Nesbitt *et al.* 2007), which have yielded abundant remains of basal sauropodomorphs (with the exception of North America) and basal neotheropods.

In this global Triassic context, the Indian dinosaur record has been previously restricted to the basal saurischian *Ahwalke-ria maleriensis* from the Lower Maleri Formation (Chatterjee 1987) and some undescribed specimens from the Upper Maleri Formation (Kutty 1969; Kutty *et al.* 1987). These Triassic dinosaur-bearing sedimentary units of India belong to the Gondwana formations of the Pranhita–Godavari Basin, a succession of continental depocenters ranging from

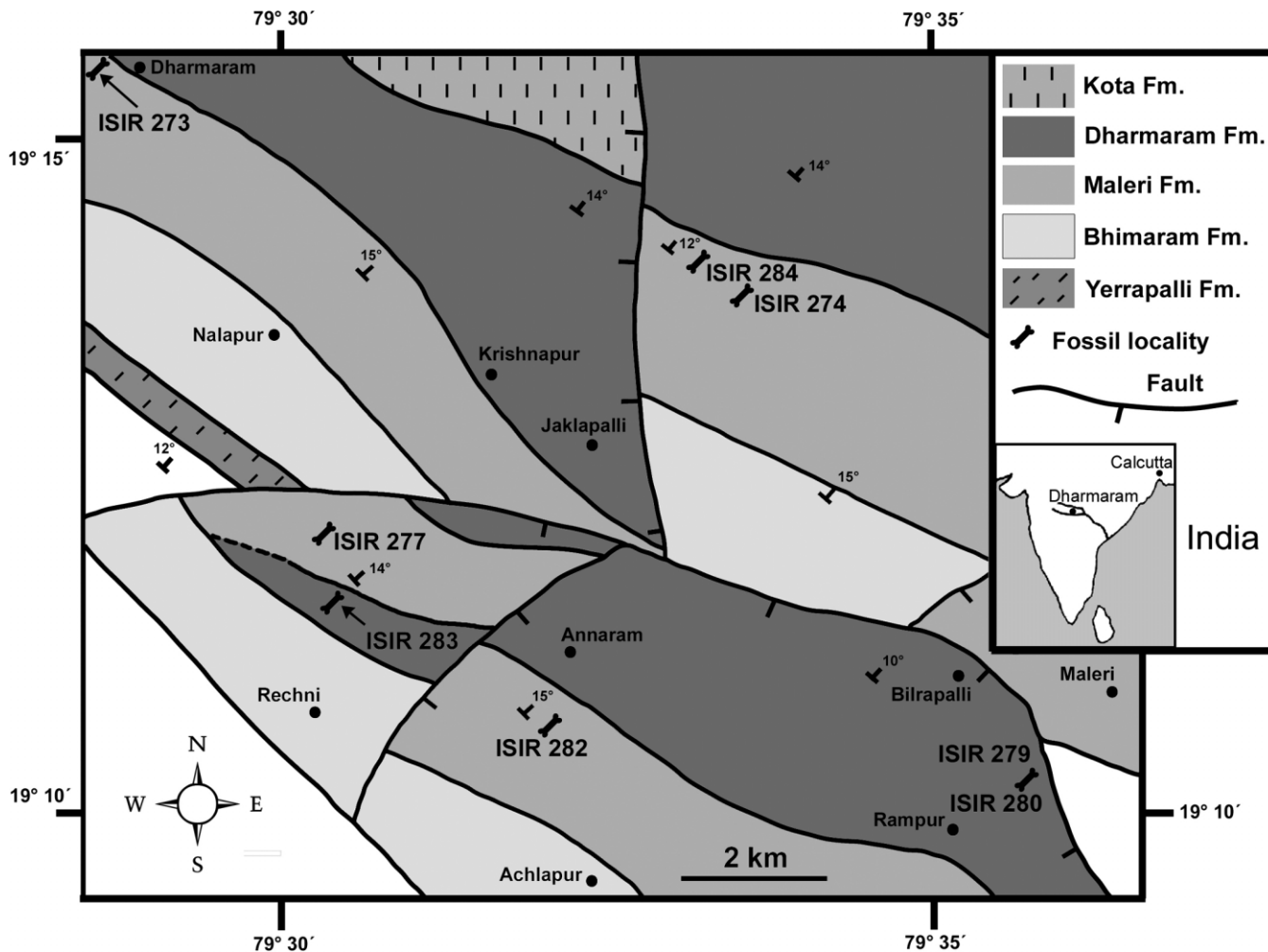


Figure 1 Geological map showing the outcrops in the Pranhita–Godavari Valley of Andhra Pradesh and the localities from which the specimens reported here were collected (modified from Kutty & Sengupta 1989).

Early Permian to Early Cretaceous in age (Chatterjee 1978; Bandyopadhyay & Sengupta 2006; Kutty *et al.* 2007). This present paper increases the known diversity of the Indian Triassic dinosaur record with the preliminary report of several dinosauriform specimens collected by one of the authors (TSK) from the Upper Maleri and Lower Dharmaram formations of the Pranhita–Godavari Basin (Fig. 1), including two new species: *Nambalia roychowdhurii* nov. gen. et nov. sp. and *Jaklapallisaurus asymmetrica* nov. gen. et nov. sp. The new dinosaur assemblages reported here allow a more comprehensive characterisation of the Indian dinosaur faunas for this time span and comparison with contemporaneous dinosaur-bearing assemblages from other regions.

Institutional abbreviations: BMNH, Natural History Museum, London, UK; BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; FZB, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; 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; MEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MLP, Museo de La Plata, Argentina; PUC, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; PULR, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Fundación “Miguel Lillo”, San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San

Juan, San Juan Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UFRGS, Universidad Federal de Rio Grande do Sul, Porto Alegre, Brazil; UFSM, Universidade Federal de Santa Maria, Santa Maria, Brazil; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; UMNH, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah, USA; UNSJ, Universidad Nacional de San Juan, Argentina; USP, Universidade de São Paulo, Brazil; ZG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

1. Dinosaur assemblages from the Triassic Pranhita–Godavari Basin of Central India

1.1. Lower Maleri Formation

The oldest of the Indian dinosaur-bearing formations is the Lower Maleri Formation (Chatterjee 1987), which has a rich fossil vertebrate fauna composed of dipnoans, xenacanthids, metoposaurs, dicynodonts, cynodonts, ‘protosauroids’, rhynchosaurs, parasuchians, aetosaurs, and dinosaurs (Roy Chowdhury 1965; Kutty 1969; Chatterjee 1974, 1978, 1980a, 1982, 1987; Kutty *et al.* 1987, 2007; Kutty & Sengupta 1989; Langer 2005; Hungerbühler *et al.* 2002; Sengupta 2002, 2003; Bandyopadhyay & Sengupta 2006). The Lower Maleri Formation has been correlated with the *Hyperodapedon* AZ (Assemblage–Zone) of the Ischigualasto–Villa Unión Basin,

based on the presence of a fauna dominated by the rhynchosaur *Hyperodapedon* and the cynodont *Exaeretodon*, and is thus interpreted as Ischigualastian in age (i.e. late Carnian–early Norian) (Langer 2005).

The enigmatic *Alwalkeria maleriensis* is the only dinosaur recorded from the Lower Maleri Formation (Chatterjee 1987), and has been the subject of discussion in several recent early dinosaur reviews (e.g. Langer 2004; Remes & Rauhut 2005; Langer *et al.* 2010). *Alwalkeria* was originally described as a basal theropod (Chatterjee 1987), but more recently it has been regarded as an indeterminate dinosaur (Novas 1989, 1997). In a recent reappraisal of the specimen, Remes & Rauhut (2005) considered that the holotype of *Alwalkeria maleriensis* (ISI R306) is a chimera composed of dinosaur (femur and astragalus) and probable pseudosuchian and prolacertiform remains. In addition, Langer (2004) and Remes & Rauhut (2005) concluded that *Alwalkeria* is a basal saurischian of uncertain relationships, an assignment that was followed by Langer *et al.* (2010). Indeed, the dinosaurian affinity of *Alwalkeria* is supported by the presence of the following dinosaur synapomorphies (Langer *et al.* 2010, Brusatte *et al.* 2010): femoral head strongly inturned and distinctly offset from the shaft; an asymmetrical fourth trochanter; astragalus with an acute anteromedial corner, a broader ascending process, and a reduced fibular articulation (ISI R306). Remes & Rauhut (2005) proposed saurischian affinities for *Alwalkeria* on the basis of an astragalus with an elliptical depression behind the ascending process (see Langer & Benton 2006, character 92) and a small horizontal shelf anterior to the ascending process (see Langer & Benton 2006, character 93). Langer (2004) pointed out some features that would indicate that *Alwalkeria* is closer to eusaurischians than to herrerasaurids (considering herrerasaurids as non-theropod saurischians). However, most of these features are related to cranial and axial elements that are now considered to belong to non-dinosaurian taxa (Remes & Rauhut 2005), and the remaining feature was the presence of an anteroposteriorly-compressed lateral portion of the astragalus body. However, the latter character is also observed in *Herrerasaurus* (PVL 2566; MACN-Pv 18060; Novas 1993). *Alwalkeria* presents an odd femoral morphology, with the presence of a hypertrophied femoral neck (ISI R306). The latter feature allows *Alwalkeria maleriensis* to be distinguished from other known dinosauriforms. The astragalus exhibits a more conservative morphology, and is very similar to that of other basal dinosaurs, such as the basal sauropodomorph *Saturnalia* (MCP 3844–PV) and *Agnosphytis* (Fraser *et al.* 2002). In particular, *Alwalkeria* resembles the latter forms in the presence of a reduced but still horizontal fibular articular facet, but the very fragmentary nature of the holotype of *Alwalkeria* prevents further comparisons. In conclusion, *Alwalkeria* can be considered a valid saurischian species with an unusual femoral morphology and a more conservative astragalus anatomy.

1.2. Upper Maleri Formation

Overlying the Lower Maleri Formation is the Upper Maleri Formation, for which a Norian (Kutty *et al.* 2007) or, more precisely, an early Norian age was advocated by previous authors based on vertebrate biostratigraphy (Bandyopadhyay & Sengupta 2006). Langer (2005) pointed out that the typical Ischigualastian taxa *Hyperodapedon* and *Exaeretodon* apparently disappear in the transition between the Lower and Upper Maleri formations; as a result, the latter must be considered post-Ischigualastian in age (i.e. Coloradian), but this is based on negative evidence (R. Irmis pers. comm. 2010). Furthermore, the change recorded in the temnospondyl faunas between the Lower Maleri Formation, composed of metopo-

saurs, and that of the Upper Maleri Formation, replaced by chigutisaurids, is an event associated with the end of the Ischigualastian (Sengupta 2002, 2003). Accordingly, this evidence suggests, as claimed by Langer (2005), that the Upper Maleri Formation is post-Ischigualastian in age, but the support for this inference is still weak (but see section 2.2.2). The vertebrate fauna of the Upper Maleri Formation is composed of the same ‘fish’ taxa from the Lower Maleri Formation, plus chigutisaurids, dicynodonts, parasuchians, aetosaurs, and dinosaurs (Kutty *et al.* 1987; Kutty & Sengupta 1989; Hungerbühler *et al.* 2002; Sengupta 2002, 2003; Bandyopadhyay and Sengupta 2006). Among dinosaurs, Kutty *et al.* (1987) originally mentioned the presence of a small sauropodomorph referred to *Massospondylus* sp. (ISI R277), but lately Kutty *et al.* (2007) suggested that this specimen would be closely related to the Brazilian basal saurischian *Guaibasaurus*. More recently, Novas *et al.* (2009) reported a more diverse dinosaur assemblage from the Upper Maleri Formation, composed of at least three different taxa of basal sauropodomorphs (ISI R273, R274, R277) (Figs 2, 3A–F) and two dinosauriforms (ISI R282, Fig. 3G; ISI R284), which are preliminarily described here. Among these, ISI R273 and ISI R274 represent two new basal sauropodomorph genera and species, which are named below.

1.2.1. Systematic palaeontology

Dinosauria Owen, 1842 *sensu* Padian & May, 1993

Saurischia Seeley, 1887 *sensu* Gauthier, 1986

Eusaurischia Padian, Hutchinson & Holtz, 1999 *sensu* Langer, 2004

Sauropodomorpha Huene, 1932 *sensu* Salgado, Coria & Calvo, 1997

Nambalia roychowdhurii nov. gen. et nov. sp.

Fig. 2

Etymology. The generic name is derived from the Indian town of Nambal, which is located close to where the holotype specimen was found. The specific name is in honour of Dr Roy Chowdhuri, for his outstanding research on the Triassic vertebrate faunas of India.

Diagnosis. Basal sauropodomorph dinosaur characterised by the following combination of apomorphies (autapomorphies marked by an asterisk): femur with an almost transversely unexpanded distal end* and a shallow distal anterior intercondylar groove; and astragalus with a pit on the anterior surface of the astragalus ascending process, anterolateral process larger than the posterolateral process in dorsal view, straight ventral margin in anterior view, and sub-triangular medial condyle in anterior view.

Holotype. Part of ISI R273, comprising the following elements found almost in articulation: a right ilium (ISI R273/1), left femur (ISI R273/2), and distal half of the left tibia and fibula with articulated astragalus and calcaneum (ISI R273/3) (Fig. 2G–J).

Paratypes. Part of ISI R273, including partial postcrania of at least two individuals of different sizes found closely associated, one of them of roughly the same size as the holotype. The large paratype is represented by ten caudal vertebrae (ISI R273/19–27) (Fig. 2A–C), a proximal right pubis (ISI R273/28), right ischium (ISI R273/29), probable metacarpals I and II, and complete right manual digits I, II, and III (ISI R273/5/1, 3; ISI R273/6/2, 4; ISI R273/7/2–4; ISI R273/13/2; ISI R273/9) (Fig. 2D–F), left astragalus lacking medial end, left metatarsals I–V with articulated and complete pedal digit I and V (ISI R273/4), first phalanx of digit II, and all the non-ungual phalanges of digit IV (ISI R273/5/2; ISI R273/6/3; ISI R273/7/1; ISI R273/15) (Fig. 2K). The

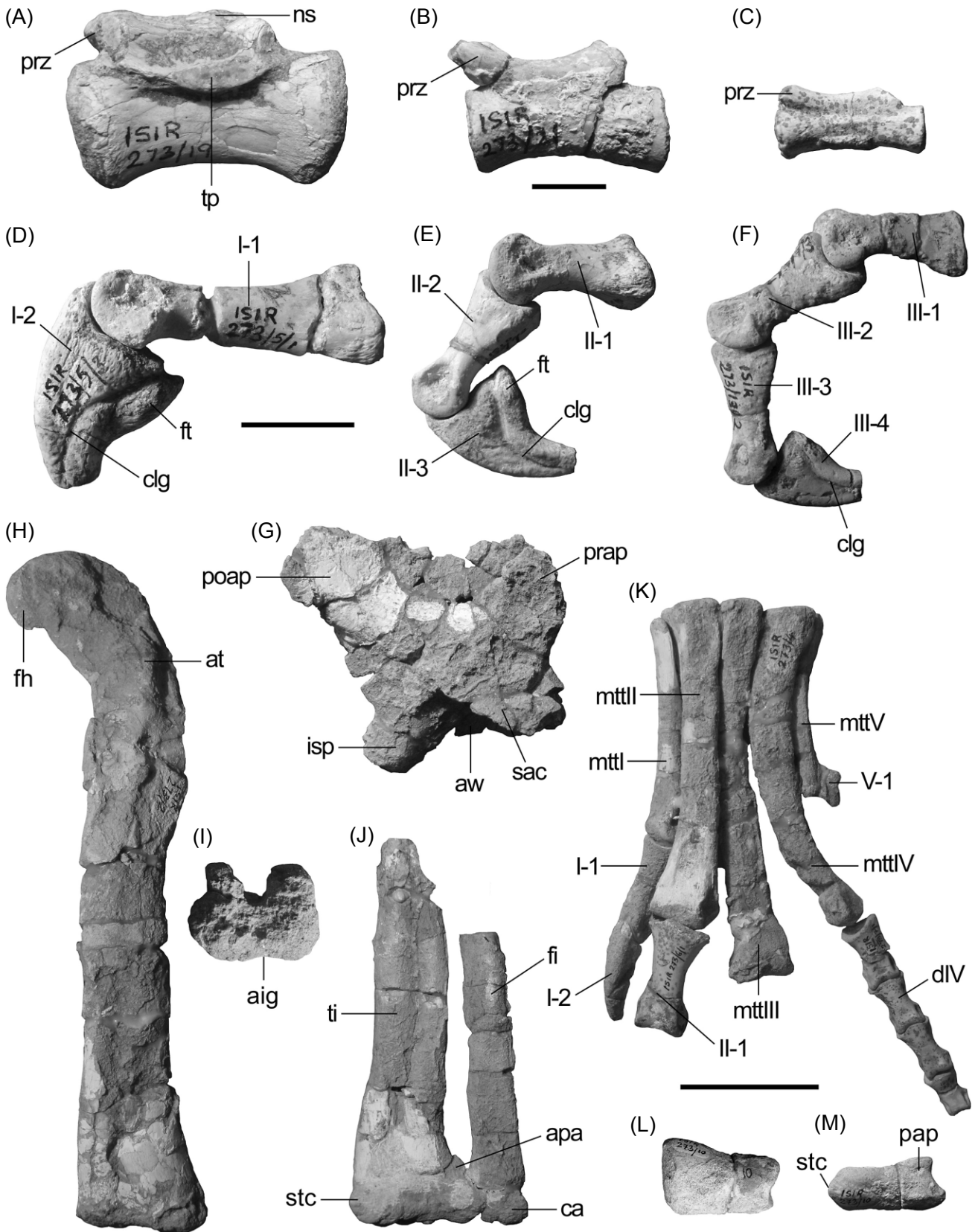


Figure 2 Selected bones of *Nambalia roychowdhurii* nov. gen. et nov. sp. from the Late Triassic Upper Maleri Formation of India (ISI R273), including holotype (G–J) and small (L–M) and large paratype (A–F, K) specimens: (A) Mid-caudal vertebra in right lateral view; (B, C) posterior caudal vertebrae in right lateral views; (D–F) left manual digits I (D) II (E) and III (F) in medial views; (G) right ilium in lateral view; (H, I) left femur in anterior (H) and distal (I) views; (J) left tibia, fibula, astragalus and calcaneum in anterior view; (K) left foot in anterior view; (L, M) left astragalus ventral (L) and anterior (M) views. Abbreviations: X-# = phalanx X-#; aig = anterior intercondylar groove; apa = ascending process of the astragalus; at = anterior trochanter; aw = acetabular wall; ca = calcaneum; clg = collateral groove; dIV = digit IV; fh = femoral head; fi = fibula; ft = flexor tubercle; isp = ischial peduncle; mttI–V = metatarsals I–V; ns = neural spine; pap = pit on the anterior surface of the ascending process; poap = postacetabular process; prap = preacetabular process; prz = prezygapophysis; sac = supraacetabular crest; stc = sub-triangular medial condyle; ti = tibia; tp = transverse process. Scale bars = 2 cm (A–F); 5 cm (G–M).

smaller paratype is represented by right metacarpals I and II (ISI R273/12/1; ISI R273/13/1), probable manual ungual of digit I (ISI R273/7/5), left manual phalanx 1-II (ISI R273/14/2), right manual phalanges 2-II (ISI R273/12/2), 3-III (ISI R273/12/3), 4-III (ISI R273/11/3), left astragalus (ISI R273/10) (Fig. 2L–M), and pedal phalanges 1-I (ISI R273/14/1), 1-III (ISI R273/13/3), 4-III (ISI R273/13/4), and 2-IV (ISI R273/14/3).

The elements catalogued as ISI R273 represent the partial postcrania of at least three different individuals collected from a small erosion slope and associated with some archosauriform teeth (e.g. 273/16–17). The three individuals each preserve the left astragalus, which exhibits the exact same morphology in all of them, including the following unique combination of characters: a pit at the anterior surface of the astragalar ascending process; larger anterolateral process of the astragalar body in dorsal view; and straight ventral margin of astragalar body. In addition, two of the astragali present the diagnostic sub-triangular medial condyle in anterior view. In this regard, all the astragali are considered as belonging to *Nambalia roychowdhurii*, and the articulated ilium, femur, tibia, fibula, astragalus and calcaneum are proposed as the holotype. The other bones belong to two size groups, were found closely associated with the holotype and the other two tarsal bones, and the shape and proportions of the small and large-sized phalanges are identical. Accordingly, these elements are considered as the paratypes of *Nambalia roychowdhurii*.

Horizon and locality. The holotype and paratypes come from the Upper Maleri Formation (?late Norian–earliest Rhaetian, Late Triassic; see below), Pranhita–Godavari Basin, north of Nambal village (79°27'E; 19°16'N), central India (Fig. 1).

Description. The preserved mid-caudal vertebrae are moderately elongated elements, with circular and concave anterior and posterior articular facets and low neural arches. The prezygapophyses are short and slightly overlap the preceding vertebra (Fig. 2A–C). The metacarpals and manual phalanges are notably gracile elements (Fig. 2D–F), resembling those of *Herrerasaurus* (Sereno 1993) and *Guaibasaurus* (Bonaparte *et al.* 2007; UFRGS PV 0725T), but in contrast to the more robust manual bones of *Lamplughsaura* and *Pradhania* (Kutty *et al.* 2007). The ilium of *Nambalia* possesses a well-developed supraacetabular crest and a fully perforated acetabulum (Fig. 2G), contrasting with the completely closed acetabulum of silesaurids (Dzik 2003) and the partially open one of guaibasaurids (Bonaparte *et al.* 1999; Langer 2003; Martinez & Alcover 2009; Ezcurra 2010a). The femur of *Nambalia* differs from that of *Alwalkeria* in the absence of a long femoral neck (ISI R306). The anterior trochanter is represented by a vertical ridge that ends proximally at the ventral margin of the femoral head, and the trochanteric shelf is absent (Fig. 2H). The fourth trochanter is asymmetric and proximally located, differing from *Lamplughsaura* and massopodan sauropodomorphs, in which this process is positioned closer to the mid-shaft of the bone (e.g. *Riojasaurus*; Bonaparte 1972). The distal end of the tibia possesses a moderately laterally-developed posterolateral process, which partially covers the ascending process of the astragalus in posterior view. The astragalus has a low ascending process with a small circular pit at its anterior surface (Fig. 2J–L, M). The astragalar body possesses a well-defined sub-triangular medial condyle in anterior view (Fig. 2J, M), which resembles the condition present in *Unaysaurus* (UFMS 11069), *Tawa* (Nesbitt *et al.* 2009, fig. 2J), and a dinosaur astragalus from Clifton (referred to *Thecodontosaurus* by Benton *et al.* 2000, fig. 18L–M), but contrast with that observed in the vast majority of basal dinosauriforms, such as *Marasuchus* (Sereno & Arcucci 1994), *Silesaurus* (Dzik 2003), *Herrerasaurus* (PVL 2566, PVSJ 373), *Alwalkeria* (ISI R306),

Pisanosaurus (PVL 2577), *Lilienstermus* (MB.R. 2175), *Guaibasaurus* (MCP 2356–PV), *Riojasaurus* (PVL 4364), *Coloradisaurus* (PVL 3967), and *Lessemsaurus* (PVL 4822). In the basal sauropodomorphs *Saturnalia* (Langer 2003) and *Plateosaurus engelhardti* (SMNS 13200), the medial condyles are rounded in anterior view, but not sub-triangular as in *Nambalia*. The astragalus has a strongly reduced and dorsolaterally oriented articular surface for reception of the fibula. The metatarsals and pedal phalanges are gracile and resemble those of other basal dinosaurs (Fig. 2K), such as *Herrerasaurus* (Novas 1993) and *Saturnalia* (Langer 2003). Pedal digit V is rudimentary and represented by a single phalanx.

Jaklapallisaurus asymmetrica nov. gen. et nov. sp.

Figs 3A–D, 7G

Etymology. The generic name is derived from the Indian town of Jaklapalli, close to where the holotype specimen was collected. The specific name is in allusion to the strongly asymmetrical astragalus of this species in distal view.

Diagnosis. Small-sized basal sauropodomorph dinosaur diagnosed by the following combination of characters (autapomorphies indicated by an asterisk): distal femur with a widely transversely open popliteal fossa in distal view*; medial condyle of distal femur sub-triangular in distal view*; distal femur with straight anterior margin; distal tibia with concave posteromedial border*; and astragalar body with a straight dorsal edge in posterior view* and a medial condyle strongly developed anteriorly, with a medial end that is 1.6 times deeper than the lateral one. Furthermore, *Jaklapallisaurus* differs from *Plateosaurus ingens* in the presence of a less strongly anteroposteriorly expanded proximal tibia.

Holotype. ISI R274, postcranial material including a fragmentary vertebra, probably from the dorsal series, a proximal caudal vertebra, distal right femur, complete right tibia and astragalus, and right metatarsals I–IV and two pedal phalanges (Fig. 3A–D).

Referred material. ISI R279, distal end of right femur.

Type horizon and locality. Upper Maleri Formation (?late Norian–earliest Rhaetian, Late Triassic; see below), Pranhita–Godavari Basin, around 3 km north of Jaklapalli village, Central India (Fig. 1).

Referred horizon and locality. Lower Dharmaram Formation (?latest Norian–Rhaetian, Late Triassic; Bandopadhyay *et al.* 2002; Langer 2005), Pranhita–Godavari Basin, around 1 km northeast of Rampur village, Central India (Fig. 1).

Description. The centrum of the proximal caudal vertebra of *Jaklapallisaurus* is around 1.5 times longer than high and slightly transversely compressed at mid-length. Both anterior and posterior articular surfaces are roughly circular and concave, with the posterior one being the most strongly excavated. The distal end of the femur of *Jaklapallisaurus* is slightly more than 1.5 times wider transversely than the anteroposterior depth across the medial condyle (Fig. 3B), resembling the condition of several sauropodomorphs (e.g. *Eucnemesaurus*: Yates 2007a; *Lessemsaurus*: PVL 4822; *Plateosaurus engelhardti*: Moser 2003; *Riojasaurus*: PVL 3808). Nevertheless, this ratio is lower in the basal dinosauriforms *Silesaurus* (ZPAL Ab III 361: equivalent ratio is 1.29), *Alwalkeria* (ISI R306: 1.3), *Herrerasaurus* (PVSJ 373: 1.33), *Staurikosaurus* (Bittencourt & Kellner 2009: 1.36), and the very basal sauropodomorphs *Saturnalia* (MCP 3844–PV: 1.18), *Pantydraco* (NHMUK P77: 1.4), *Efraasia* (SMNS 12220, 12684, 14881: 0.9–1.37), *Ruehleia* (Galton 2001b: 1.34), *Nambalia* (ISI R273: 1.35), and a femur from Clifton referred to *Thecodontosaurus* (Benton *et al.* 2000: 1.22). The anterior margin of the distal end of the femur is straight, contrasting with the strongly convex

anterior margins of *Saturnalia* (Langer 2003; MCP 3844–PV), *Herrerasaurus* (Novas 1993; PVSJ 373), *Eoraptor* (PVSJ 512), *Pantyraco* (Yates 2003a), and *Liliensternus* (MB.R. 2175). However, an almost straight anterior surface is present in *Guaibasaurus* (MCP 2355–PV) and *Glacialisaurus* (Smith & Pol 2007). The distal end of the femur of *Jaklapallisaurus* lacks an anterior intercondylar groove, contrasting with the condition present in *Nambalia* and *Plateosaurus engelhardti* (SMNS 13200). The popliteal fossa is widely transversely open in distal view (ISI R274, 279), representing a morphology not observed in other basal saurischians.

The proximal end of the tibia of *Jaklapallisaurus* has a well-developed cnemial crest, which is slightly curved laterally, as occurs in other dinosaurs (Novas 1996; Nesbitt *et al.* 2007). The posterior condyles of the proximal end of the tibia are posteriorly extended to the same extent, resembling *Plateosaurus ingens* (Galton 1986) and some specimens of *Plateosaurus engelhardti* (Moser 2003, plate 11, fig. 1e; SMNS 13200). The distal end of the tibia is transversely wider than antero-posteriorly deep and has a conspicuous lateral notch that separates the anterior articular facet for the reception of the ascending process of the astragalus from the posterolateral process. The astragal body is sub-rectangular in anterior view and has a low ascending process (Fig. 3A). A deep circular pit is present on the anterior surface of the ascending process, as also occurs in *Nambalia*. The astragal body exhibits a straight dorsal edge in posterior view, contrasting with *Nambalia* and other basal sauropodomorphs, such as *Plateosaurus engelhardti* (SMNS 13200) and *Riojasaurus* (PVL 3845, 4364), in which this border is sigmoid, and results in a strong dorsoventral reduction of the portion of the astragal body directly behind the ascending process. In distal view, the astragal body of *Jaklapallisaurus* is strongly asymmetrical with a medial margin that is more than 1.6 times deeper anteroposteriorly than the lateral one (Fig. 3D). This sharp asymmetry is associated with a strong anterior projection of the anteromedial corner of the astragalus and the same condition is observed in specimens of the massopodan sauropodomorph *Riojasaurus* (PVL 3845, 4364). However, such an anterior development of the anteromedial border of the astragalus is absent in other dinosauriforms (e.g. *Pisanosaurus*: PVL 2577; *Herrerasaurus*: PVSJ 373, PVL 2566; *Alwalkeria*: ISI R306; *Saturnalia*: MCP 3844–PV; *Nambalia*: ISI R273; *Unaysaurus*: UFSM 11069; *Plateosaurus engelhardti*: SMNS 13200; *Ignavusaurus*: Knoll 2010; *Coloradisaurus*: PVL 3967; *Lessemsaurus*: PVL 4822). The metatarsals and preserved pedal phalanges are relatively robust elements (Fig. 3A), resembling those of *Plateosaurus* (*P. engelhardti*: Moser 2003) and other non-sauropod sauropodomorphs.

Guaibasauridae Bonaparte *et al.*, 1999 *sensu* Ezcurra, 2010a
Gen. et sp. indet.

Fig. 3E, F

Material. ISI R277, two cervical vertebrae (ISI R277/7–8), posterior end of the neural arch of the last dorsal vertebra in articulation with the sacrum (ISI R277/1), which includes three sacral vertebrae, right ilium, and a fragment of the left iliac blade, articulated left femur (ISI R277/2 and 277/5), proximal half of the right femur (ISI R277/3), and left tibia, tarsus, and almost complete pes (ISI R277/4) (Fig. 3E, F).

Horizon and locality. Upper Maleri Formation (?late Norian–earliest Rhaetian, Late Triassic; see below), Pranhita–Godavari Basin, 2.5 km north of Rechni village, Central India (Fig. 1).

Description. The anterior cervical vertebrae of ISI R277 are elongate, with centra that are 2.5 times longer than the

height of the anterior articular facets, but they do not reach the extreme elongation present in *Pradhania* (Kutty *et al.* 2007). The cervical centra possess low and thin longitudinal median keels. The sacrum of ISI R277 is composed of three sacral vertebrae, resembling the condition of *Silesaurus* (Dzik & Sulej 2007), *Eoraptor* (PVSJ 512), and probably *Chromogisaurus* (Ezcurra 2010a) and *Saturnalia* (Langer 2003). The ilium possesses a very well developed and laterally directed supra-acetabular crest, as in *Guaibasaurus* (Bonaparte *et al.* 1999). As occurs in Guaibasauridae, but in contrast to *Nambalia* and *Lamplughsa* (Kutty *et al.* 2007), the acetabular wall is partially open and the length of the postacetabular process exceeds that of the acetabulum (Fig. 3E) (Ezcurra 2010a). The brevis fossa is deep and bounded by the brevis shelf and a well-developed medial shelf of the postacetabular process. ISI R277 differs from *Alwalkeria* in lacking an elongated femoral neck. The anterior trochanter of ISI R277 is a vertical ridge situated below the ventral level of the femoral head, contrasting with the condition in *Guaibasaurus* and *Saturnalia* (Bonaparte *et al.* 1999, 2007; Langer 2003) in which the anterior trochanter reaches the ventral level of the femoral head, and the trochanteric shelf is absent (Fig. 3F). The fourth trochanter is asymmetric and proximally located, contrasting with *Lamplughsa* and massopodan sauropodomorphs (e.g. *Riojasaurus*; Bonaparte 1972) in which the fourth trochanter is situated close or at mid-length of the femoral shaft. The foot of ISI R277 is gracile, and resembles that of other basal dinosaurs (e.g. *Herrerasaurus*, *Guaibasaurus*, *Saturnalia*; Novas 1993; Bonaparte *et al.* 1999; Langer 2003). The metatarsus is composed of five elements, including a reduced metatarsal V with a rounded distal end. The latter morphology resembles that described for *Guaibasaurus* (Bonaparte *et al.* 1999), *Saturnalia* (Langer 2003), and *Chromogisaurus* (Ezcurra 2010a).

Archosauria Cope, 1869 *sensu* Gauthier & Padian, 1985
Ornithodira Gauthier, 1986 *sensu* Sereno, 1991
Dinosauriformes Novas, 1992a *sensu* Novas, 1992a
Gen. et sp. indet. A

Material. ISI R282, two sacral vertebrae (corresponding to the first and third sacrals), a proximal caudal vertebra, right ilium, proximal and distal ends of the right pubis, and a probable proximal left pubis (Fig. 3G).

Horizon and locality. Upper Maleri Formation (?late Norian–earliest Rhaetian, Late Triassic; see below), Pranhita–Godavari Valley, around 1 km south of Annaram village, Central India (Fig. 1).

Description. Two sacral vertebrae of ISI R282 are preserved, but the position of their articulation with the iliac blade and the attachment scars present on the ilium indicate that the sacrum of this animal was composed of three sacrals. The latter condition is also present in *Silesaurus* (Dzik & Sulej 2007) and several basal saurischians, including *Eoraptor* (PVSJ 512), *Staurikosaurus* (Galton 2000; Bittencourt & Kellner 2009), ISI R277, *Guaibasaurus* (Bonaparte *et al.* 2007), and probably *Saturnalia* (Langer 2003) and *Chromogisaurus* (Ezcurra 2010a). In contrast, *Herrerasaurus* (Novas 1993), ‘*Caseosaurus*’ (Long & Murry 1995), and probably *Tawa* (Nesbitt *et al.* 2009) possess only two sacral vertebrae. The centrum of the proximal caudal vertebra of ISI R282 is 1.17 times longer than high. The articular facets are planar and oval, being higher than wide, in contrast with those of *Jaklapallisaurus* which are sub-circular in contour. The neural arch is very low in comparison with the height of the centrum. The pre- and postzygapophyses are very short. In contrast to herrerasaurids (Novas 1992b), the neural spine is not oriented dorsally, instead it projects posterodorsally. The ilium of ISI

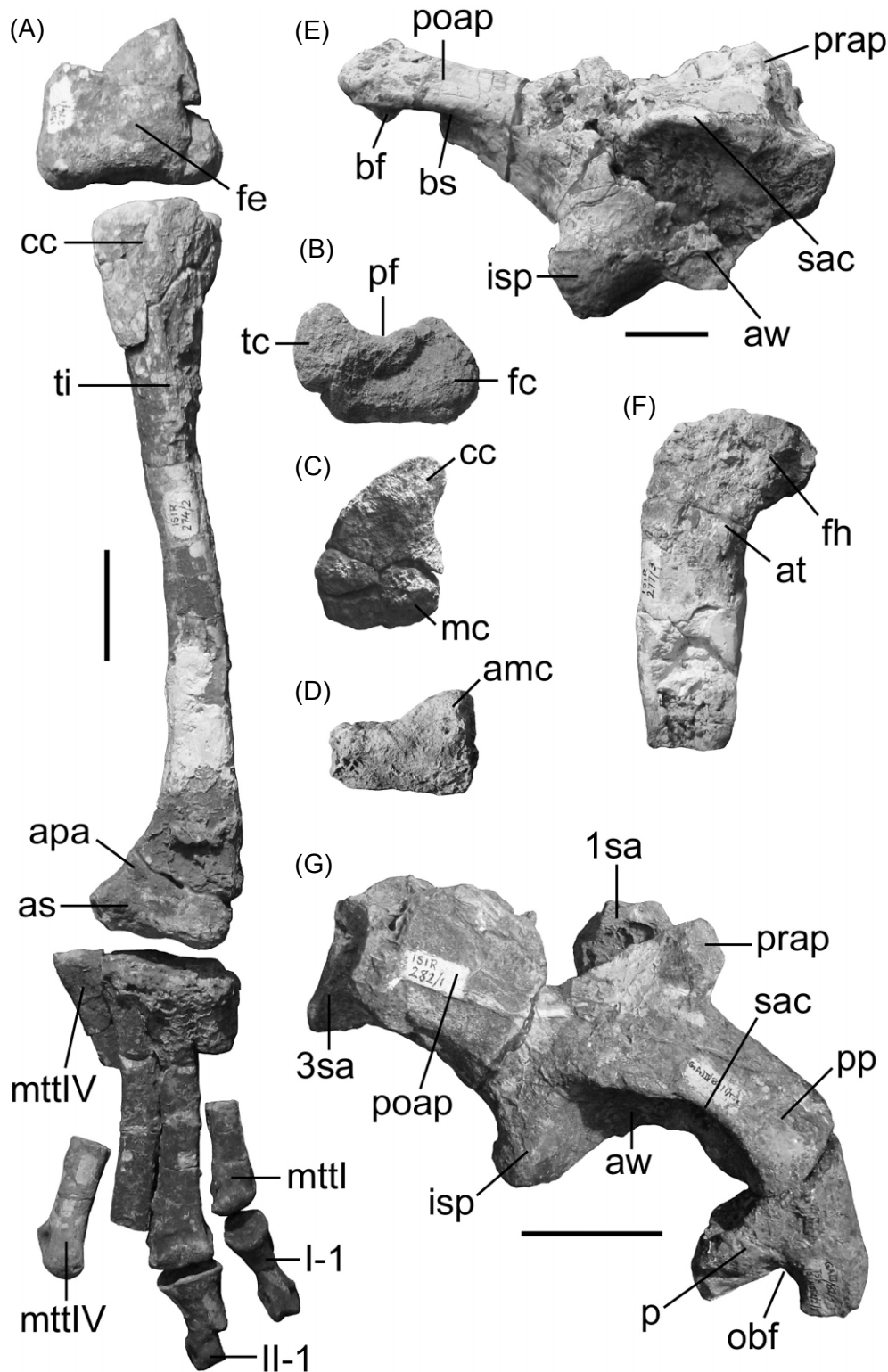


Figure 3 Selected bones of new dinosaur specimens from the Late Triassic Upper Maleri Formation of India. (A–D) ISI R274, holotype of *Jaklapallisaurus asymmetrica* nov. gen. et nov. sp.: (A) right hindlimb in anterior view; (B) femur in distal view; (C) tibia in proximal view; (D) astragalus in distal view. (E) ISI R277, right ilium in lateral view. (F) ISI R277, right femur in anterior view. (G) ISI R282, sacrum and right pelvic girdle in lateral view. Abbreviations: 1sa=first sacral vertebra; 3sa=third sacral vertebra; X-#=phalanx X-#; amc=anterior projection of the medial condyle; apa=ascending process of the astragalus; as=astragalus; at=anterior trochanter; aw=acetabular wall; bf=brevis fossa; bs=brevis shelf; cc=cnemial crest; fc=fibular condyle; fe=femur; fh=femoral head; isp=ischial peduncle; mc=medial condyle; mttI+IV=metatarsals I+IV; obf=obturator foramen; p=pubis; pf=popliteal fossa; poap=postacetabular process; pp=pubic peduncle; prap=preacetabular process; sac=supraacetabular crest; tc=tibial condyle; ti=tibia. Scale bars=5 cm (A–D, G); 2 cm (E, F).

R282 possesses a postacetabular process which lacks a brevis fossa, a condition which differs from that of most dinosaurs, including *Nambalia* and ISI R277. The supraacetabular crest is

moderately developed laterally and dorsally bounds a fully perforated acetabular wall, contrasting with silesaurids (Dzik 2003) and guibasaurids (Ezcurra 2010a). The pubic peduncle

is anteroposteriorly longer than the ischial peduncle, a morphology also observed in herrerasaurids (Novas 1992b), *Caseosaurus* (UMMP 8870), and *Tawa* (Nesbitt *et al.* 2009). The pubis of ISI R282 is orientated ventrally, as occurs in at least some guaibasaurids (Ezcurra 2010a) and *Staurikosaurus* (Galton 1977). The distal end of the pubis is only poorly expanded, contrasting with the larger distal expansions observed in herrerasaurids (Novas 1992b) and *Tawa* (Nesbitt *et al.* 2009). The lack of overlapping elements between ISI R282 and *Alwalkeria* prevents comparisons with these taxa, and few useful comparisons can be made to *Pradhania*. However, in contrast with *Pradhania*, ISI R282 seems to be a non-sauropodomorph dinosauriform (see section 2.2.2). Accordingly, although ISI R282 can be distinguished from other dinosauriforms by a unique combination of characters, a new taxon for this specimen is not erected, due to the lack of overlapping elements with *Alwalkeria*.

Gen. et sp. indet. B

Material. ISI R284, right ilium.

Horizon and locality. Upper Maleri Formation (?late Norian–earliest Rhaetian, Late Triassic; see below), Pranhita–Godavari Valley, around 3 km to the northeast of Jaklapalli village, Central India (Fig. 1).

Description. The fifth dinosaur specimen from the Upper Maleri beds is an isolated right ilium catalogued as ISI R284. This specimen was not included in the numerical phylogenetic analysis (see section 2.2.2) because of its fragmentary condition. The presence of an arched dorsal margin of the iliac blade in lateral view and a perforated acetabulum suggest that this specimen is a dinosaur, or at least more closely related to dinosaurs than to silesaurids or other basal sauropodomorphs (Ezcurra 2006a, Brusatte *et al.* 2009, 2010, Langer *et al.* 2010, Nesbitt *et al.* 2010). In addition, the preacetabular process of the iliac blade of ISI R284 is strongly compressed transversely, possessing a blade-like shape in dorsal view, resembling the condition of ornithischians (e.g. *Lesothosaurus*: NHMUK R11002; *Stormbergia*: Butler 2005), guaibasaurids (e.g. *Saturnalia*: MCP 3846–PV; *Panphagia*: PVSJ 874), *Pantydraco* (NHMUK P771), *Eoraptor* (PVSJ 512), and neotheropods (e.g. *Liliensterus*: MB.R. 2175; *Coelophysis rhodesiensis*: QG 1; *Dilophosaurus wetherilli*: UCMP 77270). Although the latter feature seems to be highly homoplastic among basal dinosaurs, its presence in ISI R284 provides further support for the dinosaur affinities of this specimen. The overall morphology of ISI R284 closely resembles that of *Nambalia roychowdhurii* and the possibility that they could represent the same species is probable, but no unambiguous apomorphies support this hypothesis. In addition, the absence of overlapping elements with *Jaklapallisaurus* and *Pradhania* prevents comparisons with these taxa. Finally, ISI R284 differs from ISI R277 in possessing a fully open acetabular wall, from ISI R282 in possessing a brevis fossa, and from *Lamplughsauro* in possessing a supraacetabular crest that is well-developed laterally.

1.2.2. Phylogenetic relationships of the dinosaurs from the Upper Maleri Formation and its implications. A numerical analysis was carried out in order to assess the phylogenetic relationships of the dinosaur specimens reported here from the Upper Maleri Formation: *Nambalia roychowdhurii* (ISI R273), *Jaklapallisaurus asymmetrica* (ISI R274, 279), ISI R277, and ISI R282. The data matrix was modified from that published by Ezcurra (2010a), which is a modified version of that originally published by Yates (2007b) and modified by Smith & Pol (2007). Several character-states have been modified in the data matrix following the changes proposed by Yates (2010), Yates *et al.* (2010), and some introduced here (see

Appendix 1 (section 5.1) for changes introduced here). Six operational taxonomic units (OTUs) (*Nambalia roychowdhurii*, *Jaklapallisaurus asymmetrica*, ISI R277, ISI R282, *Pradhania gracilis*, and *Tawa hallae*) and two characters were added (see Appendices 2–4 (sections 4.2–4.4) for scorings and new characters), and the resultant data matrix is composed of 380 characters and 56 taxa, with the ingroup focused on basal dinosaurs and basal sauropodomorphs. The non-archosaurian archosauriform *Euparkeria* was used to root the recovered most parsimonious trees (MPTs). The data matrix was analysed under equally-weighted parsimony using TNT 1.1 (Goloboff *et al.* 2008). A heuristic search of 1000 replications of Wagner trees (with random addition sequence) followed by tree bisection reconnection (TBR) branch swapping (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 most parsimonious trees (MPTs) were collapsed (i.e. rule 1 of Coddington & Scharff 1994). Multistate characters were treated as unordered and no *a priori* character polarisation was used. The results were 540 MPTs of 1210 steps (CI=0.368; RI=0.677), and the best score was hit 636 times out of the 1000 replications. With regard to the specimens described here, the analysis consistently placed ISI R282 as a dinosauriform more derived than silesaurids, and *Nambalia*, *Jaklapallisaurus* and ISI R277 as members of Sauropodomorpha (Fig. 4). It must be noted that *Tawa hallae* was found within Theropoda, as recovered by Nesbitt *et al.* (2009), but as the sister-taxon of the *Eoraptor*+Neotheropoda clade. However, the implications of the recovered phylogenetic position of *Tawa* are beyond the scope of the present paper and will be discussed elsewhere. In the strict consensus tree, ISI R277 was found within a polytomy at the base of Guaibasauridae. *Nambalia* was recovered as a sauropodomorph more derived than Guaibasauridae, *Pantydraco* and *Thecodontosaurus*, and is positioned as the sister-taxon of *Efraasia*, *Plateosauravus* and more derived sauropodomorphs. *Jaklapallisaurus* was nested within Plateosauria and the lesser inclusive clade Plateosauridae. Accordingly, *Jaklapallisaurus* was recovered as a sauropodomorph more derived than *Nambalia*.

A second search was performed with the *a priori* exclusion of ISI R282 and *Agnosphitys*, due to the unstable position of these specimens in the first analysis. The results were 30 MPTs of 1208 steps, with a CI: 0.368 and an RI: 0.678, and the best score hit 99 times out of the 100 replications. The consensus tree of the recovered MPTs exhibited better resolved interrelationships among basal dinosauriforms than in the first analysis, including a monophyletic Dinosauria, Herrerasauria, and Eusaurischia. Within Guaibasauridae, ISI R277 and *Panphagia* were found within a trichotomy at the base of the group and as the sister-taxa of the clade composed of *Guaibasaurus* and Saturnaliinae (i.e. *Saturnalia* and *Chromogisaurus*) (Fig. 5). The results of both analyses are discussed in more detail below.

Nambalia roychowdhurii was found as a member of Sauropodomorpha because of the presence of an iliac blade that is strongly curved laterally in dorsal view. Within this clade, *Nambalia* is closer to plateosaurians than to guaibasaurids, due to the presence of an ilium without a buttress between the preacetabular process and the supraacetabular crest; metatarsal I with the transverse axis of the distal end proximomedially oriented; metatarsal II with the proximal surface bearing a concave lateral margin; and metatarsal V with the transverse width of the proximal end being more than 30% of the length of the bone. Furthermore, *Nambalia* shares with *Efraasia*, *Plateosauravus*, *Ruehleia*, and plateosaurians the presence of an ilium with a directly ventrally facing brevis

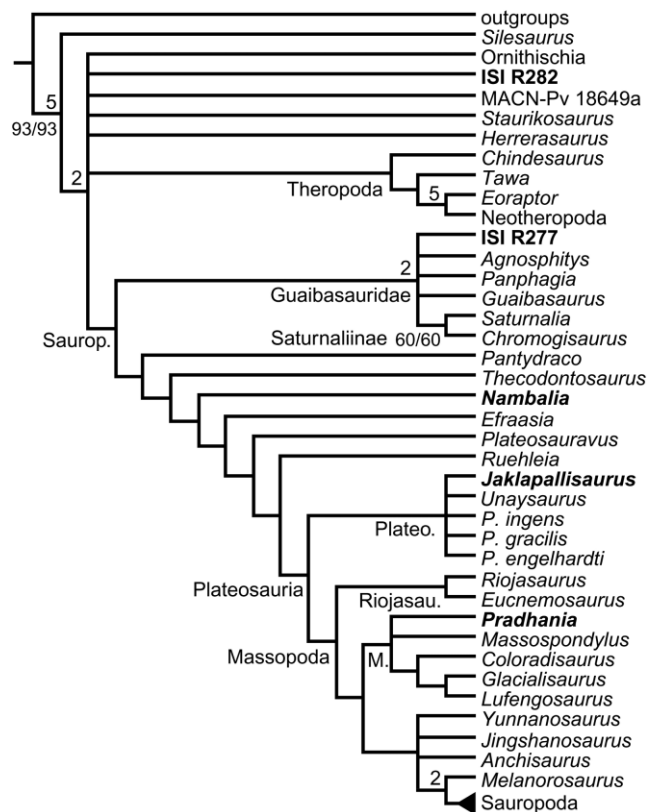


Figure 4 Strict consensus tree of 540 MPTs recovered from the heuristic analysis depicting the phylogenetic relationships of *Nambalia*, *Jaklapallisaurus*, ISI R277, ISI R282 and *Pradhania* among basal dinosaurs. Values above the nodes are decay indexes greater than 1 and below the nodes absolute (left) and GC (right) bootstrap frequencies greater than 50% (after 10,000 pseudoreplicates). Abbreviations: M.=Massospondylidae; P.=Plateosaurus; Riojasau.=Riojasauridae; Plateo.=Plateosauridae; Saurp.=Sauropodomorpha.

fossa, a distal femur with a well-developed and kidney-shaped tibiofibular crest, and a distal tibia with a transverse width greater than its anteroposterior length. *Nambalia* is recovered as the sister-taxon of the clade that includes *Efraasia* and more derived sauropodomorphs because the Indian form lacks mid-caudal centra less than twice the height of their anterior articular facets and an ischium with a sub-triangular distal outline.

Jaklapallisaurus asymmetrica was found to be closer to plateosaurians than to guaibasaurids within Sauropodomorpha because of the presence of metatarsal II with a proximal surface bearing a concave lateral margin. Furthermore, *Jaklapallisaurus* was nested in the clade including *Nambalia* and more derived sauropodomorphs due to the presence of a distal femur with a well-developed and kidney-shaped tibiofibular crest and a distal tibia with a transverse width greater than its anteroposterior length. The Indian species was nested within the clade Plateosauria because of the presence of a femoral distal transverse width greater than 1.4 times its greatest anteroposterior depth across the fibular condyle. Within Plateosauria, *Jaklapallisaurus* was found as a member of the family Plateosauridae. The apomorphy which supports the inclusion of *Jaklapallisaurus* within Plateosauridae is the presence of a proximal tibia with posterior condyles that extend posterior to the same extent (unknown in *Unaysaurus* and *Plateosaurus gracilis*, and polymorphic in *Plateosaurus engelhardti*). The affinities of the Indian species changes within Plateosauridae among the recovered MPTs, but its position as the most basal member of the family is the only hypothesis supported by non-ambiguous apomorphies. Indeed, the pos-

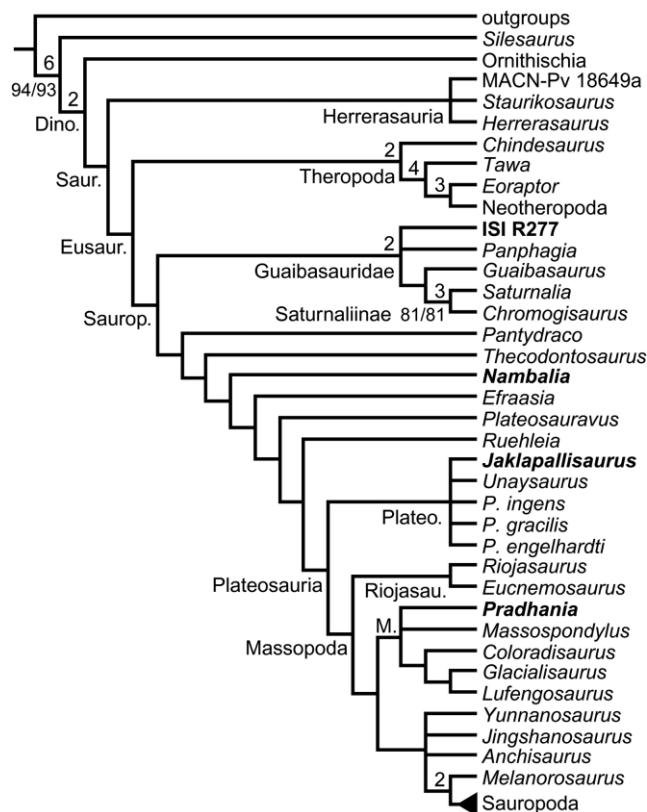


Figure 5 Strict reduced consensus tree of 30 MPTs recovered from the heuristic analysis (after the *a priori* exclusion of ISI R282 and *Agnosphitys* from the analysis) depicting the phylogenetic relationships of *Nambalia*, *Jaklapallisaurus*, ISI R277 and *Pradhania* among basal dinosaurs. Values above the nodes are decay indexes greater than 1. Abbreviations: Dino.=Dinosauria; Eusaur.=Eusaurischia; M.=Massospondylidae; P.=Plateosaurus; Plateo.=Plateosauridae; Riojasau.=Riojasauridae; Saur.=Saurischia; Saurp.=Sauropodomorpha.

ition of *Jaklapallisaurus* as the most basal plateosaurid is supported by the absence of proximal caudal vertebrae with a longitudinal ventral sulcus (unknown in *Plateosaurus ingens*) and the presence of a proximal second metatarsal with a concave medial margin (unknown in *Plateosaurus gracilis* and *Plateosaurus ingens*). Finally, *Jaklapallisaurus* is not included within Massopoda because it lacks the following synapomorphy of the clade: a distal femur with an anterior extensor median depression. Thus, the presence of the latter character in *Nambalia* is considered as homoplastic in the present analyses. The assignment of *Jaklapallisaurus* to Plateosauridae must be considered tentative because it is based on a character without a completely known distribution within the clade and polymorphic in one of its species.

ISI R277 was originally referred to *Massospondylus* sp. (Kutty *et al.* 1987), but more recently it was suggested to be closely related to the basal saurischian *Guaibasaurus* (Kutty *et al.* 2007). The present phylogenetic analyses support the latter interpretation, in which ISI R 277 was nested within guaibasaurid sauropodomorphs. Indeed, ISI R277 was recovered as a member of Sauropodomorpha due to the presence of anterior cervical centra (cervical 3–5) that are longer than 2.5 times the height of their anterior articular facets, laminae of cervical neural arches 4–8 that are weakly-developed low ridges, and an iliac blade that is strongly laterally curved in dorsal view. The guaibasaurid affinity of ISI R277 is supported by the presence of an ilium with an incipiently open acetabular wall and a postacetabular process that is longer than the distance between the pubic and ischial peduncles (Ezcurra 2010a). When *Agnosphitys* is *a priori* pruned from the

analysis, the interrelationships within Guaibasauridae are better resolved. ISI R277 and *Panphagia* are found within a trichotomy at the base of Guaibasauridae, as the sister-taxon of the clade containing *Guaibasaurus* and Saturnaliinae. Indeed, ISI R277 is excluded from the *Guaibasaurus*+Saturnaliinae (i.e. *Saturnalia*+*Chromogisaurus*) clade by the absence of a femur with the proximal tip of the anterior trochanter at the same level as the ventral margin of the femoral head (unknown in *Agnosphitys*, *Chromogisaurus* and *Panphagia*). Finally, ISI R277 is excluded from Saturnaliinae by the absence of an iliac postacetabular process with a pointed posteroverventral corner and a rounded posterodorsal margin, and the lack of a strong and anterodorsally tapering trapezoidal rugosity, presumably for the origin of the *Mm. flexor tibialis* and *iliotibialis*, extended along the whole height of the posterior third of this process (Ezcurra 2010a).

ISI R282 was found lying within a polytomy at the base of the clade including dinosauriforms more derived than Silesauridae, with its positions in the MPTs ranging from a trichotomy together with Ornithischia and Saurischia (i.e. the position of ISI R282 as the sister taxon of Dinosauria is depicted by a zero length branch) to a deeply nested saurischian. The position of ISI R282 as a dinosauriform more derived than silesaurids is supported by the presence of an ilium with a fully open acetabulum and a nearly straight pubic shaft. Furthermore, ISI R282 is excluded from Sauropodomorpha, thus preventing possible affinities with *Nambalia*, *Jaklapallisaurus* and ISI R277, due to the absence of an ilium with a pubic peduncle longer than twice the anteroposterior length of its distal end, a supraacetabular crest extending along the entire pubic peduncle and contacting the distal end as a well developed crest, and a strongly laterally curved iliac blade. Accordingly, the phylogenetic position of ISI R282 is regarded as highly problematic.

The phylogenetic position recovered for the Early Jurassic Indian genus *Pradhania* has implications for the taxonomy of the Upper Maleri dinosaurs. In the original description of *Pradhania*, this taxon was found as a sauropodomorph more basal than other members of the clade, except for *Saturnalia* and *Pantyraco* (Kutty *et al.* 2007). However, in the present analysis *Pradhania* was found as a more derived sauropodomorph, a member of Massopoda, and nested within the Massospondylidae. Indeed, *Pradhania* presents the following synapomorphies of Massospondylidae recovered in the current phylogenetic analysis: a dentary with a symphyseal end strongly ventrally curved (also present in Plateosauridae); and anterior cervical vertebrae with a centrum that is four times longer than the height of its anterior articular facet (also present in *Omeisaurus* and *Mamenchisaurus*). The probable affinities of *Pradhania* with massospondylids must be further tested in future analyses, but represents an interesting hypothesis. It would imply a wider geographical distribution for the clade, which would be present in latest Triassic to Early Jurassic times and occurring in South America, Antarctica, Africa, Asia, and India (Cooper 1981; Yates 2007b; Smith & Pol 2007). Furthermore, the phylogenetic position of *Pradhania* suggests that none of the Upper Maleri specimens reported here belong to this genus or to the *Pradhania* lineage.

The composition of the dinosaur fauna of the Upper Maleri Formation roughly approaches that of the early post-Ischigualastian (late Norian) Brazilian Caturrita Formation. Indeed, the presence of the unnamed guaibasaurid dinosaur (ISI R277) and the probable plateosaurid *Jaklapallisaurus asymmetrica* matches with that observed in the Brazilian assemblage, from which the guaibasaurid *Guaibasaurus candeleriensis* and the plateosaurid *Unaysaurus tollentoi* were recovered. These observations bolster previous assumptions of a

post-Ischigualastian age for the Upper Maleri Formation, which is here considered as probably late Norian to earliest Rhaetian due to its poor temporal constraint. Furthermore, although based on negative evidence, no typical Ischigualastian tetrapods found in the Lower Maleri Formation are reported from the Upper Maleri Formation (e.g. *Hyperodapedon*, *Exaeretodon*). Non-massopodan or very basal massopodan sauropodomorphs are also recorded in presumed post-Ischigualastian outcrops of Europe (e.g. Löwenstein and Trossingen formations; Yates 2003b; Galton & Upchurch 2004) and South Africa (i.e. lower Elliot Formation; Yates 2007a), but no unequivocal sauropodomorph remains are currently known from the Triassic of North America (Ezcurra 2006b; Nesbitt *et al.* 2007; Irmis *et al.* 2007b). The Upper Maleri Formation resembles coeval European beds in the presence of parasuchians and sauropodomorph dinosaurs; it approaches North American assemblages in the presence of parasuchians, and South American faunas in the sauropodomorph assemblage. Besides the mixture of palaeobiogeographic affinities among the vertebrate fauna of the Upper Maleri Formation and those of other roughly coeval depositional centers, the Indian assemblage exhibits an alpha-level dinosaur diversity of at least four different dinosaur species, which approaches or slightly exceeds that currently known for post-Ischigualastian beds of North America (Chinle Formation), South America (Caturrita Formation), and Europe (Löwenstein Formation) (see Fig. 6). This high dinosaur alpha diversity of the Upper Maleri Formation approaches that recorded in the lower levels of the Ischigualasto Formation (Ezcurra 2010a) and is slightly lower than that observed in the lower Elliot Formation (Langer *et al.* 2010). Thus, it provides support to the idea that high dinosaur species richness was maintained after Ischigualastian times in at least some dinosaur-bearing assemblages. At the moment, it cannot be determined if the lower dinosaur alpha diversity recorded in other roughly coeval assemblages (e.g. the Caturrita Formation of Brazil) is a real signal, or an artifact of incomplete sampling or taphonomic biases.

1.3. Lower Dharmaram Formation

The fossil vertebrate fauna of the Lower Dharmaram Formation includes the same 'fish' genera known from the Lower and Upper Maleri formations, but tetrapods are only represented by archosaurs, including aetosaurs (cf. *Paratyphothorax*), parasuchians (cf. *Nicrosaurus*) (Bandyopadhyay & Sengupta 2006; Kutty *et al.* 2007), and dinosaur specimens (Novas *et al.* 2009). The dinosaurs are represented by fragmentary remains of sauropodomorphs (ISI R279, 280, 281) (Fig. 7A–B, E–G) and neotheropods (ISI R283) (Fig. 7C–D). The presence of an archosaur-dominated tetrapod fauna resembles presumed post-Ischigualastian assemblages, such as that of the La Esquina Fauna of the Los Colorados Formation, the Trossingen Formation of the German Keuper, the lower Elliot Formation and the Chinle Formation. It must be also noted that no rhynchosaurs and therapsids have been found to date in the Lower Dharmaram Formation. Accordingly, we agree with previous authors in considering the Lower Dharmaram Formation as probably latest Norian–Rhaetian in age (Bandyopadhyay & Sengupta 2006; Kutty *et al.* 2007).

The dinosaurs collected from the Lower Dharmaram Formation are represented by isolated bones (ISI R279, 280, 281, 283), which were not included in the numerical phylogenetic analysis. ISI R279 is a distal right femur that possesses a combination of apomorphies that seems shared only by *Jaklapallisaurus* among basal dinosaurs, including autapomorphic widely transversely open popliteal fossa and medial condyle of distal femur sub-triangular in distal view (Fig. 7G).

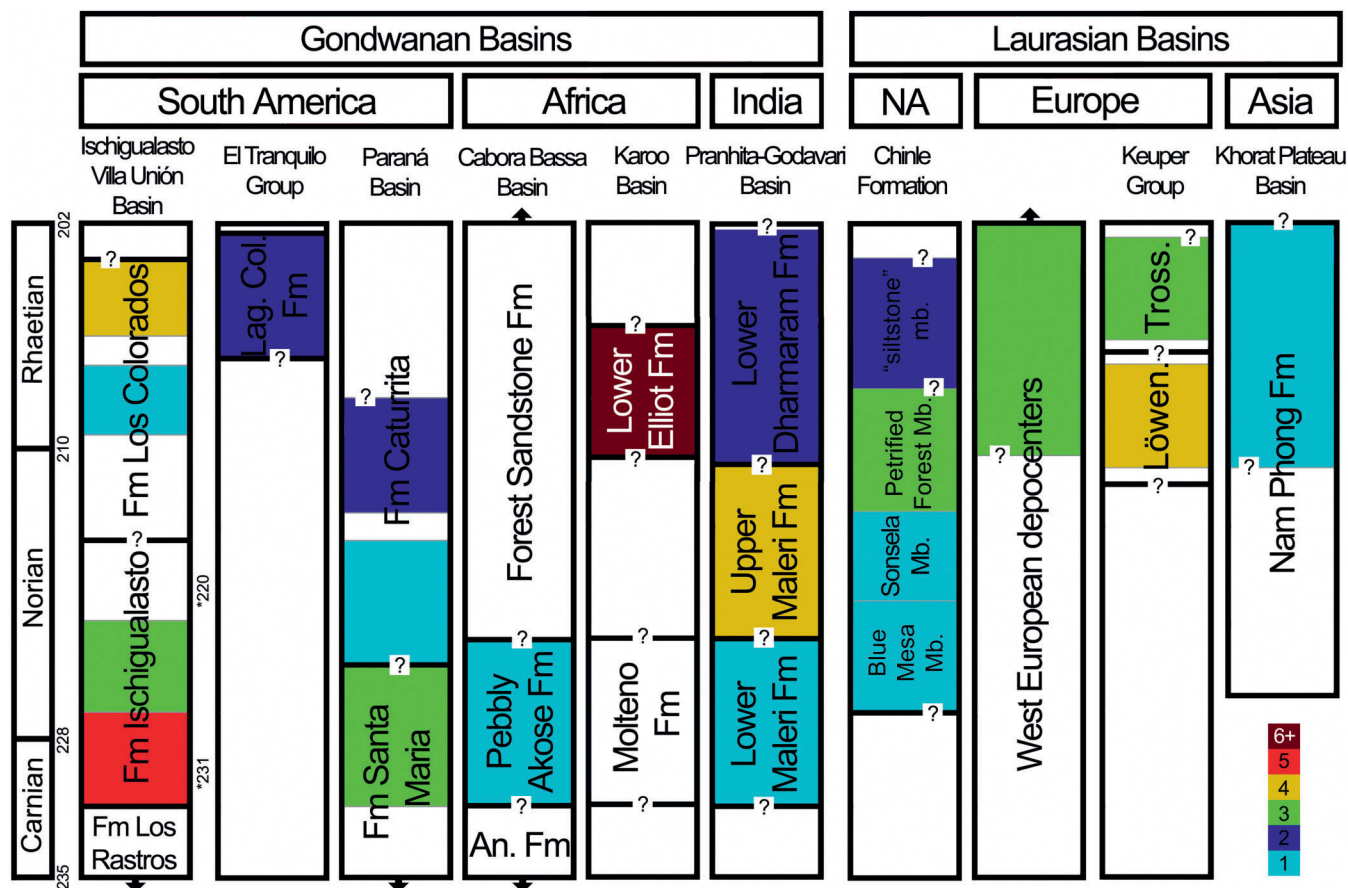


Figure 6 Biostratigraphic sequence of dinosaur-bearing Triassic depocentres (based on Brusatte *et al.* 2010; Langer *et al.* 2010; Ezcurra 2010a; Ezcurra & Brusatte in press). The different colours depict the alpha-taxonomic diversity of each dinosaur-bearing assemblage. Note that the age of the boundaries between the sedimentary units are uncertain and only approximately estimated. Abbreviations: An.=Angwa Sandstone; Fm=Formation; Löwen.=Löwenstein Formation; Mb/mB=Member; NA=North America; Tross.=Trossingen Formation.

Thus, ISI R279 is here referred to *Jaklapallisaurus asymmetrica*. An isolated left astragalus, ISI R280, can be assigned to Sauropodomorpha due to the presence of an astragal body with a strongly anteroposteriorly-expanded medial end and a downturned posterolateral border (Fig. 7E–F). ISI R281 is based on the proximal half of a left femur, assigned to Sauropodomorpha because of its rounded head and a vertical and reduced anterior trochanter (Yates 2007b) (Fig. 7A–B). Finally, a left femur that lacks its distal end (ISI R283) can be assigned to Neotheropoda due to the presence of a strongly inturned femoral head that forms an angle of less than 90° to the main axis of the shaft and a well-developed and pyramidal anterior trochanter (Rauhut 2003). ISI R283 can be excluded from *Averostra* (*sensu* Ezcurra & Cuny 2007) because it lacks a proximally well-developed anterior trochanter extending beyond the level of the ventral margin of the femoral head (Rauhut 2003; Ezcurra 2006a). Accordingly, ISI R283 is interpreted as a non-*averostran* neotheropod (Fig. 7C–D). This indicates the presence of at least two or three different dinosaur taxa in the Lower Dharmaram Formation: basal sauropodomorphs and an indeterminate basal neotheropod.

2. Discussion

The Gondwanan fossil record has been a key source of information in understanding the macroevolutionary processes and patterns involved in the origin and early radiation of dinosaurs during the Triassic. The new and rich dinosaur fauna from presumed post-Ischigualastian beds of central

India reported here enhances our knowledge of these ancient southern biotas.

Three distinct faunistic patterns can be distinguished in the dinosaur-bearing assemblages from the Late Triassic–Early Jurassic Gondwana formations of the Pranhita–Godavari Basin (Table 1). First, a rhynchosaur-dominated fauna is documented in the Lower Maleri Formation, in which dinosaurs were apparently a minor and poorly diverse component. This pattern contrasts with coeval South American beds (i.e. La Peña and Cancha de Bochas members of the Ischigualasto Formation of Argentina and Alemoa Member of the Santa Maria Formation of Brazil), in which dinosaurs were diverse, primarily in the Argentinean unit, but still not abundant (Ezcurra 2010a) (Fig. 6). The low dinosaur alpha-diversity of the Lower Maleri Formation does not appear to represent a sampling artifact, because numerous specimens of other tetrapods have been collected from this unit (e.g. *Hyperodapedon*, *Buettneria*, *Parasuchus*; von Huene 1940; Chatterjee 1974, 1980b; Chatterjee & Roy Chowdhury 1974; Benton 1983). Accordingly, the currently available evidence suggests that the oldest known dinosaur assemblages were not homogeneous, but more diverse in South America than in India.

The second interval is an archosaur-dominated tetrapod assemblage documented from the Upper Maleri and Lower Dharmaram formations. These units yielded abundant basal sauropodomorphs, as occurs in coeval beds from South America and Europe but sharply contrasting with North American assemblages. The absence of sauropodomorphs in the latter landmass is intriguing, and faunal provincialism

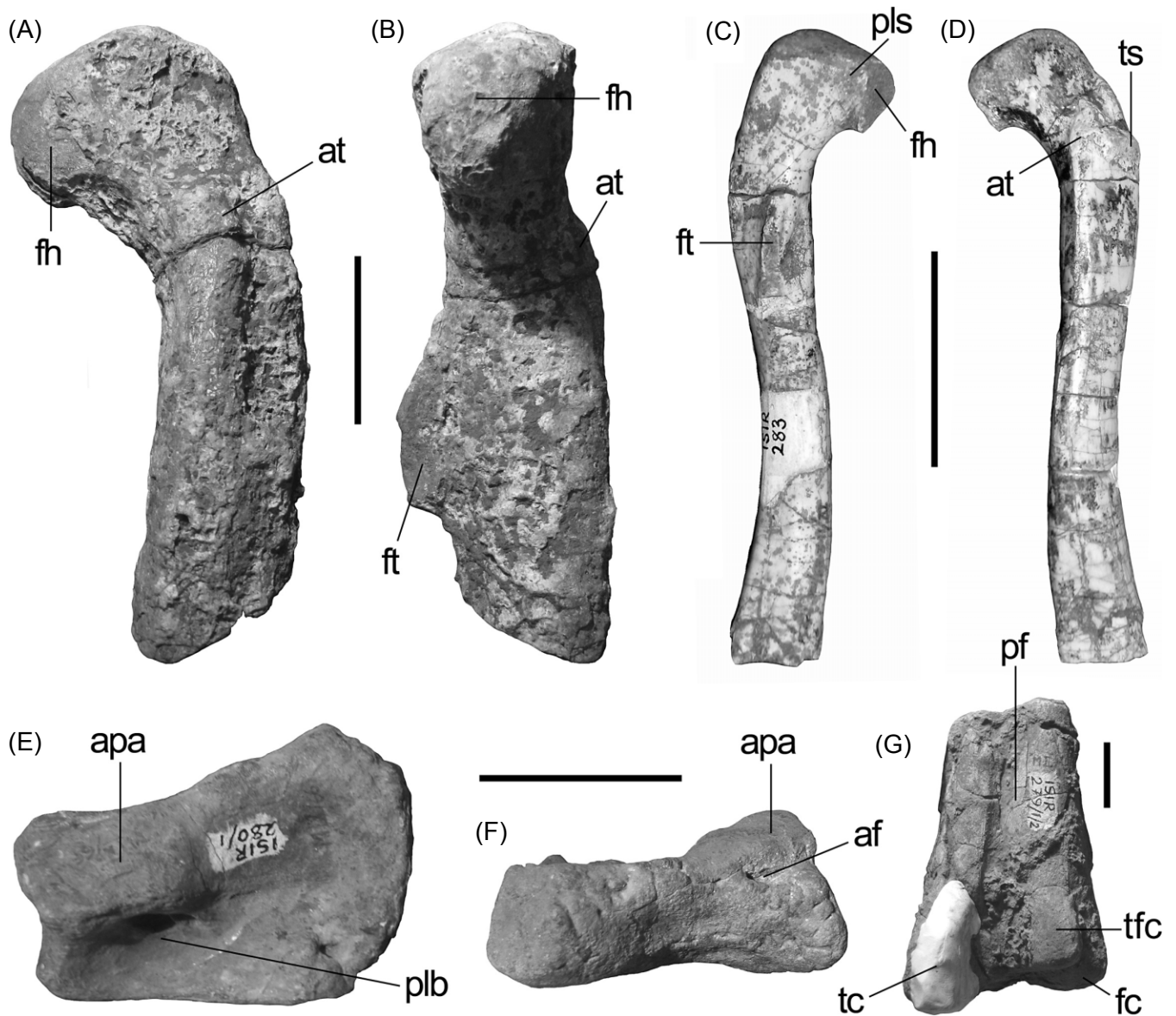


Figure 7 Selected bones of new dinosaur specimens from the Late Triassic Lower Dharmaram Formation of India: (A, B) ISI R281, right femur in anterior (A) and medial (B) views; (C, D) ISI R283, right femur in posterior (C) and anterior (D) views; (E, F) ISI R280, left astragalus in dorsal (E) and anterior (F) views; (G) referred specimen of *Jaklapallisaurus asymmetrica* nov. gen. et nov. sp. (ISI R279), right femur in posterior view. Abbreviations: af=anterior fossa; apa=ascending process of the astragalus; at=anterior trochanter; fc=fibular condyle; fh=femoral head; ft=fourth trochanter; pf=popliteal fossa; plb=posterolateral basin; pls=posterolateral sulcus; tc=tibial condyle; tfc=tibiofibular crest; ts=trochanteric shelf. Scale bars=5 cm (A–F); 2 cm (G).

related to palaeolatitudinal differences has been proposed (Ezcurra 2006b, 2010b; Irmis *et al.* 2007b; Nesbitt *et al.* 2009). The Indian fossil assemblages extend the Triassic record of sauropodomorphs into this region and further emphasise the provincialism of the contemporary North American dinosaur faunas. Furthermore, the presence of a neotheropod dinosaur in the latest Norian–Rhaetian of India constitutes the second Triassic record of this group from the Southern Hemisphere (Ezcurra & Novas 2007). Thus, this specimen widens the geographic distribution of Neotheropoda in Gondwana. In addition, the new Indian dinosaur specimens described from the Upper Maleri and Lower Dharmaram formations suggests that dinosaurs were the most taxonomically diverse tetrapods during the time of deposition of these sedimentary units (Table 1).

The patterns documented in the Triassic assemblages of the Indian Pranhita–Gondavari Basin suggest that dinosaurs radiated during post-Ischigualastian times in this area. The latter contrasts with the situation observed in the Ischigualasto–Villa

Unión Basin, in which the initial radiation of dinosaurs appears to have occurred earlier, because the late Carnian dinosaur assemblage is already quite taxonomically diverse (Fig. 6; Ezcurra 2010a). The pattern observed in the Pranhita–Godavari Basin agrees with a radiation of dinosaurs after the late-Ischigualastian extinction event (Benton 1983, 1984, 1988, 2006), in which the rhynchosaur-dominated fauna disappeared. However, the radiation of dinosaurs recorded in the Upper Maleri Formation did not occur in an empty ecospace, contrasting with a non-competitive model (Benton 1983), because pseudosuchians and dicynodonts were also conspicuous members of this tetrapod fauna. Accordingly, as previously suggested by other authors (e.g. Irmis *et al.* 2007b; Nesbitt *et al.* 2009), it seems that the early radiation of dinosaurs was not synchronous at a worldwide level, and the evidence described here for India suggests that diachronous faunal changes may have occurred even within Gondwana.

Radioisotopic dates currently available from South and North American Triassic beds allow a more precise dating of

Table 1 Updated list of vertebrates from the Triassic dinosaur-bearing formations of the Pranhita–Godavari Valley, India (modified from Kutty *et al.* (2007) and Bandyopadhyay & Sengupta (2006)). Genera abbreviations: A. = *Alwalke-ria*; B. = *Buettneria*; Ce. = *Ceratodus*; Co. = *Compsocerops*; E. = *Exaeretodon*; H. = *Hyperodapedon*; J. = *Jaklapallisaurus*; K. = *Kuttycephalus*; M. = *Malerisaurus*; N. = *Nambalia*; P. = *Paleorhinus*; X. = *Xenacanthus*. The specimens described in the present paper are in bold.

Formation	Lower Maleri	Upper Maleri	Lower Dharmaram
Age	(late Carnian–early Norian)	(?late Norian–earliest Rhaetian)	(?latest Norian–Rhaetian)
Xenacanthidae	<i>X. indicus</i>	<i>X. indicus</i>	<i>X. indicus</i>
Dipnoi	<i>Ce. negeswari</i> <i>Ce. virapa</i>	<i>Ce. negeswari</i> <i>Ce. hunetrianus</i>	<i>Ce. negeswari</i> —
Chigutisauridae	—	<i>Co. cosgriffi</i> <i>K. triangularis</i>	—
Metoposauridae	<i>B. malerensis</i>	—	—
Dicynodontia	—	cf. <i>Ischigualastia</i>	—
Cynodontia	<i>E. statisticae</i>	—	—
Prolacertiformes	<i>M. robinsonae</i>	—	—
Rhynchosauria	<i>H. huxleyi</i>	—	—
Parasuchia	<i>P. hislopi</i> cf. <i>Angistorhinus</i>	<i>Angistorhinus</i> cf. <i>Leptosuchus</i>	cf. <i>Nicrosaurus</i> —
Aetosauria	cf. <i>Typhothorax</i>	Aetosauria indet.	cf. <i>Paratyphothorax</i>
Basal dinosauriformes	<i>A. malerensis</i>	ISI R282, 284	—
Sauropodomorpha	—	<i>N. roychowdhurii</i> <i>J. asymmetrica</i>	<i>J. asymmetrica</i> ISI R280
	—	ISI R277	ISI R281
Neotheropoda	—	—	ISI R283

the first appearance of dinosaurs. Dinosaurs first appeared in North American beds slightly more than 10 million years after their first records in Gondwana (Furin *et al.* 2006; Irmis & Mundil 2008), a time span greater than the entire Carnian stage (*sensu* Muttoni *et al.* 2004). The radiation of the earliest dinosaur clades seems to have occurred during the middle–late Carnian, a time span during which the group is only recorded from Gondwanan assemblages. This could be an artifact of the fossil record, but it may also suggest a Gondwanan origin of dinosaurs and a subsequent dispersal to Laurasia (Nesbitt *et al.* 2009).

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4. Appendices

4.1. Appendix 1. Modifications made to the data-matrix of Ezcurra (2010a)

Character 258: the posterior end of the postacetabular process of *Agnosphitys* is broken, thus the state of this character cannot be assessed in this taxon. Thus, this character has been re-scored as (?) instead of (0) for *Agnosphitys*.

Character 304: the proximal ends of the tibiae of *Plateosaurus engelhardti* exhibit intraspecific variation regarding the posterior development of their posterior condyles. In some specimens, the medial condyle is anteriorly displaced in comparison with the lateral one (Moser 2003, plate 12, fig. 1b); in others, both condyles are posteriorly extended to the same degree (Moser 2003, plate 11, fig. 1e). In at least one individual this dimorphism occurs within a single individual (SMNS 13200). Accordingly, the scoring of this character has been changed from (1) to (01) for *Plateosaurus engelhardti*.

Character 325: in *Saturnalia* (Langer 2003; MCP 3844–PV) and *Herrerasaurus* (MACN-Pv 18060; PVSJ 373), the lateral surface of the calcaneum bears a distinct groove on its lateral surface and it is not simple as described by state (0) of this character (*contra* Yates (2007b) and Ezcurra (2010a)). Accordingly, this character has been re-scored as (1) instead of (0) in the present data-matrix for *Saturnalia*.

Character 353: in the holotype of *Plateosaurus ingens*, the femur is not preserved (Rütimeyer 1856; Galton 1986), because of that the scoring of this character has been changed from (4) to (?) for this species.

Character 355: in *Anchisaurus polyzelus*, the distal articular surface of the astragalus is weakly convex, but not ‘roller-shaped’ (Galton 1976, fig. 22b, d). Accordingly, the scoring of this character has been changed from (?) to (0) for *Anchisaurus*.

Character 360: this character was introduced by Smith & Pol (2007), and state (1) refers to the presence of a distinctly

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11??0?0????0?0?10????0?????0?0?????1011100-?01?01???????

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