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Notes

Non-dinosaurian Dinosauromorpha

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Abstract: Ichnological evidence suggests that dinosauromorphs originated by the Early Triassic, and skeletal remains of non-dinosaur representatives of the clade occur from the Anisian to the end of the Triassic. These taxa are small- to medium-sized, vary in feeding and locomotor features, and occurred over most of western Pangaea. They include the small lagerpetids from the Mid–Late Triassic of Argentina and the United States, and the larger, quadrupedal Silesauridae, with records in the Middle Triassic of Africa and Argentina, and in the Late Triassic of Europe, the Americas and northern Africa. The former group represents the earliest diverging dinosauromorphs, whereas silesaurids are more closely related to Dinosauria. Other dinosauromorphs include the archetypal early dinosauriform *Marasuchus lilloensis* (Middle Triassic of Argentina) and poorly known/controversial taxa such as *Lewisuchus admixtus* and *Saltopus elginensis*. The earliest diverging dinosauromorphs may have preyed on small animals (including insects), but cranio-dental remains are rare; by contrast, most silesaurids probably included plant material in their diet, as indicated by their modified jaw apparatus and teeth. Our knowledge of the anatomy and thus relationships of non-dinosaurian Dinosauromorpha is still deficient, and we suspect that future discoveries will continue to reveal novel patterns and hypotheses of palaeobiology and biogeography.

The clade Dinosauromorpha includes all taxa more closely related to birds than to pterosaurs, and therefore includes non-avian dinosaurs and their flying, avialan descendants. Yet, unlike their dinosaurian evolutionary offspring, few of the archosaurs currently regarded as non-dinosaurian Dinosauromorpha (Fig. 1) were known before the palaeontological 'cladistic-revolution' 30 years ago. *Saltopus elginensis* was described by Huene (1910) as a dinosaur, an assignment followed until fairly recently (Steel 1970; Norman 1990). Likewise, in his series of contributions describing the Chañares Formation tetrapods, Romer (1971, 1972a, b) acknowledged dinosaur (particularly 'coelurosaur') affinities for the long-limbed *Lagerpeton chanarensis*, *Lewisuchus admixtus* and '*Lagosuchus talampayensis*', but assigned them to the contempory wastebasket group 'Pseudosuchia'. A similar approach was taken by authors such as Bonaparte (1975), Krebbs (1974) and Thulborn (1975). By the mid- to late-1980s, a series of non-numerical phylogenetic studies started recognizing a clade exclusively composed of all known dinosaurs, plus some of those Chañares forms at the base (Paul 1984a, b; Brinkman & Sues 1987; Benton & Clark 1988; Novas 1989; Sereno 1991), as previously hinted by Bakker & Galton (1974). Later, this view was detailed in numerical studies specifically focused on the Chañares forms *Lagerpeton chanarensis* and *Marasuchus lilloensis* (Sereno & Arcucci 1994a, b), with the former recovered as the earliest diverging dinosauromorph and the latter as more closely related to dinosaurs. Parrish (1993) regarded *Lewisuchus admixtus* as a pseudosuchian archosaur, and Novas (1996) found *Pseudolagosuchus major* Arcucci (1987) to be the sister taxon of dinosaurs. Their suggested synonymy by Arcucci (1997, 1998) was the last revisionary work on the subject in the 20th century. At the time, all those small-bodied forms were accepted plesiomorphically as carnivores/insectivores and shared a bipedal mode of locomotion with early dinosaurs.

A key advancement for our understanding of early dinosauromorph evolution was the discovery of *Silesaurus opolensis* from the Late Triassic of Poland (Dzik 2003). Its combination of unexpected
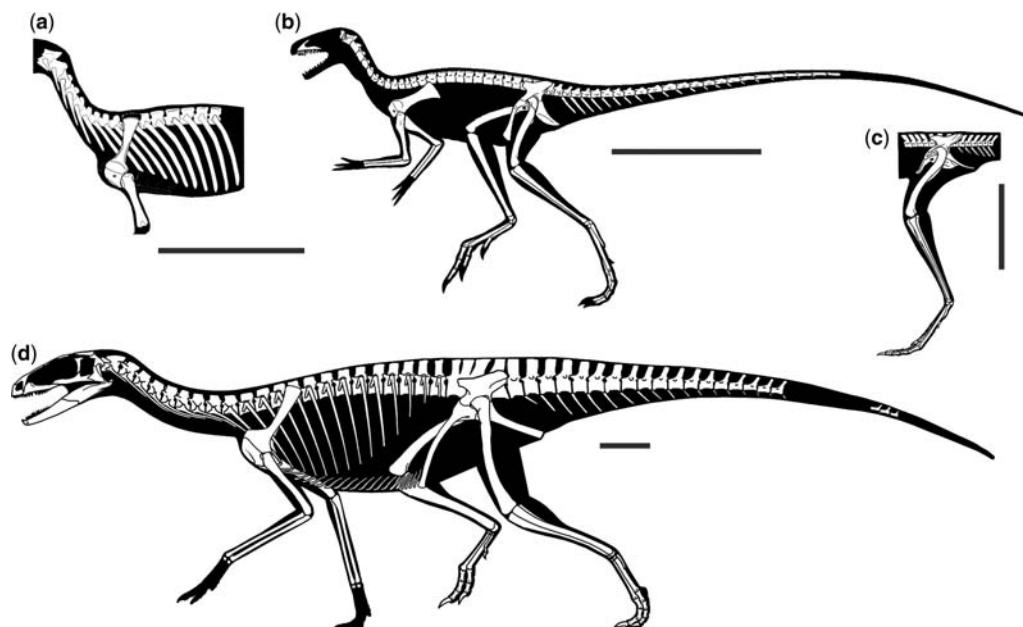
Fig. 1. Skeletal reconstructions of non-dinosaur dinosauromorphs in left lateral view, with preserved parts indicated: (**a**) neck and trunk of *Lewisuchus admixtus* (modified from Remes 2007); (**b**) skeleton of *Marasuchus lilloensis* (modified from Sereno & Arcucci 1994*b*); (**c**) hindquarter of *Lagerpeton chanarensis* (from Sereno & Arcucci 1994*a*); (**d**) skeleton of *Silesaurus opolensis* (modified from Dzik 2003). Scale bars, 10 cm.

anatomical traits (e.g. long arms, toothless beak, leaf-shaped teeth) was suggestive of a facultative quadrupedal mode of locomotion and a herbivorous/omnivorous diet. Following its description, various new (Parker *et al.* 2006; Ferigolo & Langer 2007; Irmis *et al.* 2007*a*; Small 2009; Nesbitt *et al.* 2010; Peecook *et al.* 2011; Kammerer *et al.* 2012) and previously known (Ezcurra 2006; Nesbitt *et al.* 2007) taxa were considered close relatives of *Silesaurus opolensis*, all or some of which form a diverse clade (Silesauridae) that is usually recovered as the sister group of Dinosauria. In contrast, some workers have proposed the hypothesis that all or some of the 'silesaurids' are nested within Ornithischia (Ferigolo & Langer 2007; Niedzwiedzki *et al.* 2009), as evidenced by the putative homology of their toothless mandibular tip with the predentary bone of those dinosaurs. However, the most recent comprehensive archosaur phylogenies, with widespread sampling of early Dinosauriformes and early archosaur outgroups (Ezcurra 2006; Irmis *et al.* 2007*a*; Brusatte *et al.* 2010; Nesbitt 2011), agree on the non-dinosaurian affinities of Silesauridae (see 'Systematics and evolution').

Here, we synthesize the current understanding of non-dinosaurian dinosauromorphs. We summarize the definitions and diagnoses of recognized clades, synthesize the geographical and chronological distribution of known taxa, and provide an overview of their osteology. Furthermore, we highlight current consensus and controversies on their taxonomy and evolutionary history, and discuss aspects of their palaeobiology. Finally, we suggest some directions for future work on those animals.

Definitions and diagnoses

Beyond the characters of the pelvis and hindlimb, diagnostic traits for Dinosauromorpha and Dinosauriformes are hard to establish because these are the only anatomical parts well-known for lagerpetids, the single putative group of non-dinosauriform dinosauromorphs. However, potentially diagnostic traits from other parts of the skeleton are summarized in Novas (1996) and Nesbitt (2011). Considering that the monophyletic status of Silesauridae *sensu lato* is uncertain (see 'Systematics and evolution'), it is possible that some of the diagnostic traits listed below may diagnose more inclusive clades. Indeed, diagnoses are particularly volatile in the context of shifting phylogenetic hypotheses such as those for early dinosauromorphs, and the discovery of new forms may easily modify the inclusivity (thus the characteristic anatomical traits) of defined clades.

Dinosauromorpha Benton 1985

Node-based definition (Sereno 1991): *Lagerpeton chanarensis*, *Marasuchus lilloensis*, *Pseudolagosuchus major*, Dinosauria (incl. Aves), and all descendants of their most recent common ancestor.

Comments. The name Dinosauromorpha was coined by Benton (1985) to include dinosaurs, ornithosuchids and birds, but was first phylogenetically defined by Sereno (1991; see above) in a manner that matches current orthodoxy on the inclusivity of the group, which excludes ornithosuchids. Dinosauromorph synapomorphies (Novas 1996; Nesbitt 2011) include ventrally descended facies articularis antitrochanterica on the femoral head, straight cnemial crest, astragalus with acute craniomedial corner, reduced calcaneum, reduced articular facet for metatarsal V on the lateral surface of distal tarsal 4, elongated metatarsus with reduced metatarsals I and V, and metatarsal V with proximal portion not 'hooked' and with articular surface for distal tarsal 4 subparallel to the shaft axis. However, not all early Dinosauromorpha share these diagnostic traits.

Lagerpetidae Arcucci 1986

Stem-based definition (Nesbitt *et al.* 2009): all taxa more closely related to *Lagerpeton chanarensis* Romer 1972a than to *Alligator mississippiensis* Daudin 1801, *Eudimorphodon ranzii* Zambelli 1973, *Marasuchus lilloensis* Sereno & Arcucci 1994a, *Silesaurus opolensis* Dzik 2003, *Triceratops horridus* Marsh 1889, *Saltasaurus loricatus* Bonaparte & Powell 1980 and *Passer domesticus* Linnaeus 1758.

Comments. Lagerpetidae was proposed as Lagerpetonidae by Arcucci (1986) to include only *Lagerpeton chanarensis*, and was first phylogenetically defined by Nesbitt *et al.* (2009; see above). According to the ICZN (1999) rules, the name Lagerpetonidae had to be replaced because it was formed (before 1999) based on an incorrect identification of the type–genus stem, which is *Lagerpet-* instead of *Lagerpeton-*. Nesbitt *et al.* (2009) diagnosed lagerpetids based on the following unambiguous synapomorphies: femoral head hook-shaped, with a ventrolateral emargination and enlarged medial tuber, distal femur with enlarged crista tibiofibularis and craniomedial corner forming an angle near or less than 90°, and astragalus with a caudally placed ascending process. Further potential synapomorphies according to Nesbitt (2011) include an acetabular antitrochanter on the ilium, proximal femur with flat craniolateral face, astragalus with 'posterior ascending process', no calcaneal tuber, and metatarsal IV longer than metatarsal III.

Dinosauriformes Novas 1992a

Node-based definition (modified from Novas 1992b): the most recent common ancestor of *Marasuchus lilloensis*, Dinosauria, and all taxa stemming from it.

Comments. Novas (1992a) created the name Dinosauriformes for the minimal clade uniting *Lagosuchus* and dinosaurs. His latter (Novas 1992b) node-based phylogenetic definition fits the inclusivity of the group as currently understood, and is slightly modified (see above) to fit the updated taxonomy of Sereno and Arcucci (1994b). Synapomorphic traits of Dinosauriformes (Novas 1996; Ezcurra 2006; Nesbitt 2011) include pubis longer than ischium and with articular surfaces for ilium and ischium separated by a groove or gap; ischium with articular surfaces for ilium and pubis separated by a fossa, reduced antitrochanter and reduced pubic contact; proximal femur with trochanteric shelf and protruding lesser trochanter (forming a steep proximal margin to the shaft), also seen in large specimens of the Lagerpetidae *Dromomeron gregorii* (Nesbitt *et al.* 2009); distal tibia with a proximodistally oriented lateral groove; and astragalus with cranial ascending process. As with dinosauromorphs, not all early Dinosauriformes share these diagnostic traits.

Silesauridae Langer et al. 2010

Stem-based definitions: all archosaurs closer to *Silesaurus opolensis* than to *Heterodontosaurus tucki* and *Marasuchus lilloensis* (Langer *et al.* 2010); or the most inclusive clade containing *Silesaurus opolensis* Dzik 2003 but not *Passer domesticus* Linnaeus 1758, *Triceratops horridus* (Marsh 1889) and *Alligator mississippiensis* Daudin 1801 (Nesbitt *et al.* 2010).

Comments. Silesauridae was first named and phylogenetically defined by Langer *et al.* (2010; see above), and independently by Nesbitt *et al.* (2010; see above). The group was first diagnosed by Nesbitt *et al.* (2010) based on the following unique combination of character states: rugose ridge on the rostrolateral edges of the supraoccipital, ilium with a straight ventral margin of the acetabulum, and femoral head with ventral notch and straight transverse groove on the proximal surface. Other potential synapomorphies according to Nesbitt (2011) include exits of the hypoglossal nerve (XII) nearly aligned in a dorsoventral plane, cerebral branches of internal carotid artery on the ventral surface of the braincase, rostral tip of the lower jaw edentulous and tapering to a sharp point, teeth fused to the bone of attachment and with subtriangular and

apicobasally short crowns, cervical centra 3–5 longer than mid-trunk centra, sacral ribs shared between two sacral vertebrae, humerus with proximal articular surface continuous to the deltopectoral crest, femur with straight medial articularfacet of the proximal portion and distal condyles of the divided caudally between one-quarter and one-third the shaft length, and pedal unguals dorsolaterally compressed.

Fossil record

Geographical and chronological distribution

Taken as a whole, Triassic non-dinosaur dinosauromorphs had a widespread distribution, which is expected given the configuration of the continents into one landmass, Pangaea (Fig. 2), but they are not completely cosmopolitan. Prior to 2003, all recognized specimens were known from the Middle Triassic Chañares Formation in northwestern Argentina. Following the description of *Silesaurus opolensis*, there has been an explosion in the number of non-dinosaurian dinosauromorphs from Middle and Late Triassic localities (Table 1), as well as older footprint records (Brusatte *et al.* 2011). Middle Triassic dinosauromorph occurrences are restricted to southern Pangaea, with possibly Anisian occurrences of silesaurids from Tanzania and Zambia (Nesbitt *et al.* 2010; Peecook *et al.* 2011). The only Ladinian occurrence is the aforementioned Los Chañares assemblage, which includes *Lagerpeton chanarensis*, *Marasuchus*

lilloensis and probable silesaurids, that is, *Pseudolagosuchus major* and *Lewisuchus admixtus* (Romer 1971; Bonaparte 1975; Arcucci 1986, 1987; Sereno & Arcucci 1994*a*, *b*; Nesbitt *et al.* 2010). As of now, there are no clear body fossils of dinosauromorphs from the Middle Triassic of north Pangaea.

Among Late Triassic occurrences, the only clear Carnian records are two unpublished isolated specimens (a lagerpetid and a silesaurid) from the lower part of the Ischigualasto Formation of NW Argentina (R. N. Martinez, unpublished data). This is latest Carnian in age, although the formation as a whole may span to the earliest Norian (Rogers *et al.* 1993; Furin *et al.* 2006; Martinez *et al.* 2011). *Silesaurus opolensis* from Poland was initially considered late Carnian in age based on vertebrate biostratigraphy (Dzik 2003), but there is equal if not stronger evidence for an early Norian age (see discussion in Irmis 2011, p. 409), and the same is true for a newly reported 'Carnian' Polish site preserving isolated remains of a silesaurid (Sulej *et al.* 2011). Similarly, a Carnian–Norian age has been attributed to the Lossiemouth Sandstone Formation in Scotland (Benton & Walker 2011), which yielded *Saltopus elginensis*, but this relies on a poorly constrained tetrapod-based transcontinental correlation. Kammerer *et al.* (2012) suggested a broadly late Carnian–Norian age for the Moroccan silesaurid *Diodorus scytobrachion* from the Timezgadiouine Formation in the Argana Basin. Olsen *et al.* (2000, 2003) used convincing cyclostratigraphic and tectonostratigraphic
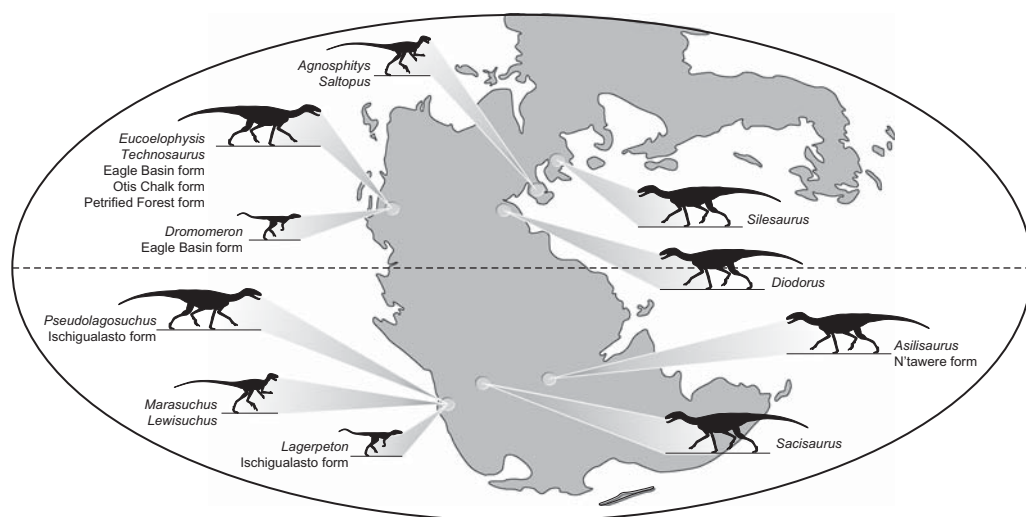
Fig. 2. Distribution of all Triassic deposits with non-dinosaur dinosauromorph records on a Late Triassic palaeomap redrawn from Blakey (2006). Generalized black silhouettes of 'lagerpetids' (small biped), 'silesaurids' (quadruped) and other early dinosauromorphs, adapted from various sources and not at the same scale.

Table 1. *Summary of dinosauromorph taxa*

Taxa	Occurrence	Age	Material
DINOSAUROMORPHA Benton (1985)			
LAGERPETIDAE Arcucci (1986)			
Dromomeron gregorii Irmis *et al.* 2007*a*, b	Colorado City Fm., Dockum Grp./Texas, USA	Late Triassic: middle Norian	Hindlimb elements
Dromomeron romeri Nesbitt *et al.* 2009	Petrified Forest Mb., Chinle Fm./New Mexico, USA	Late Triassic: late Carnian– early Norian	Hindlimb
Lagerpeton chanarensis Romer 1971	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Posterior presacral, sacral and anterior caudal vertebrae, pelvic girdle, and articulated hindlimb
'Eagle Basin form' Small 2009	Chinle Fm./Colorado, USA	Late Triassic: Norian– Rhaetian	Femora
'Ischigualasto form' Martinez unpublished data	Ischigualasto Fm./San Juan, Argentina	Late Triassic: late Carnian	Femur
DINOSAURIFORMES Novas 1992			
Lewisuchus admixtus Romer 1972*a*	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Partial skull, presacral vertebrae, scapulacoracoid, humerus and tibia
Marasuchus lilloensis (Romer 1972*b*, gen. Sereno et Arcucci, 1993)	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Nearly complete skeleton lacking some cranial and pectoral elements
Saltopus elginensis Huene 1910	Lossismouth Sandstone Fm./Morayshire, Scotland	Late Triassic: late Carnian	Impression of an articulated skeleton with presacral, sacral and caudal vertebrae, and hindlimbs
SILESAURIDAE Langer *et al.* 2010			
Asilisaurus kongwe Nesbitt *et al.* 2010	Lifua Mb., Manda Beds/Ruvuma, Tanzania	Middle Triassic: late Anisian	Disarticulated elements from all over the skeleton, manus lacking
Diodorus scytobrachion Kammerer *et al.* 2011	Timezgadiouine Fm./ Marrakesh-Tensift-El Haouz, Morocco	Late Triassic: late Carnian	Lower jaw, humerus, and hindlimb elements
Eucoelophysis baldwini Sullivan et Lucas 1999	Petrified Forest Mb., Chinle Fm./New Mexico, USA	Late Triassic: mid Norian	Vertebrae, ilium, possible pubis, and hindlimb elements
Pseudolagosuchus major Arcucci 1987	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Pubis and partial hindlimb (holotype) and various referred specimens
Sacisaurus agudoensis Ferigolo & Langer 2006	Caturrita Fm./Rio Grande do Sul, Brazil	Late Triassic: late Carnian– early Norian	Isolated maxilla, postorbital, partial lower jaws, vertebrae, scapula, and pelvic elements
Silesaurus opolensis Dzik 2003	Drawno Beds, Krasiejów claypit/Opole, Poland	Late Triassic: late Carnian– early Norian	Nearly complete skeleton lacking some cranial elements and manus

(*Continued*)

Table 1. *Continued*

Taxa	Occurrence	Age	Material
Technosaurus smalli Chatterjee 1984	Bull Canyon Fm., Dockum Grp./Texas, United States	Late Triassic: Norian	Premaxilla and dentary with teeth
'Eagle Basin form' Small 2009	Chinle Fm./Colorado, USA	Middle Triassic: Norian–Rhaetian	Ilium and femora
'Petrified Forest form' Parker *et al.* 2006	Petrified Forest Mb., Chinle Fm./Arizona, USA	Late Triassic: Norian	Femur
'Otis Chalk form' Nesbitt *et al.* 2010	Colorado City Fm., Dockum Grp./Texas, USA	Late Triassic: late Carnian–early Norian	Humerus, femur and tibia
'N'tawere form' Peecook *et al.* 2011	N'tawere Fm./Luangwa Valley, Zambia	Middle Triassic: late Anisian	Pelvis
'Ischigualasto form' Martinez unpublished data	Ischigualasto Fm./San Juan, Argentina	Late Triassic: late Carnian	Ilium
PROBLEMATICA			
Agnosphitys cromhallensis Fraser *et al.* 2002	Cromhall Quarry fissure deposits/Avon, England	LateTriassic: Norian–Rhaetian	Ilium (holotype), maxilla, tooth, humerus and astragali
NOMINA DUBIA			
Lagosuchus talampayensis Romer 1971	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Articulated vertebrae and partial appendicular skeleton

evidence to correlate this unit to the Wolfville For-mation in the conjugate Fundy Basin, Nova Scotia. Correlation of the Wolfville Formation to the better studied Newark Basin indicates it is late Carnian in age (Olsen *et al.* 2011). Thus, if these correlations are correct, they would indicate that *Diodorus scytobrachion* is one of the few Carnian non-dinosaurian dinosauromorphs.

Norian records of non-dinosaurian dinosauro-morphs are the most widespread if considered as a whole. However, the only reported Norian lager-petid remains are those of *Dromomeron* spp. from southwestern North America (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009; Small 2009). The real driver of this widespread early dinosauromorph distribution is the Norian record of silesaurids. Apart from *Silesaurus opolensis*, this includes many specimens from throughout southwestern North America (Ezcurra 2006; Parker *et al.* 2006; Nesbitt *et al.* 2007, 2010; Irmis *et al.* 2007*a*) that span the early–middle Norian (Irmis *et al.* 2011), and *Saci-saurus agudoensis* from the likely Norian Caturrita Formation of southern Brazil (Ferigolo & Langer 2007; Langer *et al.* 2007), although the age of this stratigraphic unit is very poorly constrained.

Oldest record

The oldest known body fossils of any dinosauro-morph are silesaurid specimens (Nesbitt *et al.* 2010; Peecook *et al.* 2011), which is surprising because this clade is well-nested within Dino-sauromorpha (Ezcurra 2006; Nesbitt *et al.* 2010; Nesbitt 2011). The records include *Asilisaurus kongwe* from the Lifua Member of the Manda Beds, in the western portion of the Ruhuhu Basin of southwestern Tanzania (Nesbitt *et al.* 2010), and an indeterminate form recovered from the N'ta-were Formation of the Luangwa Basin of Zambia (Peecook *et al.* 2011). Although there are no radioisotopic ages, both the Lifua Member and the N'tawere Formation can be assigned to the late Anisian through vertebrate biostratigraphic cor-relation (cynodont and dicynodont synapsids) with the 'Cynognathus subzone C' of the Karoo Super-group in South Africa (Rubidge 2005). Unfortu-nately, 'Cynognathus subzone C' has also not been radioisotopically dated, and therefore cannot be directly correlated with the marine-defined sta-ges of the Triassic timescale (e.g. Mundil *et al.* 2010), so the exact age of any deposits correlated with that biostratigraphic unit is not clear. In any case, coupled with the record of the earliest pseudosuchians, that is, *Ctenosauriscus koeneni* from the Early Triassic of Germany (Butler *et al.* 2011) and *Xilousuchus sapingensis* from the Early–Middle Triassic of China (Nesbitt *et al.* 2011), and the fact that the oldest pterosaur

records are Late Triassic in age (Barrett *et al.* 2008), these Middle Triassic (?Anisian) silesau-rids indicate the presence of significant ghost line-ages at the base of both Dinosauromorpha and Pterosauromorpha.

The next oldest dinosauromorphs are found in the famous Middle Triassic Chañares Formation of NW Argentina and include *Lagerpeton chan-arensis*, '*Lagosuchus talampayensis*', *Lewisuchus admixtus*, *Marasuchus lilloensis* and *Pseudolago-suchus major*. Like the Lifua Member, the Chañares Formation has never been radioisotopically dated. The best age constraint is an absolute minimum age of *c.* 231 Ma from near the base of the Ischigual-asto Formation (Rogers *et al.* 1993; Furin *et al.* 2006; Martinez *et al.* 2011). This unit overlies the Los Rastros Formation, which itself conformably overlies the Chañares Formation (Rogers *et al.* 2001; Mancuso & Marsicano 2008). Thus, we can at least say that the Los Rastros and Chañares for-mations are older than late Carnian; a Ladinian age for the Los Chañares assemblage is based broadly on vertebrate (mostly cynodonts) biostrati-graphic 'stage of evolution' arguments and long-distance correlations with other south Pangaean Middle Triassic units that also lack precise absolute age constraints.

Nonetheless, despite the age uncertainty, this assemblage is particularly important because it is the oldest to preserve taxa referred to both major early dinosauromorph clades, lagerpetids and sile-saurids, together with *Marasuchus lilloensis*. Fur-thermore, the completeness and early date of discovery of many of these remains mean that this assemblage has been particularly influential in our understanding of dinosauromorph and dinosaur origins (e.g. Romer 1971, 1972*a*; Bonaparte 1975; Arcucci 1986, 1987; Novas 1989, 1992*b*, 1996; Sereno & Arcucci 1994*a*, *b*; Sereno 1997; Benton 1999, 2004, 2006), and has shaped ideas about the transition from synapsid- to archosauromorph-dominated faunas during the early Mesozoic (Romer 1966, 1970; Bakker 1968, 1975; Bonaparte 1982; Charig 1984; Shubin & Sues 1991), as these dinosauromorphs co-existed with a diversity of other archosauriforms such as proterochampsids, doswelliids, *Gracilisuchus* and 'rauisuchians' (e.g. Rogers *et al.* 2001), as well as abundant cynodonts and dicynodonts (e.g. Abdala & Giannini 2000; Rogers *et al.* 2001).

Brusatte *et al.* (2011) recently described foot-prints from the late Early Triassic (Olenekian) of Poland that they assigned to a lagerpetid dinosauro-morph trackmaker. If this is correct, it represents the oldest occurrence of dinosauromorphs; these sequences are well dated by palynomorph and con-chostracan biostratigraphy (Brusatte *et al.* 2011). The footprints show the impressions of digits

I–IV, which gradually increase in size towards digit IV. Although this morphology compares in a general sense with the pes of *Lagerpeton chanarensis*, the only lagerpetid with a well-preserved foot (Sereno & Arcucci 1994*a*), there are some important differences. In *Lagerpeton chanarensis*, digit II is approximately half the length of digits III and IV, which are nearly subequal (Sereno & Arcucci 1994*a*, fig. 5), whereas in the footprints, digit II is approximately three-quarters the size of digit III, and digit III is slightly smaller than digit IV (Brusatte *et al.* 2011, fig. 2). Also, digits II–IV in *Lagerpeton chanarensis* are so much longer than digit I that it is not clear that this digit would consistently make an impression in the substrate, unlike the Polish tracks where digit I is consistently and clearly preserved. These differences do not mean that the Polish trackmaker was not a dinosauromorph, but they do complicate the identification of the animal. Because *Lagerpeton chanarensis* is the only lagerpetid with a well-preserved pes, there is no way to evaluate variation in digit ratios across other taxa (e.g. *Dromomeron* spp.).

Youngest record

Until recently, it was thought that non-dinosaurian dinosauromorphs went extinct around the time the first dinosaurs appeared (e.g. Sereno 1997; Benton 2004). This view changed quickly with the discovery that a minimum of two dinosauromorph lineages outside of Dinosauria persisted well into the Late Triassic, and co-existed with early dinosaurs (Ezcurra 2006; Irmis *et al.* 2007*a*; Nesbitt *et al.* 2007). Because the recognition of this pattern is so recent, we are unlikely to have reached the asymptote of the collector's curve of Late Triassic dinosauromorphs, and this makes it difficult to pinpoint exactly when lagerpetids and silesaurids went extinct. Among published records, the other major difficulty is the poor geochronological constraints for the Late Triassic timescale in general (Mundil *et al.* 2010), and even worse geochronological control for most Late Triassic non-marine vertebrate assemblages (Irmis *et al.* 2010, 2011). This means that relative stratigraphic placement of different late occurrences is often ambiguous at best. Such uncertainty will hopefully be resolved as better radioisotopic age data are brought to bear on the problem (e.g. Irmis *et al.* 2011; Ramezani *et al.* 2011).

The youngest well-dated records of dinosauromorphs are lagerpetid and silesaurid remains from the upper Chinle Formation of the Chama Basin in northern New Mexico, USA (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009). Specimens of the lagerpetid *Dromomeron romeri* and a silesaurid similar to *Eucoelophysis baldwini* from the Hayden Quarry (Irmis *et al.* 2007*a*) are associated with a high-precision U–Pb zircon age of 211.9 ± 0.7 Ma, which represents a maximum age constraint, indicating a late Norian age (Irmis *et al.* 2011). An isolated *Dromomeron* astragalocalcaneum from the stratigraphically slightly higher Snyder Quarry (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009) is therefore the youngest record in this basin, and post-dates the Hayden Quarry by an unknown amount of time. These data demonstrate that dinosaurs and dinosauromorphs co-existed for a minimum of 18 million years (Irmis *et al.* 2011). Lagerpetid and silesaurid specimens from the uppermost Chinle Formation of the Eagle Basin in western Colorado (Small 2009) could be younger than the Chama Basin records if regional lithostratigraphic correlations are correct (e.g. Dubiel 1992, 1994), but these units cannot easily be traced because of discontinuities in outcrops. Therefore, placement of the Eagle Basin records as the youngest non-dinosaurian dinosauromorph occurrences awaits better geochronological control. In addition, if its phylogenetic position and geological age were better constrained, *Agnosphitys cromhallensis* from the Norian–Rhaetian fissure deposits of Avon (Fraser *et al.* 2002) could also represent the youngest record of a non-dinosaur dinosauromorph. Alternatively, this taxon has been considered either a theropod (Yates 2007) or a sauropodomorph (Ezcurra 2010) dinosaur. It would be tempting to conclude that lagerpetids and/or silesaurids did or did not persist until the Triassic–Jurassic boundary, but their record is simply too poorly sampled to make a conclusion either way.

Anatomy

Non-dinosaurian dinosauromorph anatomy has been described, figured and/or commented on by Arcucci (1986, 1987, 1997, 1998, 2005), Benton and Walker (2011), Bittencourt *et al.* (2011), Bonaparte (1975), Chatterjee (1984), Dzik (2003), Dzik and Sulej (2007), Ezcurra (2006), Ferigolo and Langer (2007), Fraser *et al.* (2002), Irmis *et al.* (2007*a*, *b*), Kammerer *et al.* (2012), Nesbitt (2011), Nesbitt *et al.* (2007, 2009, 2010), Novas (1989, 1996), Parker *et al.* (2006), Peecook *et al.* (2011), Romer (1971, 1972*a*, *b*), Sereno and Arcucci (1994*a*, *b*), Small (2009), Sulej *et al.* (2011) and Sullivan and Lucas (1999). Unless explicitly mentioned, these primary descriptions and revisions form the basis for the osteological review provided below, but they are not quoted to avoid tedious repetition.

The skull is poorly known for most non-dinosaurian dinosauromorphs. *Silesaurus opolensis* is by far the best represented in this respect

(Fig. 3b), with few unknown elements (prefrontal, parts of the palate). Unfortunately, this late-surviving taxon is unlikely to represent the general skull shape of all early dinosauromorphs given its derived position within Silesauridae and divergent morphology, with possible herbivorous/omnivorous adaptations. The pre-orbital portion of the skull of *Silesaurus opolensis* is rather short, and the mandibular glenoid fossa is displaced ventrally relative to the tooth line (Fig. 3b), as in herbivorous dinosaurs. *Asilisaurus kongwe* has a long lacrimal forming the entire antorbital bar and a very broad prefrontal. The jugal of *Silesaurus opolensis* bears a robust lateral ridge extending parallel
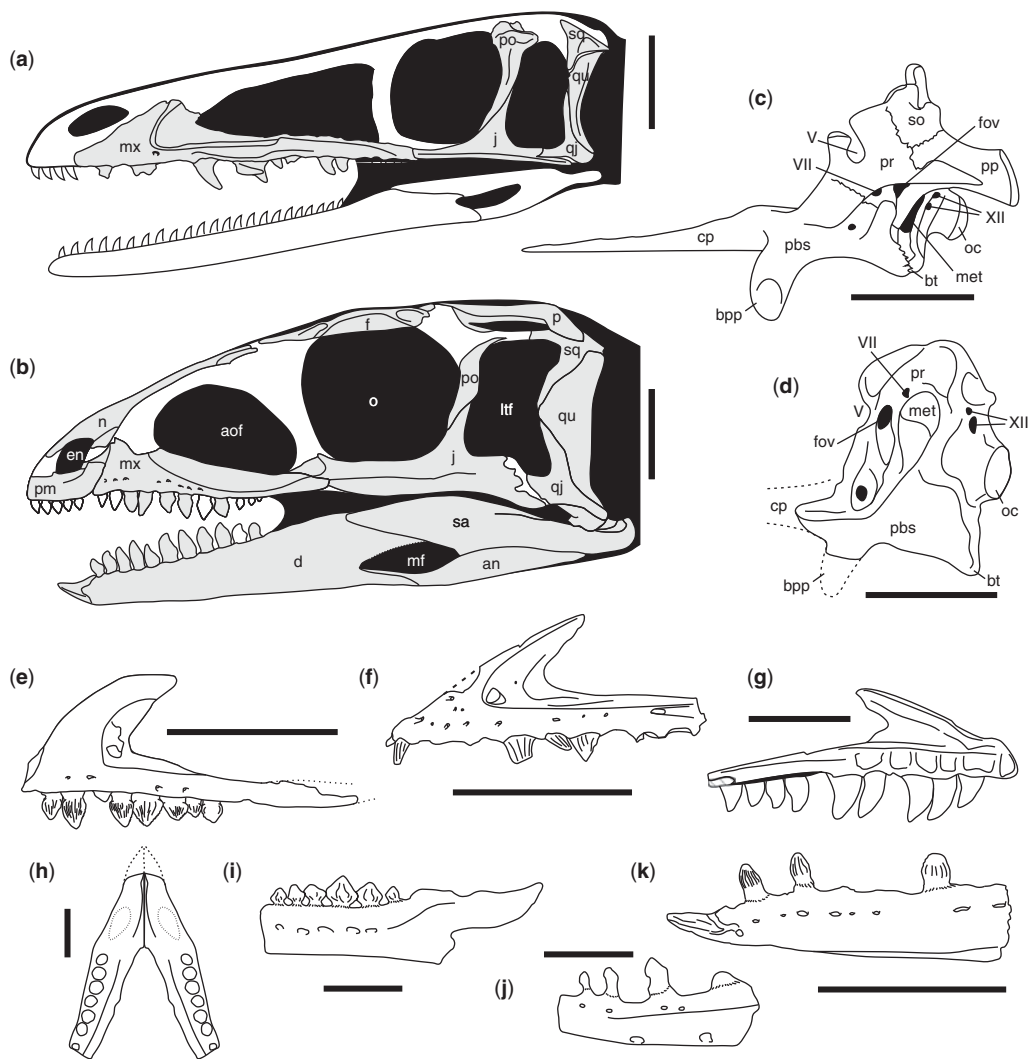
Fig. 3. Skull remains of non-dinosaur dinosauromorphs: (**a**) skull reconstruction of *Lewisuchus admixtus*; (**b**) skull reconstruction of *Silesaurus opolensis* (modified from Dzik 2003; Dzik & Sulej 2007); (**c**) braincase reconstruction of *Silesaurus opolensis* (from Dzik 2003); (**d**) right side (reversed) of the braincase of *Marasuchus lilloensis* (from Sereno & Arcucci 1994*b*); (**e**) right (reversed) maxilla of *Sacisaurus agudoensis* (MCN PV10041); (**f**) left maxilla of *Agnosphitys cromhallensis* (modified from Fraser *et al.* 2002); (**g**) left maxilla of *Marasuchus lilloensis* (PVL 3870) in medial view; (**h**) reconstruction of the cranial part of the lower jaw of *Asilisaurus kongwe* (modified from Nesbitt *et al.* 2010) in dorsal view; (**i**) left partial dentary of *Technosaurus smalli* (modified from Nesbitt *et al.* 2007); (**j**) right (reversed) partial dentary of *Diodorus scytobrachion* (modified from Kammerer *et al.* 2012); (**k**) left partial lower jaw of *Sacisaurus agudoensis* (MCN PV10050). (a–f, i–k) lateral view. Scale bars, 2 cm (a–c, e–f, i–k) and 5 mm (d, g, h).

to its ventral margin and an unusually broad caudal ramus, which resembles that of some early ornithischians (Haubold 1991; Pol *et al.* 2011), but is also seen in other early archosaurs. In *Silesaurus opolensis* and *Lewisuchus admixtus*, both the quadratojugal and the squamosal overlap the quadrate body laterally, forming the caudal margin of the dorsoventrally elongated lower temporal fenestra. For the latter taxon, if the referred temporal area and maxilla are assembled together (Fig. 3a), the result is an unusually long skull, twice the length of the humerus and longer than the referred tibia.

Among the upper tooth-bearing elements (Figs 3c–k), the premaxillae of *Silesaurus opolensis* and *Technosaurus smalli* bear five alveoli. The teeth are absent in the caudal portion of the maxillae in *Silesaurus opolensis* and *Sacisaurus agudoensis*, whereas they continue to the caudal border of maxillae attributed to *Marasuchus lilloensis*, *Lewisuchus admixtus* and *Agnosphitys cromhallensis*. The dorsal rami of the maxilla is caudally inclined in the latter three taxa, but more vertical in *Silesaurus opolensis* and *Sacisaurus agudoensis*. The antorbital fossa excavates both the dorsal and caudal rami of the maxilla, diminishing caudally along the later ramus in most forms, but not in *Silesaurus opolensis*, where it has a convex ventral margin. Pterygoid teeth have been recognized in *Lewisuchus admixtus*.

Braincase material is preserved for *Marasuchus lilloensis*, *Asilisaurus kongwe*, *Silesaurus opolensis* and *Lewisuchus admixtus*. Their lateral surface is formed mainly by the prootic and the parabasisphenoid. The lateral surface of the prootic preserves rostral and caudal recesses that respectively harbour the facial nerve (VII) foramen and the fenestra ovalis. In *Silesaurus opolensis* and *Lewisuchus admixtus*, the metotic strut extends from the ventral surface of the exoccipital to the basitubera, and forms the caudal wall of the metotic fenestra. The holotype of *Lewisuchus admixtus* has a short, rod-like right stapes associated to the stapedial groove into the columellar recess. At least in *Silesaurus opolensis* and *Lewisuchus admixtus*, the hypoglossal (XII) foramina lie subvertically on the exoccipital surface, rostrally bound by the metotic strut and caudally by the basioccipital condyle. Early dinosauromorphs are convergent with suchians in possessing an auricular (=floccular) recess encased by the prootic and supraoccipital/epiotic (Nesbitt 2011). The recess is present externally as a lobe-like projection of the braincase, dorsal to the trigeminal foramen. The ventral surface of the parabasisphenoid of *Silesaurus opolensis* is pierced by the lateral foramina for the internal carotid artery, cranially to the parabasisphenoid recess. In *Marasuchus lilloensis* and *Lewisuchus admixtus* an equivalent opening is located more

dorsally on the cranial recess of the prootic. The occipital region is better exposed in *Silesaurus opolensis* and *Lewisuchus admixtus*; their similarities include the participation of the supraoccipital in the foramen magnum (not necessarily exclusive among archosaurs), the presence of a rugose crest on the edge between that bone and the paraoccipital process (suggested as a shared apomorphy by Nesbitt *et al.* 2010), and exoccipitals meeting at the midline (also in *Marasuchus lilloensis*). The paraoccipital processes of *Lewisuchus admixtus* have a projected ventrodistal corner, and are slightly ventrolaterally directed, rather than completely laterally as in *Silesaurus opolensis*.

Dentaries are known for *Silesaurus opolensis*, *Diodorus scytobrachion*, *Sacisaurus agudoensis*, *Asilisaurus kongwe*, the Hayden Quarry taxon and *Technosaurus smalli*, whereas there is no clear evidence that the lower jaw (the post-dentary part of which is apparently lost) attributed to *Lewisuchus admixtus* belongs to that taxon. The most peculiar feature of the silesaurid dentary is its tapering, toothless tip, as present in *Silesaurus opolensis*, *Asilisaurus kongwe* and *Sacisaurus agudoensis*. This is depressed relative to the rest of the mandible and bears longitudinal striations and/or small foramina, suggesting that it was covered with a keratinous beak. Its correspondence to the predentary of ornithischians was suggested by Ferigolo and Langer (2007), but it differs from that bone because it is paired, and not clearly separated from the dentary.

Typically carnivorous-like teeth (elongated, mediolaterally compressed, recurved, serrated) occur in maxillae attributed to *Lewisuchus admixtus* (nine spatulate serrations per millimetre), *Marasuchus lilloensis* and *Agnosphitys cromhallensis*. Yet, the more caudally positioned teeth of *Marasuchus lilloensis* are somewhat leaf-shaped. Dentary teeth of *Asilisaurus kongwe* are closely packed and peg-like, but the occolusal tip of the crowns bear tiny serrations on their carinae. In contrast, upper and lower jaw teeth of *Silesaurus opolensis* and *Sacisaurus agudoensis*, as well as those of the dentaries of *Technosaurus smalli*, *Diodorus scytobrachion* and the Hayden Quarry taxon, are larger and have strongly labiolingualy flattened crowns. The former two taxa have a reduced number of teeth (12–15 in the dentary and *c.* 10 in the maxilla), which diminish in size both rostrally and caudally; this is also evident in *Diodorus scytobrachion* and *Technosaurus smalli*. The base of the crowns is mesiodistally expanded, often overlapping the adjacent teeth, and labiolingually expanded, especially on the medial side, where a cingulum may occur (e.g. *Sacisaurus agudoensis*). The crowns are generally leaf-shaped rostrally and more subtriangular in the caudal part of the series, and frequently

bear longitudinal striations. Ornamentation on the carinae ranges from large denticles, subparallel to the long axis of the tooth, to smaller elements, perpendicular to the margin of the crown. Nesbitt *et al.* (2010; see also Kammerer *et al.* 2012) suggested that most silesaurids, including *Silesaurus opolensis*, *Diodorus scytobrachion*, *Asilisaurus kongwe*, *Sacisaurus agudoensis* and the Hayden Quarry taxon, have socketed teeth ankylosed to the bone of attachment (i.e. ankylosed thecodonty of Edmund 1969 or ankylothecodonty of Chatterjee 1974). Those taxa have a bulbous 'collar' of a distinct kind of bony material connecting the teeth to the alveolar wall, frequently with resorption pits on the lingual face of the alveolus. A similar macroscopic pattern is seen in the referred maxilla of *Agnosphitys cromhallensis*, but not in *Lewisuchus*

admixtus and *Marasuchus lilloensis*, the latter of which has square-shaped lingual structures that resemble interdental plates.

The vertebral column is relatively well known only in *Marasuchus lilloensis* and *Silesaurus opolensis*, but other early dinosauromorphs also have associated vertebrae (Fig. 4). The dorsal margin of the axial neural spine of *Lewisuchus admixtus* is convex along its extension, but straight in both *Marasuchus lilloensis* and *Silesaurus opolensis*. The neck is sigmoidal, as inferred from articulated specimens and the parallelogram-shaped centra of *Silesaurus opolensis* and *Marasuchus lilloensis*. Unambiguous silesaurids (Table 1) and *Lewisuchus admixtus* also share elongated cervical centra 3–5 relative to mid-trunk (5–10) elements, and the cervical neural arches are notably high in early
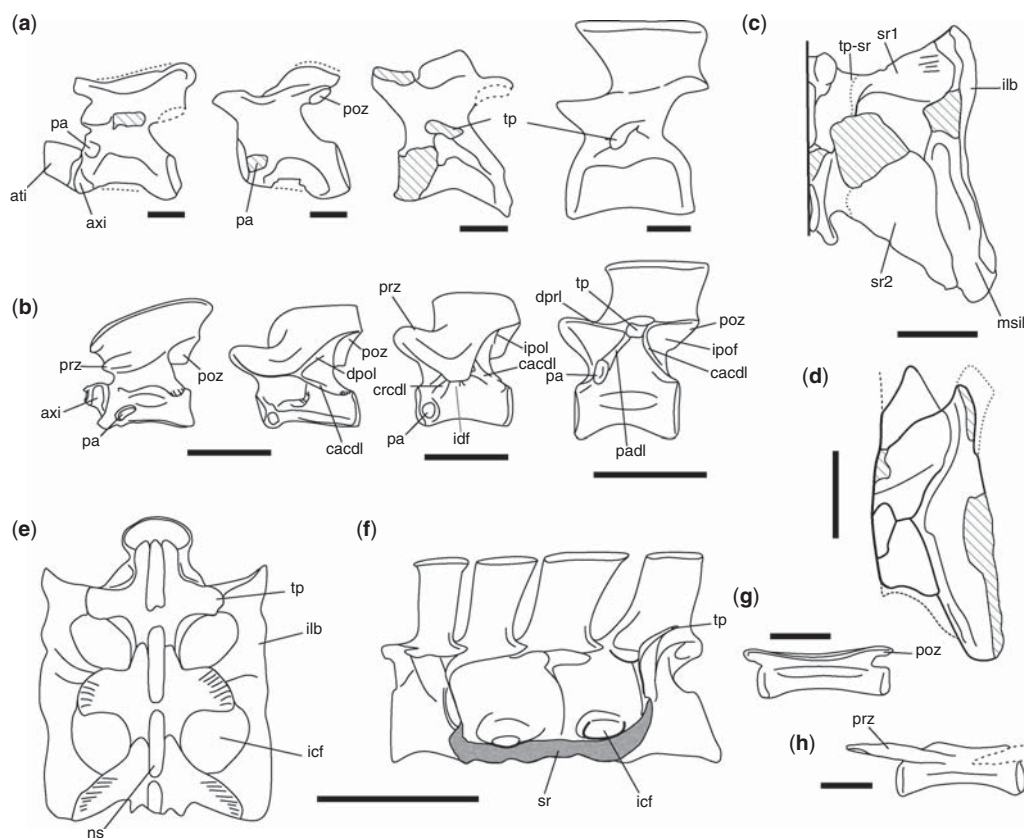
Fig. 4. Vertebral remains of non-dinosaur dinosauromorphs: (**a**) atlas-axis, 3rd and 7th cervical, and 7th trunk (16th presacral) vertebrae of *Marasuchus lilloensis* (modified from Sereno & Arcucci 1994*b*); (**b**) reconstruction of axis, 3rd and 7th cervical, and 6th trunk vertebrae of *Silesaurus opolensis* (modified from Piechowski & Dzik 2010); (**c**) sacrum of *Lagerpeton chanarensis* (PVL 4619); (**d**) sacrum of *M. lilloensis* (modified from Sereno & Arcucci 1994*b*); (**e, f**) Reconstruction of the sacrum of *S. opolensis* (modified from Dzik & Sulej 2007); (**g**) middle caudal vertebra of *M. lilloensis* (modified from Sereno & Arcucci 1994*b*); (**h**) mid-distal caudal vertebra of *S. opolensis* (ZPAL unnumbered). (a, b, f–h) lateral and (c–e) dorsal views. Scale bars, 1 cm (c, h), 2 cm (a, b) and 5 cm (d–g).

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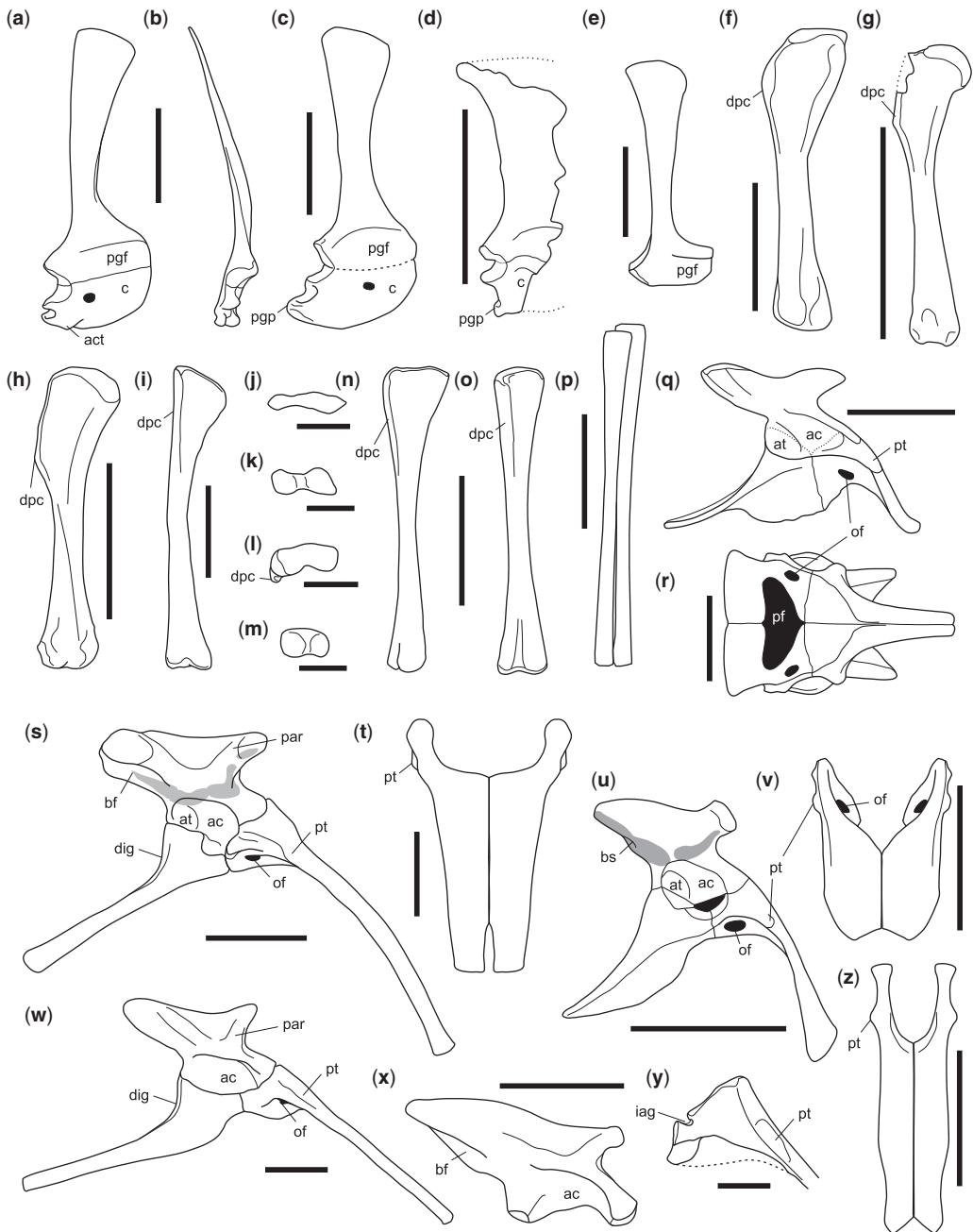
Fig. 5. Pectoral and pelvic girdle and forelimb remains of non-dinosaur dinosauromorphs: (**a**, **b**) pectoral girdle reconstruction of *Silesaurus opolensis* (modified from Dzik 2003); (**c**) right pectoral girdle of *Lewisuchus admixtus* (modified from Remes 2007); (**d**) left (reversed) partial pectoral girdle of *Marasuchus lilloensis* (PVL 3871); (**e**) right scapula of *Sacisaurus agudoensis* (MCN PV10033); (**f**) left (reversed) humerus of *L. admixtus* (modified from Remes 2007); (**g**) left (reversed) humerus of *M. lilloensis* (PVL 3871); (**h**) right humerus of *Agnosphitys cromhallensis* (modified from Fraser *et al.* 2002); (**i**–**k**) right humerus of *Diodorus scytobrachion* (modified from Kammerer *et al.* 2012); (**l**–**o**) right humerus of *S. opolensis* (modified from Dzik 2003); (**p**) right radius and ulna of *S. opolensis* (modified from Dzik 2003); (**q**, **r**) Pelvic girdle of *Lagerpeton chanarensis* (modified from Sereno & Arcucci 1994*a*); (**s**) pelvis reconstruction of *S. opolensis* (modified from Dzik 2003); (**t**) paired pubes of *S. opolensis* (modified from Dzik 2003);

dinosauromorphs. In general, cervical and trunk centra are laterally excavated in early dinosauromorphs by shallow fossae, but these are not distinctly rimmed, so they cannot be considered pneumatic pleurocoels. The cervical neural spines of *Lewisuchus admixtus* are possibly covered with a single row of osteoderms (Romer 1972*a*; Arcucci 1997; Bittencourt *et al.* 2011), although this would be unique among early dinosauromorphs and is not universally accepted (Nesbitt *et al.* 2010). Silesaurids share a conspicuous pattern of vertebrate lamination (in both cervical and trunk series), similar to early dinosaurs and some pseudosuchians (Butler *et al.* 2012). By contrast, with the possible exceptions of *Silesaurus opolensis* (ZPAL AbIII 411/7) and *Asilisaurus kongwe*, early dinosauromorphs differs from dinosaurs by lacking epipophyses on the postzygapophyses. The parapophyses shift to the neural arch by the sixth trunk vertebra in *Silesaurus opolensis*, where they project laterally on rod-like stalks. At least silesaurids (e.g. *Silesaurus opolensis*, *Asilisaurus kongwe*) have hyposphene–hypantrum intervertebral articulations in the trunk vertebrae, and gastralia have also been recorded in *Silesaurus opolensis*. The neural spines of *Marasuchus lilloensis* and *Lewisuchus admixtus* trunk vertebrae have their cranial margins inclined forward. In *Lagerpeton charanesis*, both the cranial and caudal margins were reconstructed in that way (Sereno & Arcucci 1994*a*). In *Marasuchus lilloensis* and *Lewisuchus admixtus*, the neural spines of the mid-trunk vertebrae are lateromedially expanded towards the apex.

Early dinosauromorphs usually have two sacral vertebrae, which correspond to the primordial elements of early archosauriforms. An exception is *Silesaurus opolensis*, which possesses a three-vertebra sacrum, and Nesbitt (2011) suggested that the additional vertebra was inserted between the two primordial sacrals. Rib attachments are shared between adjacent sacral centra in silesaurids *sensu stricto* (Table 1). The proximal caudal vertebrae of *Marasuchus lilloensis* have laterally excavated centra with a ventral longitudinal sulcus, and low and caudally displaced neural spines. In *Silesaurus opolensis*, the proximal caudal vertebrae are more similar to those of dinosaurs, because the neural spines are plate-like and the transverse processes are buttressed by subtle infradiapophyseal laminae.

Some isolated mid to distal tail vertebrae of *Silesaurus opolensis* have elongated zygapophyses, which overlap about a quarter of the adjacent centrum length. This is frequently cited as a synapomorphy of theropod dinosaurs and is absent in *Marasuchus lilloensis*.

The pectoral girdle and forelimbs are poorly known for early dinosauromorphs, with almost no records of manual elements (Fig. 5). This hampers defining the plesiomorphic condition for the dinosaur manus, the anatomy of which varies greatly and is important for evolutionary studies of the group. Confirmed scapulocoracoid remains are known for *Asilisaurus kongwe*, *Saltopus elginensis*, *Silesaurus opolensis*, *Lewisuchus admixtus* and *Sacisaurus agudoensis*. These taxa share an elongated and distally expanding scapular blade, whereas the scapula referred to the holotype of *Marasuchus lilloensis* (Fig. 5d; but see Remes 2007) has a significantly shorter blade. The scapula of *Silesaurus opolensis*, *Asilisaurus kongwe* and *Lewisuchus admixtus* bears a sharp ridge forming the dorsal margin of the 'preglenoid fossa' (Madsen & Welles 2000). These taxa also share a complex subglenoid area, with a well-developed 'acrocoracoid tuberosity' for the origin of Mm. coracobrachialis and biceps (Langer *et al.* 2011). This connects to a caudomedially curved ridge that forms an elongated postglenoid process in *Asilisaurus kongwe* and *Lewisuchus admixtus*. The shaft of the humerus of *Silesaurus opolensis* and *Diodorus scytobrachion* is nearly straight, but medially concave. Their deltopectoral crest is very poorly developed, but extends for about one-third the length of the humerus, similar to dinosaurs. The crest is more expanded in *Lewisuchus admixtus*, *Asilisaurus kongwe* and *Marasuchus lilloensis*, with its apex placed more distally in the latter (but see Remes 2007), more proximally in *Asilisaurus kongwe* (as in *Silesaurus opolensis* and *Diodorus scytobrachion*) and midway along its length in *Lewisuchus admixtus*. The radius and ulna of *Silesaurus opolensis* (Fig. 5p), *Saltopus elginensis* and *Asilisaurus kongwe* are nearly featureless tubular elements, with a severely reduced olecranon process in the ulna. In *Silesaurus opolensis*, the pectoral epipodium is longer than the humerus, as in *Scleromochlus taylori* and pterosaurs (Benton 1999). This condition is uncommon for other dinosauromorphs, except in some

Fig. 5. (*Continued*) (**u**) pelvic girdle of *M. lilloensis* (modified from Sereno & Arcucci 1994*b*); (**v**) paired pubes of *M. lilloensis* (modified from Sereno & Arcucci 1994*b*); (**w**) pelvis reconstruction of *S. agudoensis*; (**x**) left (reversed) ilium of *A. cromhallensis* (modified from Fraser *et al.* 2002); (**y**) proximal right pubis of *Eucoelophysis baldwini* (modified from Sullivan & Lucas 1999); (**z**) paired pubes of *Pseudolagosuchus major* (PVL 4629). (a, c–e, q, s, u, w–y) lateral, (b) caudal, (f–i, n, p, t, v, z) cranial, (j, l) proximal, (k, m) distal, (o) medial and (r) ventral views. Scale bars, 1 cm in (j, k), 2 cm in (c–i, l, m, q, r, u–y) and 5 cm in (a, b, n–p, s, t, z).

theropods and quadrupedal ornithischians (e.g. Carpenter 2002; Horner *et al.* 2004). The pectoral elements referred to the holotype of *Marasuchus lilloensis* (but see Remes 2007) also include relatively long, tubular radius and ulna (*c.* 80–90% of the humeral length), but this contrasts with the proportionally much shorter same elements in the holotypes of '*Lagosuchus talampayensis*' and *Saltopus elginensis.* In the former case, this might point to the non-dinosauromorph affinity of those elements, which are preserved separately from the rest of the skeleton (Sereno & Arcucci 1994*b*) in a slab that also contains other archosauriforms (e.g. the proterochampsid *Tropidosuchus*) to which they might belong (M. Ezcurra, pers. comm.). *Silesaurus opolensis* and *Saltopus elginensis* are the only early dinosauromorphs with preserved carpal elements, and the latter is the only taxon with a partially preserved manus. This includes subequal metacarpals I–IV and a smaller and divergent metacarpal V.

Partial to completely articulated pelvic girdles (Fig 5q–z) are known for nearly all early dinosauromorphs. In *Lagerpeton chanarensis*, the acetabulum is completely closed and the ventral margin of the ilium is markedly convex. The acetabulum of *Marasuchus lilloensis* and *Silesaurus opolensis* is also closed, but there may be a small gap present in the contact of the three pelvic bones. The ventrally concave acetabular wall of *Agnosphitys cromhallensis* (Fig. 5x) is most similar to that of early dinosaurs. The pelves of all early dinosauromorphs have a well-developed antitrochanter (Novas 1996; Fraser *et al.* 2002). In *Lagerpeton chanarensis*, this is restricted to the ischium, whereas the antitrochanter extends onto the caudal portion of the ilium among Dinosauriformes. The ilia of early dinosauromorphs share a short preacetabular ala that does not extend cranially to the pubic peduncle. Its lateral surface is crossed by a blunt 'preacetabular ridge' (Langer 2003), which extends from the supra-acetabular crest and forms a well-developed 'preacetabular fossa' (Hutchinson 2001). The dorsal margin of the ilia of *Silesaurus opolensis*, *Sacisaurus agudoensis* and the Eagle Basin silesaurid has a concave saddle-like dorsal profile (Small 2009), but this may be enhanced by the loss of the fragile dorsal iliac lamina. The postacetabular ala is much longer, and bears a distinct lateral fossa ('brevis fossa') for the origin of M. caudofemoralis brevis in *Silesaurus opolensis*, *Agnosphitys cromhallensis*, *Sacisaurus agudoensis* and the N'twere silesaurid. This is absent in *Lagerpeton chanarensis*, *Asilisaurus kongwe* and *Marasuchus lilloensis*, but a faint shelf forms the dorsal margin of M. caudofemoralis brevis origin in the latter taxon.

Like all ornithodirans, the dinosauromorph pubis is significantly longer than the ischium. Among Dinosauriformes, especially silesaurids, the pubis is even more elongate compared to that of *Lagerpeton chanarensis*. The shape of the pubic shaft varies greatly among early dinosauromorphs; it is plate-like in *Lagerpeton chanarensis* and *Marasuchus lilloensis*, and its laterodistal corner is caudally bent in the latter taxon (Sereno & Arcucci 1994*b*). A 'pubic boot' is unknown in early dinosauriforms, although the distal margin of the pubes expands slightly in both *Silesaurus opolensis* and *Pseudolagosuchus major*. The pubic shaft of these two latter taxa is lateromedially compressed, particularly in the distal half, and has a thickened lateral margin. The iliac and ischiadic articulations are continuous in the pubis of *Lagerpeton chanarensis*, but separated by a recess in *Marasuchus lilloensis*. Silesaurids possess an ischio–acetabular groove (Sulivan & Lucas 1999) separating the caudal process of the pubis (Langer 2003) from the iliac and femoral articulations. The ischium of *Lagerpeton chanarensis* meets the pubis at a dorsoventrally extensive articulation, whereas that contact is reduced in dinosauriforms. The ischial shaft is plate-like in *Lagerpeton chanarensis* and *Marasuchus lilloensis*, but rod-like in *Sacisaurus agudoensis*, *Saltopus elginensis*, *Silesaurus opolensis* and *Asilisaurus kongwe*. *Silesaurus opolensis* and *Asilisaurus kongwe* are the only non-dinosaur dinosauromorphs with a slightly expanded distal ischium.

Hindlimb bones, especially the femora and tibiae, are known for nearly all early dinosauromorphs (Fig. 6). The femur is sigmoid in lateral/medial aspects. The head is craniomedially directed, usually forming an angle of *c.* 45° with the long axis of the distal condyles. In lagerpetids (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009), the ventral surface of the head is marked by a distinct emargination that gives the femur a hook-shaped profile. In lateromedial view, the femoral head of silesaurids is medially flattened and possesses a ventral 'notch' at its distal extent. The medial tuber (Novas 1996) occupies most of the caudomedial surface of the femoral head in lagerpetids, but is reduced in *Marasuchus lilloensis*, *Pseudolagosuchus major* and *Asilisaurus kongwe*, and nearly absent in *Silesaurus opolensis*, *Eucoelophysis baldwini*, *Diodorus scytobrachion*, *Sacisaurus agudoensis* and the Hayden Quarry taxon. By contrast, a well-developed, distinctly angular cranial tuber (=anterolateral tuber in Nesbitt 2011) is typical of silesaurids, but more subtle in *Marasuchus lilloensis* and absent in lagerpetids. The femoral head of most silesaurids is subtriangular in proximal view, lacking a well-developed facies articularis antitrochanteica, but bearing a longitudinal groove. A dorsolateral trochanter (Bonaparte *et al.* 1999) is present in *Asilisaurus kongwe*, *Silesaurus opolensis*, *Diodorus scytobrachion*, *Eucoelophysis baldwini* and

Sacisaurus agudoensis, but not in lagerpetids and *Marasuchus lilloensis*. It may also be present in some specimens referred to *Pseudolagosuchus major* (UPLR 053), but is not clearly seen in its holotype. Except for large specimens of *Dromomeron gregorii*, an anterior trochanter (=lesser trochanter of some) is absent in lagerpetids, but occurs in all early dinosauriforms. It is usually a knob or finger-like structure, and it is separated from the femoral shaft by a cleft in *Silesaurus opolensis*, *Sacisaurus agudoensis* and *Eucoelophysis baldwini*. A trochanteric shelf is present in *Marasuchus lilloensis*, *Peudolagosuchus major* (likely in its holotype and more clearly in the referred UPLR 053), *Saltopus elginensis*, *Asilisaurus kongwe*, some specimens of *Silesaurus opolensis* and larger specimens of *Dromomeron gregorii*, but is absent in *Eucoelophysis baldwini*, *Diodorus scytobrachion* and *Sacisaurus agudoensis*; the occurrence of this trait is probably ontogenetically related (Nesbitt *et al.* 2009), but it may have some systematic significance. The femoral ('fourth') trochanter corresponds to a proximodistally elongated structure that is weakly projected in *Eucoelophysis baldwini*, *Diodorus scytobrachion*, *Sacisaurus agudoensis* and some specimens of *Silesaurus opolensis*, but more pronounced in other specimens of the latter taxon, as well as in *Marasuchus lilloensis* and *Lagerpeton chanarensis*. In contrast, this ridge is replaced by a rugose surface in *Dromomeron romeri* (Nesbitt *et al.* 2009). The distal end of the femur of lagerpetids is characterized by a distinct scar for the origin of M. femorotibialis externus, a large lateral condyle that includes an enlarged crista tibiofibularis (Nesbitt *et al.* 2009), and a craniomedial corner that forms a *c.* 90° angle (Fig. 6d, e). Generally, the lateral and medial condyles of dinosauromorph femora are separated by a deep caudal groove, which is proximally expanded in silesaurids.

The tibia of early dinosauromorphs is usually longer than the femur, but the reverse is true in at least *Silesaurus opolensis*. All dinosauromorph tibiae display an expanded proximal articulation that includes a variously developed cnemial crest and broad medial and fibular condyles. On the lateral surface of the tibia, a fibular crest is present in both *Silesaurus opolensis* and *Sacisaurus agudoensis*. A caudal descending process (lateral malleolus) and a proximodistally elongated groove cranial to that structure is absent in lagerpetids, but occurs in all Dinosauriformes. The descending process is usually short, but expands laterally in *Silesaurus opolensis* and *Sacisaurus agudoensis*. The fibula is more slender than the tibia, and articulates distally to both astragalus and calcaneum. In lagerpetids, the astragalocalcaneum is co-ossified. The early dinosauromorph astragalus is subrectangular in distal/proximal views, and slightly overlaps the calcaneum dorsally, especially at the caudal edge. In lagerpetids, it bears a laminar caudal ascending process and an oblique ridge crossing the tibial articular facet. In *Silesaurus opolensis* and *Agnosphitys cromhallensis*, the cranial ascending process of the astragalus corresponds to a wedge-shaped structure that fits on a flat surface cranial to the descending process of the tibia. It is caudally bordered by a broad slot that receives the tibial descending process ('pb' in Fig. 6). Astragali of *Pseudolagosuchus major* and *Asilisaurus kongwe* also bear a wedged ascending process, incompletely preserved in *Pseudolagosuchus major* (Novas 1996), but the caudal slot is reduced. The caudal astragalar groove is present in *Marasuchus lilloensis*, *Asilisaurus kongwe* and *Pseudolagosuchus major*, but not in lagerpetids or *Silesaurus opolensis*. The calcaneum of early dinosauromorphs typically lacks well-developed projections and bears a concave proximal articulation for the fibula. *Marasuchus lilloensis*, *Asilisaurus kongwe* and *Pseudolagosuchus major* depart from this condition, with a protruding calcaneal tuber that bears a convex proximal surface forming a complex fibular articulation. Two distal tarsals, usually recognized as the third and fourth elements (as they are for early dinosaurs), are present in early dinosauromorphs. The medial elements are small and rounded, whereas the larger lateral distal tarsal is waisted at mid-length and has a deep caudal portion that forms an articulation-free heel on the flexor aspect of the tarsus.

The metatarsi of dinosauromorphs is unique because metatarsals II–IV are significantly longer than both outer elements and are tightly bunched to one another at their proximal half, forming a single functional unit. As a whole, the metatarsal length is reasonably conservative, corresponding to more than half of the tibial length, but the relative length of the elements varies considerably. In *Lagerpeton chanarensis*, lateral elements are gradually longer, whereas metatarsals III and IV are subequal and longer than metatarsal II in *Marasuchus lilloensis* and '*Lagosuchus talampayensis*'. As in dinosaurs, *Saltopus elginensis* and *Silesaurus opolensis* have subequal metatarsals II and IV that are shorter than metatarsal III. The partial metatarsus of *Eucoelophysis baldwini* does not allow the estimation of relative lengths. The outer metatarsals are much shorter in early dinosauromorphs, particularly for *Lagerpeton chanarensis*, metatarsal V of *Saltopus elginensis*, and probably metatarsal I of *Silesaurus opolensis*. Partially articulated phalanges are known for *Lagerpeton chanarensis*, *Dromomeron romeri*, *Marasuchus lilloensis*, *Saltopus elginensis* and *Silesaurus opolensis*, and agree on a 2–3–4–5–0 formula where preserved.
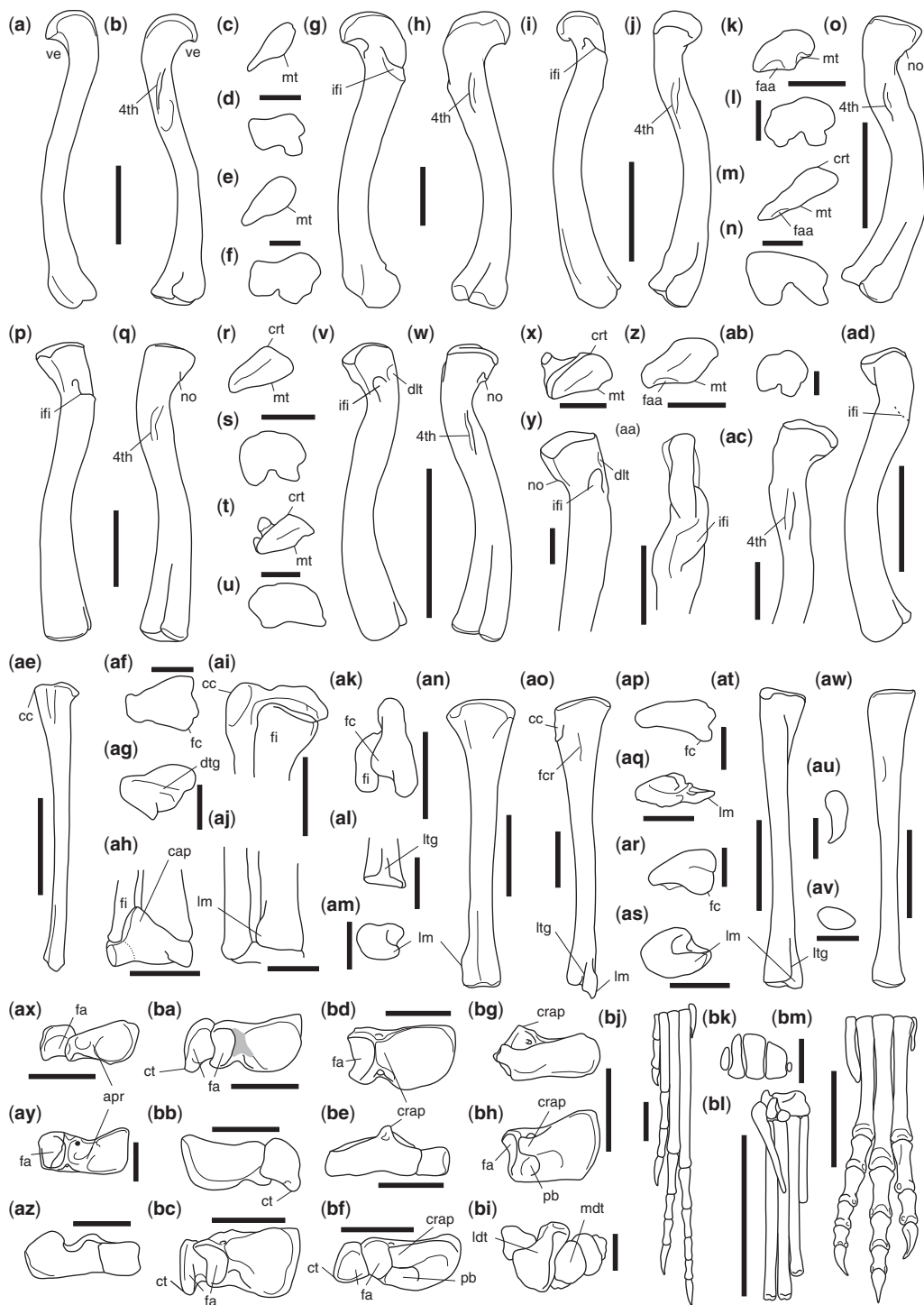
Fig. 6. Hindlimb remains of non-dinosaur dinosauromorphs: (**a–d**) right (reversed) femur of *Lagerpeton chanarensis* (modified from Nesbitt *et al.* 2009); (**e–h**) right (reversed) femur of *Dromomeron gregorii* (modified from Nesbitt *et al.* 2009); (**i, j**) left femur of *Marasuchus lilloensis* (PVL 3871); (**k**) left femur of *M. lilloensis* (modified from Novas 1996);

Systematics and evolution

A poor fossil record has broadly hampered taxonomic and phylogenetic studies of early dinosauromorphs. Few vertebrate fossil assemblages preserve reasonably complete and articulated specimens. Exceptions include the Chañares Formation, in Argentina, and the Krasiejów Claypit, in the Germanic Basin of Poland. However, the number of closely related but different species-level taxa in the Chañares Formation has led to another set of problems: the referral of partial specimens to named taxa based on limited evidence. For example, Sereno and Arcucci (1994b) reported that the holotype of *Lagosuchus talampayensis* was undiagnostic, and referred specimens to the new genus *Marasuchus*. Likewise, mixing of elements from different archosauriforms and ascribing them to a single taxon appears to be common. For example, both *Marasuchus lilloensis* and *Lewisuchus admixtus* have elements of their type material that may not belong to the same individual, or even the same taxon (Arcucci 1998; Remes 2007), and there has been confusion about mixed elements between the type of *Lagosuchus* and a closely associated specimen of the suchian *Gracilisuchus* (Sereno & Arcucci 1994b). The most challenging Chañares dinosauromorph taxa are *Pseudolagosuchus major* and *Lewisuchus admixtus*. The holotype of the former includes a partial hindlimb that is clearly different from all other Chañares Formation dinosauromorphs (Arcucci 1987). However, various

other specimens consisting of overlapping and non-overlapping elements have been assigned to the taxon (Arcucci 1987; Novas 1992b, 1996), without proper documentation of autapomorphies or a unique combination of character states shared with the holotype. Its hypothesized synonymy with *Lewisuchus admixtus* (Arcucci 1997, 1998, 2005; Nesbitt *et al.* 2010; Nesbitt 2011) is potentially reasonable because some studies suggest they are both silesaurids (e.g. Nesbitt *et al.* 2010; Nesbitt 2011). However, synonomy cannot be directly supported because the holotypes of *Pseudolagosuchus major* and *Lewisuchus admixtus* have only one possible overlapping element, the tibia (ambiguously assigned in the holotype of *Lewisuchus admixtus*), and an *a priori* assumption of synonomy should be avoided in phylogenetic studies. Other early dinosauromorphs such as *Asilisaurus kongwe* and *Sacisaurus agudoensis* are known from a reasonable amount of the skeleton, but caution is warranted because the skeletons are largely disarticulated and the evidence for the association of their referred material is partially circumstantial, though they appear to be from monodominant bonebeds. These taxa may be coded in phylogenetic studies, but we urge caution when deciding what elements are clearly referrable to a single species. Perhaps the best example of this situation is *Agnosphitys cromhallensis*. The taxon comprises unassociated disarticulated elements (the holotype ilium and referred maxilla, tooth, humerus and astragalus) from a multitaxic fissure fill assemblage and was

Fig. 6. (*Continued*) (**l**) right (reversed) femur of *M. lilloensis* (modified from Sereno & Arcucci 1994b); (**m**–**o**) left femur of *Diodorus scytobrachion* (modified from Kammerer *et al.* 2012); (**p**–**s**) left femur of *Silesaurus opolensis* (modified from Dzik 2003); (**t**–**w**) right (reversed) femur of *Sacisaurus agudoensis* (MCN 10014); (**x**, **y**) left femur of *Eucoelophysis baldwini* (modified from Ezcurra 2006); (**z**) right (reversed) femur of *Asilisaurus kongwe* (NTM RB102); (**aa**) right femur of *A. kongwe* (NTM RB112); (**ab**) left femur of *A. kongwe* (NTM RB110); (**ac**) left femur referred to *Pseudolagosuchus major* (modified from Ezcurra 2006); (**ad**) left femur of *P. major* (PVL 4629); (**ae**–**ag**) left tibia of *Dromomeron romeri* (modified from Nesbitt *et al.* 2009); (**ah**) right (reversed) crux of *L. chanarensis* (modified from Sereno & Arcucci 1994a); (**ai**) left proximal tibia and fibula of *M. lilloensis* (modified from Novas 1996); (**aj**) right (reversed) crux of *M. lilloensis* (modified from Sereno & Arcucci 1994b); (**ak**) left tibia and fibula of *M. lilloensis* (modified from Sereno & Arcucci 1994b); (**al**, **am**) distal left tibia referred to *P. major* (modified from Novas 1989); (**an**) right (reversed) tibia of *A. kongwe* (NTM RB20); (**ao**–**aq**) right (reversed) tibia of *S. agudoensis* (MCN PV10020) (modified from Ferigolo & Langer 2007); (**ar**–**at**) left tibia of *S. opolensis* (modified from Dzik 2003); (**au**–**aw**) left fibula of *S. opolensis* (modified from Dzik 2003); (**ax**) left astragalocalcaneum of *L. chanarensis* (modified from Sereno & Arcucci 1994a); (**ay**, **az**) right (reversed) astragalocalcaneum of *D. romeri* (modified from Nesbitt *et al.* 2009); (**ba**, **bb**) left astragalocalcaneum of *P. major* (modified from Novas 1989); (**bc**) left astragalocalcaneum of *M. lilloensis* (modified from Sereno & Arcucci 1994a); (**bd**) Right (reversed) astragalus of *A. kongwe* (NTM RB138); (**be**, **bf**) Right (reversed) astragalocalcaneum of *S. opolensis* (modified from Dzik 2003); (**bg**, **bh**) left astragauls of *Agnosphitys cromhallensis* (modified from Fraser *et al.* 2002); (**bi**) right (reversed) distal tarsals and metatarsus of *L. chanarensis* (Sereno & Arcucci 1994a); (**bj**) reconstruction of the left metatarsus and pes of *L. chanarensis* (modified from Nesbitt 2011); (**bk**) reconstruction of the right (reversed) metatarsus of *S. opolensis* (modified from Dzik 2003); (**bl**) reconstruction of the right (reversed) tarsus and metatarsus of *M. lilloensis* (modified from Sereno & Arcucci 1994b); (**bm**) reconstruction of the right (reversed) metatarsus and pes of *S. opolensis* (modified from Dzik 2003). (a, g, i, p, v, y, ad, ae, ai, al, ao) lateral, (b, h, j, o, q, w, ac, an) medial, (c, e, k, m, r, t, x, z, af, ak, ap, ar, au, ax, ay, ba, bc, bd, bf, bh–bi, bk) proximal, (d, f, l, n, s, u, ab, ag, am, aq, as, av, bb) distal, (aa, ah, aj, bg, bl) caudal and (at, aw, az, be, bj, bm) cranial views. Scale bars, 5 mm in (k, l, aj, al, am, bc, bi), 1 cm in (c–f, m, n, t, u, ab, af–ai, ak, ap, aq, ax–bb, bg, bh, bj) 2 cm in (a, b, g–j, o, r, s, x–aa, ac, ao, ar, as, au, av, bd–bf, bk, bl) and 5 cm in (p, q, v, w, ad, ae, an, at, aw, bm).

originally described as non-dinosaurian dinosauriform (Fraser *et al.* 2002). Later workers have debated about its phylogenetic position within Dinosauriformes with little consensus (Langer 2004; Yates 2007; Ezcurra 2010). Unfortunately, the referral of all the material to one taxon is questionable and it is possible that they could represent multiple dinosauriform taxa. Poor specimen preservation has also hindered detailed phylogenetic placement. For example, *Saltopus elginensis* is known from a partial articulated skeleton, but the poor preservation of small vertebrates in the Lossiemouth Sandstone Formation (where the fidelity of natural moulds of small bones is limited by the grain size of the matrix) precludes a detailed assessment of its anatomy.

As depicted above, the scenario for systematic/evolutionary studies of non-dinosaur dinosauromorphs appears awful at first glance. Despite these challenges, dinosauromorph workers have recently applied a number of techniques aimed at ameliorating these problems. For example, Nesbitt *et al.* (2010) and Nesbitt (2011) attacked the synonymy problem of *Pseudolagosuchus major* and *Lewisuchus admixtus* by scoring the two taxa separately in the first run of their phylogenetic analyses, identifying potential Silesauridae synapomorphies in both taxa, and found them closely related to one another (but not as sister taxa) at the base of the Silesauridae–Dinosauria split. After this treatment they were combined into one terminal taxon. Furthermore, Irmis *et al.* (2007*a*) named the lagerpetid *Dromomeron romeri* based on a holotype femur, but reasoned using explicit character and phylogenetic evidence that other elements from the same locality (tibia, astragalocalcaneum) were also from a lagerpetid, most likely from *Dromomeron romeri*. These assignments were later corroborated by articulated specimens (Nesbitt *et al.* 2009; Irmis and Nesbitt unpublished data).

The last ten years have witnessed a renewal of early dinosauromorph studies largely because of careful taxonomic assignments, phylogenetic reasoning for referrals of elements to taxa, a reappraisal of alpha taxonomy, new forms of data and new technologies. These types of study include osteohistology (Fostowicz-Frelik & Sulej 2010; Werning *et al.* 2011), ontogenetic changes in surface morphology (Nesbitt *et al.* 2009), computed tomography scans to help interpret morphology (Benton & Walker 2011), more comprehensive phylogenetic analyses (Nesbitt 2011) and detailed comparative studies using apomorphy-based identifications (Ezcurra 2006; Irmis *et al.* 2007*a*, *b*; Nesbitt *et al.* 2007, 2009, 2010). In the following discussion, we focus on recent and more robustly supported inferences about early dinosauromorph relationships. The hypotheses that herrerasaurs fall outside the

Ornithischia–Saurischia dichotomy, as non-dinosaurian dinosauriforms (Brinkman & Sues 1987; Fraser *et al.* 2002), and that silesaurids are within Ornithischia (Ferigolo & Langer 2007) have never been supported by rigorous quantitative phylogenetic analyses (but see Langer & Ferigolo, this volume, in press) and are not discussed further.

Lagerpetids are the earliest diverging dinosauromorphs (but see Bennett 1996) and the only non-Dinosauriformes members of the group (Fig. 7). This phylogenetic position was first posited solely on the partial skeleton of *Lagerpeton chanarensis* (Sereno & Arcucci 1994*a*), but, more recently, two species of *Dromomeron – D. romeri* and *D. gregorii –* were added to Lagerpetidae (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009). New anatomical information from *Dromomeron* combined with that for *Lagerpeton chanarensis* helped further support an early splitting of Lagerpetidae among Dinosauromorpha in the most recent large-scale phylogenetic studies of archosaurs (Brusatte *et al.* 2010; Nesbitt 2011). *Lagerpeton chanarensis* is from Middle Triassic high-palaeolatitude areas of Argentina, whereas *Dromomeron* spp. represent late-surviving (Norian–?Rhaetian) members of the clade in low-palaeolatitude areas of North America (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2009; Small 2009). Together with new records in the late Carnian of Argentina (Martinez, unpublished data), the North American lagerpetids reveal a seemingly broader distribution of the clade compared to that of the Middle Triassic. Nevertheless, the recognition of this long-lived and widely distributed clade is very recent and we suspect that new discoveries will be made in other parts of Pangaea.

Recent discoveries demonstrate that silesaurids are another group of dinosauromorphs that have a more complex evolutionary history than previously thought. The close affinity of *Silesaurus opolensis* to other early dinosauromorphs such as *Eucoelophysis baldwini* (previously thought to be a coelophysoid) and *Pseudolagosuchus major* was first hypothesized by Nesbitt *et al.* (2005, 2007) and Ezcurra (2006). The latter author recovered those three forms as successive sister taxa to Dinosauria, with *Pseudolagosuchus major* at the base of the 'grade' and *Eucoelophysis baldwini* closest to dinosaurs. Yet, all subsequent studies (Irmis *et al.* 2007*a*; Nesbit *et al.* 2009, 2010; Brusatte *et al.* 2010; Benton & Walker 2011; Nesbitt 2011; Kammerer *et al.* 2012) found Silesauridae to be a more inclusive clade that is sister group to Dinosauria (Fig. 7). Minimally, all these studies include *Silesaurus opolensis* and *Eucoelophysis baldwini* within Silesauridae, but there is no disagreement on the placement of *Sacisaurus agudoensis*, *Asilisaurus kongwe* and *Diodorus scytobrachion* within the clade, and these can be considered Silesauridae
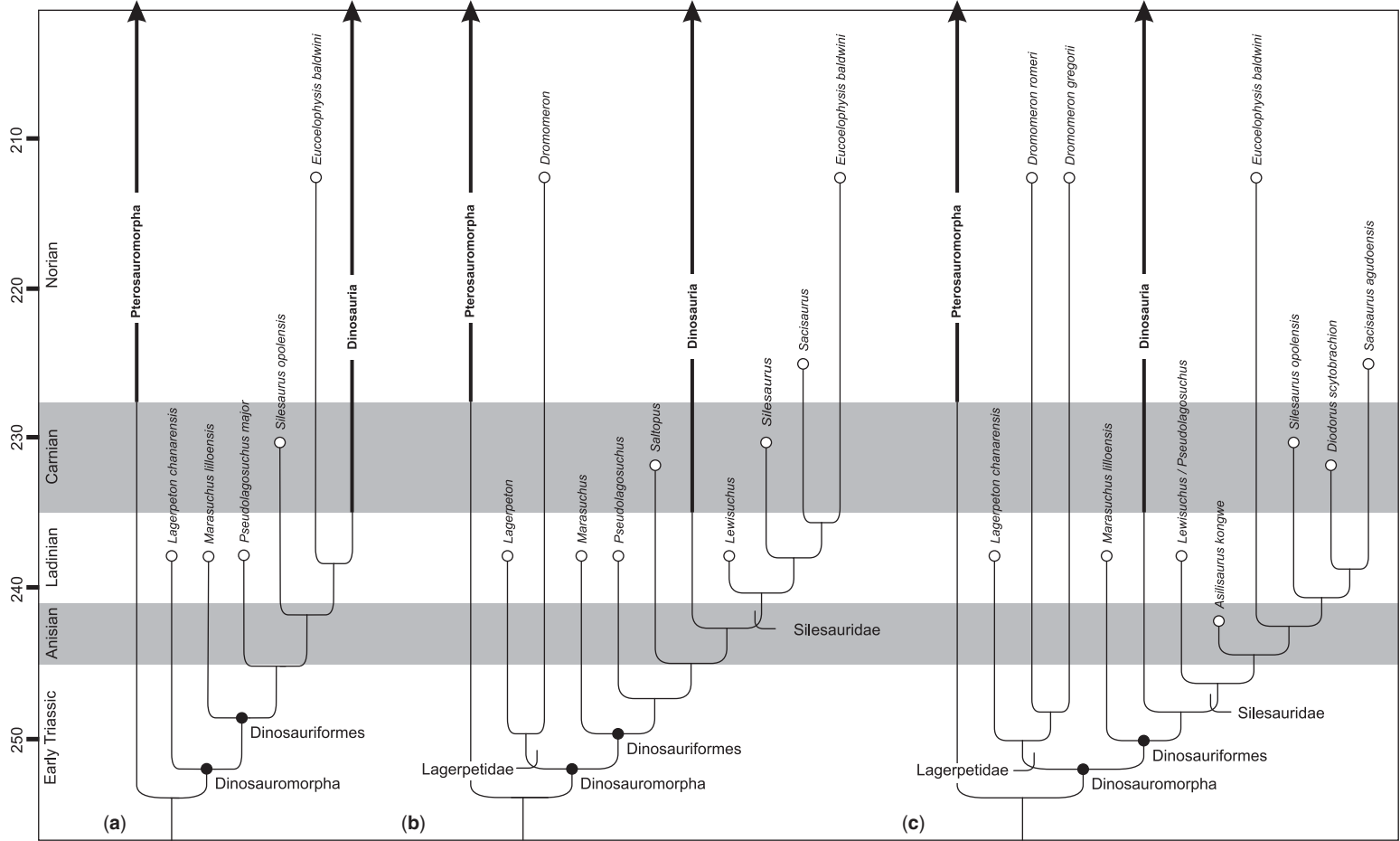
Fig. 7. Time-calibrated phylogenies of ornithodirans: (**a**) Ezcurra (2006); (**b**) Benton & Walker (2011) from the data set of Brusatte *et al.* (2010); (**c**) Kammerer *et al.* (2012) from the data set of Nesbitt *et al.* (2010). Curved line, branch-based taxon; black circle, node-based taxon.

sensu stricto. Yet, *Diodorus scytobrachion* was included in only one recent analysis (Kammerer *et al.* 2012) and *Asilisaurus kongwe* in three studies that derive from the same data set (Nesbitt *et al.* 2010; Nesbitt 2011; Kammerer *et al.* 2012), so their positions have yet to be tested independently. The internal relationships of core silesaurids also show some variations in different studies. For example, Nesbitt *et al.* (2010) found a sister taxon relationship between *Silesaurus opolensis* and *Sacisarus agudoensis* to the exclusion of *Eucoelophysis baldwini*, whereas in the studies of Brusatte *et al.* (2010) and Benton and Walker (2011), a sister taxon relationship was found between *Eucoelophysis baldwini* and *Sacisaurus agudoensis* to the exclusion of *Silesaurus opolensis.*

Although *Marasuchus lilloensis* is consistently found in a position between lagerpetids and members and potential members of Silesauridae + Dinosauria (Sereno & Arcucci 1994*b*; Benton 1999; Ezcurra 2006; Irmis *et al.* 2007; Brusatte *et al.* 2010; Nesbitt *et al.* 2010), other interrelationships of early dinosauromorphs are debated (Fig. 7). For example, Ezcurra (2006), Brusatte *et al.* (2010) and Benton and Walker (2011) found *Pseudolagosuchus major* outside the Silesauridae + Dinosauria clade, with *Lewisuchus admixtus* within Silesauridae in Brusatte *et al.* (2010) and Benton and Walker (2011). On the other hand, Nesbitt *et al.* (2010) found both of these taxa at the base of Silesauridae when coding them both separately and combining the scores into a single terminal taxon. Yet, if the analysis of Nesbitt (2011) is run with those two taxa separated, they are ambiguously placed in a politomy with the lineages leading to Dinosauria and to 'core-Silesauridae'. In some cases, *Pseudolagosuchus major* is found outside a Silesauridae + Dinosauria clade, but it may also nest closer to Dinosauria than to 'core-Silesauridae'. We suggest that this more conservatively represents the poor resolution of the absolute positions of *Pseudolagosuchus major* and *Lewisuchus admixtus*, although the character and taxon sampling of Nesbitt (2011) is not as focused on Dinosauromorpha as that of Nesbitt *et al.* (2010).

The hypothesized age of *Asilisaurus kongwe* sets a minimal Anisian date for the divergence of Pterosauromorpha, Lagerpetidae and Silesauridae. Furthermore, these data also suggest that taxa such as *Marasuchus lilloensis* and *Saltopus elginensis*, from the Ladinian and Carnian respectively, represent late surviving members of a greater radiation that is poorly sampled by the fossil record, although the phylogenetic position of *Saltopus elginensis* is poorly supported because of its poor preservation. As with lagerpetids, all Middle Triassic records of Dinosauriformes are from high palaeolatitudes of southern Pangaea (i.e. Argentina, Tanzania and Zambia). Dinosauromorph body fossils are so far absent from the similarly aged low-latitude upper Moenkopi Formation (Holbrook and Anton Chico members) of the southwestern USA (Nesbitt 2005) and mid-latitude Germanic Basin in Europe (Schoch *et al.* 2010), although some footprints in these units might pertain to this clade (Brusatte *et al.* 2011). Similarly, there are no unambiguous silesaurid records in the Ladinian, although *Lewisuchus admixtus* and *Pseudolagosuchus major*, together or separately, may fill this gap. In the Late Triassic, early dinosauromorphs are well documented and more widespread, reaching northern parts of Pangaea. Except for a new Ischigualasto Formation specimen (Martinez, unpublished data) and *Sacisaurus agudoensis* (Ferigolo & Langer 2007) from south high-palaeolatitude areas, Late Triassic records of Silesauridae are restricted to the mid to low palaeolatitudes of the northern hemisphere, including Europe (Dzik 2003; Sulej *et al.* 2011), North Africa (Kammerer *et al.* 2012) and western North America (Irmis *et al.* 2007*a*; Nesbitt *et al.* 2007, 2010). Based on limited available age constraints (e.g. Irmis *et al.* 2011), it appears that the North American occurrences, at the western Pangaean border, post-date those from the Tethyan margin in Europe and North Africa. Despite these intriguing patterns in the distribution of early Dinosauriformes, at present it is premature to interpret their significance, given that the occurrence of the group totals less than 20 occurrences worldwide over *c.* 35–40 million years. Additionally, the acceleration of new early dinosauromorph discoveries over the past ten years suggests that many new occurrences are still to be identified. Indeed, the absence of records in the eastern parts of Pangaea could be a real biogeographical pattern, but the scarcity of late Triassic tetrapod-bearing deposits in those areas jeopardizes such assumptions, as these chronological and geographical distribution patterns are more probably related to the poor fossil record of early dinosauromorphs.

Palaeobiology

The palaeobiology of the closest relatives of dinosaurs directly influences our understanding of the early evolution of dinosaurs because it helps understand the plesiomorphic dinosaurian condition and suggests reasons why dinosaurs became so successful relative to their other reptilian cousins. With the recent discovery of new taxa and more complete specimens of poorly understood species, it is clear that many classic dinosaur character states relating to anatomy (Sereno & Arcucci 1994*a, b*; Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007*a*;

Nesbitt *et al.* 2007, 2010; Brusatte *et al.* 2010; Langer *et al.* 2010; Nesbitt 2011), locomototion (Sereno & Arcucci 1994*a*; Kubo 2011), growth and physiology (Fostowicz-Frelik & Sulej 2010; Werning *et al.* 2011), and other inferred behaviour aspects (e.g. diet; Barrett *et al.* 2011) have a deeper phylogenetic history, and were inherited from their close relatives, the non-dinosaurian dinosauromorphs. Consequently, what makes dinosaurs unique? And how does the heavily studied Pterosauria clade, which is the sister group of Dinosauromorpha, inform the acquisition of features we consider to be dinosaurian? For example, soft tissue reconstructions, behaviours and autoecological aspects hypothesized for both pterosaurs and dinosaurs are very likely present in non-dinosaurian dinosauromorphs following the tenants of phylogenetic bracketing. In the following paragraphs, we synthesize the growing body of studies that target the palaeobiology of early dinosauromorphs.

Growth and body size

The growth strategies of dinosaurs illuminated through bone histology have been the focus of intense research over the past 30 years (e.g. Horner *et al.* 2000; Erickson *et al.* 2001, 2009; Padian *et al.* 2001, 2004; Starck & Chinsamy 2002; Sander *et al.* 2004; Erickson 2005; Sander & Klein 2005) and significant recent work has focused on early dinosaurs (Padian *et al.* 2001, 2004; de Ricqlès *et al.* 2003, 2008; Sander & Klein 2005; Knoll *et al.* 2010). In general, dinosaurs grew at faster rates than their pseudosuchian cousins (Padian *et al.* 2001, 2004). Yet, in these studies, the closest histologically studied relatives of Dinosauria were the highly modified pterosaurs *Dimorphodon macronyx* and '*Eudimorphodon*' *cromptonellus* (Padian *et al.* 2004), several pseudosuchians (de Ricqlès *et al.* 2003), and a single outgroup to crown archosaurs, *Erythrosuchus africanus* (Gross 1934; de Ricqlès *et al.* 2008). Until very recently, no dinosaur 'precursor' was available for histological sampling because early dinosauromorph fossils were so rare. However, this has now changed as a result of abundant new discoveries (e.g. Dzik 2003; Irmis *et al.* 2007*a*; Nesbitt *et al.* 2010), and workers are starting to build an extensive database of histological data for early Dinosauromorpha and its successive sister taxa (e.g. Werning *et al.* 2011).

Fostowicz-Frelik and Sulej (2010) were the first to publish an osteohistological study of a non-dinosaurian dinosauromorph, *Silesaurus opolensis*. Their sampling of multiple long bones specimens (e.g. femora and tibiae) indicates that *Silesaurus opolensis* grew more similarly to early dinosaurs than to pseudosuchians; these sections are dominated by woven bone, which is diagnostic of rapid growth and is characteristic of (although not unique to) dinosaurs (de Ricqlès *et al.* 2008). However, *Silesaurus opolensis* did show some peculiarities, including lower vascularization density and smaller vascular canal size relative to a dinosaur of similar body size (e.g. *Coelophysis* sp.; Padian *et al.* 2001). Ongoing work by Werning *et al.* (2011) has sampled additional early dinosauromorphs and a wide variety of other early archosauriforms, concluding that components of the dinosaurian growth strategy evolved well before dinosaurs, and perhaps even before the last common ancestor of all archosaurs. Although preliminary, these two studies suggest that all ornithodirans shared similar elevated growth rates relative to extant crocodylians, but that this growth strategy may have much deeper phylogenetic origins. These results are corroborated by recent studies by Botha-Brink and Smith (2011), which found fast growth rates among Early–Middle Triassic non-archosaur archosauriforms.

In concert with dinosaurian growth dynamics, the evolution of body size at the base of Dinosauria and Dinosauromorpha has been addressed by several recent studies (Irmis 2011; Sookias *et al.* 2012). Most early dinosauromorphs were small (femur length of *c.* 7–15 cm), but taken together in a phylogenetic context, they display the beginnings of a phyletic increase in body size that occurred several times in early dinosaur evolution (Irmis 2011). Furthermore, among Silesauridae, there is a slight increase in body size from the oldest member (*Asilisaurus kongwe*) to younger members such as *Silesaurus opolensis* and *Eucoelophysis baldwini* (Irmis 2011). Nonetheless, all known non-dinosaurian dinosauromorphs were small animals dominated in size by most contemporary non-archosaur archosauriforms (e.g. proterochampsids and parasuchians) and pseudosuchians (e.g. aetosaurs and 'rauisuchians').

Locomotion and functional morphology

All dinosaurs had an erect posture, where the limbs were aligned parasagittally underneath the girdles (Bakker 1968, 1971; Bakker & Galton 1974; Bonaparte 1982; Irmis 2011). This posture, however, was not unique to dinosaurs, but inherited from their closest relatives. Specifically, early dinosaurs and dinosauromorphs share gracile hindlimbs, elongated metatarsals and the reduction of outer pedal digits – a configuration that resulted in a digitigrade style of locomotion (Padian 1984; Gauthier 1986). The earliest diverging dinosauromorph clade, the Lagerpetidae, took this further and was functionally didactyl (Romer 1971), a unique condition among early archosaurs. Following Romer

(1971), Sereno and Arcucci (1994*a*) interpreted these forms as fleet-footed cursosor saltators (but see Fechner 2009). The hindlimb proportions and alignment of *Marasuchus lilloensis* and silesaurids are essentially identical to those of early representatives of Ornithischia, Sauropodomorph and Theropoda (Nesbitt 2011). There is even some evidence that a parasagittal stance may have been plesiomorphic for all or most archosaurs (Padian *et al.* 2010). On the other hand, some rotational components were identified in the locomotion of dinosaurs with an incompletely inturned femoral head (Langer 2003), which may have been more evident for non-dinosaur dinosauromorphs with their even less inturned femoral heads.

The limb configuration of non-dinosaur dinosauromorphs is similar to that of all dinosaurs, but the interpretation of these forms as bipeds or quadrupeds is hotly debated, with hypotheses based on both osteological (Bonaparte 1975; Dzik 2003; Fechner 2009; Piechowski & Dzik 2010; Kubo 2011) and ichnological (Haubold & Klein 2000; Brusatte *et al.* 2011) evidence. The transition from a quadruped to a biped gait is rare among diapsids. It occurred at least once in Pseudosuchia (Nesbitt 2007; Bates & Schachner 2011) and once in Avemetatarsalia, near or just before the split between dinosaurs and pterosaurs (Padian 2008). Bipedalism is probably plesiomorphic for Dinosauria (Langer *et al.* 2010) and has previously been considered a key feature of the group (Gauthier 1986; Sereno 1997; Langer *et al.* 2010). However, the discovery of *Silesaurus opolensis* complicates our understanding of dinosaur evolutionary transitions in locomotion, because its elongate forelimbs offer a close comparison to that of distinctly quadrupedal archosaurs. Yet, the forelimb-to-hindlimb length ratio, while informative (e.g. Padian 2008), can be ambiguous when interpreting bipedal/quadrupedal locomotion, especially when animals are facultative quadrupeds (e.g. Forster 1990). In fact, precisely for this reason, at least one team of authors has argued that *Silesaurus opolensis* was bipedal (Piechowski & Dzik 2010), as suggested by its slender forelimbs. These may have not endured the same amount of stress as the hindlimbs did and were not used for high-speed locomotion (see Fariña 1995), but this hypothesis is still to be fully tested. Other than simple limb length ratios, one of the only other informative functional morphological features (but see Christian & Preuscoft 1996) that have been investigated among dinosaurs is the requirement that digitigrade quadrupedal animals must be able to pronate their forelimb (Bonnan 2003; Bonnan & Senter 2007; Bonnan & Yates 2007; Yates *et al.* 2010). No detailed functional morphological study of this range of motion has been made for early dinosauromorphs, although

the rounded and very simple proximal articular surfaces of the radius and ulna of *Sileasaurus opolensis* (Dzik 2003, fig. 9) suggest that pronation was possible. Ideally, more complex biomechanical models need to be applied to this question, with limb movements, muscle attachments and centre of mass being modelled, using sensitivity analyses that address analytical uncertainty (Hutchinson & Gatesy 2006; Hutchinson *et al.* 2011; Hutchinson 2012). Of course, the ultimate limitation is the general lack of relatively complete forelimbs among non-dinosaurian dinosauromorphs, but we suspect that this problem will be quickly ameliorated as more complete material is discovered.

Feeding ecology

After their decline at the end of the Permian, large synapsid herbivores became rarer in the Triassic (Benton 1983; Sahney & Benton 2008; Sookias *et al.* 2012), although dicynodonts remain dominant elements of some fossil assemblages (Sennikov 1996; Langer *et al.* 2007; Fiorelli *et al.* 2011). By the Triassic–Jurassic transition, dinosaur herbivores were widespread and successful (Barrett *et al.* 2011; Irmis 2011). However, the Triassic origins of dinosaur feeding ecology are unclear. Most sauropodomorphs and ornithischians appear to be herbivorous, whereas their earliest representatives are more ambiguous to interpret (Martinez & Alcober 2009), and all early theropods are strict carnivores (Barrett 2000; Barrett *et al.* 2011). Complicating matters is the difficulty in distinguishing reptilian omnivores and herbivores based on tooth morphology, as feeding ecology is a spectrum that is not necessarily cleanly parsed by distinct tooth morphotypes (Barrett 2000; Irmis *et al.* 2007*b*).

Inferring the feeding ecology of the dinosaur forerunners has only become more complex with the discovery of *Silesaurus opolensis* and its set of ornithischian-like teeth and a possible beak at the rostral portion of the lower jaw (Dzik 2003). A similar morphology is present in a number of other silesaurids (*Asilisaurus kongwe*, *Sacisaurus agudonensis* and *Diodorus scytobrachion*), indicating that *Silesaurus opolensis* was part of an ecologically distinct radiation, not an aberrant form (Nesbitt *et al.* 2010). Thus, evidence for omnivory/herbivory is present in three closely related dinosauriform clades: silesaurids, ornithischians and sauropodomorphs. Consequently, it appears that such a diet could be optimized as a single acquisition that is plesiomorphic for Dinosauria (Langer *et al.* 2010; Barrett *et al.* 2011; Kubo 2011). Yet, the phylogenetic placement of some taxa (e.g. *Eoraptor lunensis*, *Lewisuchus admixtus*), the interpretation of their feeding ecology and the inferred ancestral condition in pterosaurs has a large effect on the

optimization of plesiomorphic diets within Ornitho-dira (Barrett *et al.* 2011). Nesbitt *et al.* (2010) suggested that all three groups of omnivorous/her-bivorous dinosauriforms acquired their tooth and skull features independently from one another, which may preclude an omnivorous/herbivorous common ancestor. The absence of cranial material for lagerpetids and taxa such as *Pseudolagosuchus major*, combined with ambiguous correlations between tooth shape and diet, further hampers reconstructions. Indeed, forms such as *Marasuchus lilloensis* lack clear tooth specializations to either an omnivorous/herbivorous or more carnivorous diet, which may well be the common pattern among basal dinosauromorphs. In any case, if *Lewisuchus admixtus* is the earliest diverging silesaurid, as hypothesized by Nesbitt *et al.* (2010), and if the referred skull/maxilla indeed belongs to its holotype, then it provides evidence that silesaurids independently acquired their herbivorous char-acteristics. At this point, the primitive feeding ecology for dinosauromorphs and dinosaurs is unclear. What is important is that at least three groups of dinosauriform evolved dentitions and cranial features that deviate from general features of carnivorous reptiles. Just like the complexities of interpreting locomotor posture, the dichoto-mization of taxa as either omnivore/herbivore or carnivore oversimplifies the spectrum of possible ecologies.

Breathing and pneumaticity

The mechanics of breathing and its relation to osteological features in the skeletons of dino-saurs has long been a topic of extensive research. Recent palaeontological work suggests that uni-directional lung flow, once thought to be restricted to birds, was also present in saurischian dinosaurs (O'Connor & Claessens 2005; Wedel 2009; Yates *et al.* 2012) and pterosaurs (Claessens *et al.* 2009). Even more exciting new physiological work demon-strates that it is present in extant Crocodylia (Farmer & Sanders 2010; Sanders & Farmer 2012), which generates immediate questions about how deep in the archosaur tree this feature originated. Thus, the common ancestor of birds and crocodylians and all of their descendants (including dinosauromorphs) probably had a highly efficient respiratory avian-like system (Brown *et al.* 1997; O'Connor 2006; Farmer & Sanders 2010). Schachner *et al.* (2009) demonstrated that rib morphology and the corre-sponding attachments with the presacral vertebrae in birds were very similar to those of non-avian saur-ischian dinosaurs and even early dinosauriforms (i.e. *Silesaurus opolensis*), and hypothesized that this configuration of the axial column correlates with the presence of a rigid avian-like lung.

Specimens of *Silesaurus opolensis* bear a full com-plement of ribs corresponding to vertebrae, a rar-ity among early dinosauromorphs, including early dinosaurs. As such, it is difficult to tell how far down the ornithodiran lineage these features go, but we hypothesize that most dinosauromorphs had an avian-like rigid lung.

Breathing mechanics (i.e. unidirectional air-flow) tie directly to pneumatic structures of the post-cranial skeleton in extant birds (Druncker 1971), although postcranial skeletal pneumaticity (PSP) is not a requirement for unidirectional airflow (Far-mer & Sanders 2010). Because PSP has osteolog-ical correlates that can be identified in the fossil record (O'Connor 2006), research has centred around understanding the evolution of these pneu-matic structures in dinosaurs (Wedel 2003, 2009; O'Connor & Claessens 2005; Benson *et al.* 2012; Yates *et al.* 2012), pterosaurs (Butler *et al.* 2009; Claessens *et al.* 2009) and early archosauriforms (Gower 2001; Butler *et al.* 2012). Most workers examining dinosaurs focus on the larger and geolo-gically younger forms, but there has been a clear shift to examining the early members of Dinosauria in search of homology. Among early dinosaurs, unambiguous PSP is recognized in the neck of early theropods (e.g. *Tawa hallae*, Nesbitt *et al.* 2009), neotheropods (*Coelophysis bauri*) and many sauropodomorphs (Wedel 2007; Yates *et al.* 2012), but absent in early ornithischians and the earliest sauropodomorphs. Outside of Dinosauria, PSP is present in early pterosaurs (Butler *et al.* 2009; Claessens *et al.* 2009), suggesting that some kind of airsac may have been present, primitively, in all ornithodirans. However, this is not clear, because no unambiguous PSP has been reported in any non-dinosaurian dinosauromorphs. *Silesaurus opolensis* vertebrae have a complex configuration of thin vertebral laminae and deep fossae, which are present in dinosaurs with PSP, but the pneumatic nature of these features is ambiguous in that taxon (Butler *et al.* 2012). Nevertheless, Butler *et al.* (2012) hypothesized that avian-like pulmonary air sacs may be present in all ornithodirans (including dinosauromorphs) given that both pterosaurs and saurischians bear signs of unambiguous PSP and that an airsac system could exist without invading the skeleton. Their hypothesis puts forth a number of predictions for non-dinosaurian dinosauromorphs that are testable with new fossils. For example, PSP may be present in the neck of non-dinosaurian dinosauromorphs as it is in early dinosaurs (Butler *et al.* 2012), but this region is either absent or poorly preserved in most specimens. Furthermore, all non-dinosaurian dinosauromorphs are small and it is entirely possible that unambiguous evidence of PSP would only be present in larger forms, as it tends to manifest in larger taxa (O'Connor 2004;

Wedel 2009; Benson *et al.* 2012; Yates *et al.* 2012; Smith 2012).

Integument

The last 15 years has witnessed the spectacular discovery of well-preserved feathered dinosaurs (Norell & Xu 2005; Xu & Norell 2006). At first, feathered dinosaur discoveries were restricted to the coelurosaurian clade (Ji & Ji 1996; Ji *et al.* 1998), but more recently include ceratopsian (Mayr *et al.* 2002) and heterodontosaurid (Zheng *et al.* 2009) ornithischians with similar integumentary structures. Even though the oldest records of dinosaurs with feather-like integumentary structures date back to the Middle Jurassic (Liu *et al.* 2012), phylogenetic bracketing (Witmer 1995) allows us to hypothesize that the common ancestor of all dinosaurs (that of theropods and ornithischians) had a similar covering. In fact, filamentous integumentary structures may be present in the common ancestor of pterosaurs + dinosaurs (ornithodirans) given that a diversity of pterosaurs have also been found covered in a similar integument (e.g. Bakhurina & Unwin 1995; Lu 2002; Kellner *et al.* 2009). If the integumentary coverings of dinosaurs and pterosaurs are homologous, then it is highly likely that all early dinosauromorphs were covered in similar structures, which implies that this integument was plesiomorphic for dinosaurs. If sufficiently abundant, such a coverage could play a thermoregulatory function (insulation), probably implying a higher thermal inertia (Regal 1975, 1985; Wu *et al.* 2004). At the moment, however, no skin or soft tissue has been discovered with any non-dinosaur dinosauromorph specimen.

Future directions

The number of new specimens of non-dinosaurian dinosauromorphs has increased by an order of magnitude since the discovery of *Silesaurus opolensis* in 2003. These new specimens, and associated new taxa and anatomical information, have led to a stabilization of the basic tree of Dinosauromorpha in some respects, but eroded support in others. Indeed, a number of trials remain. A comprehensive alpha-taxonomic revision of the Chañares dinosauromorphs is necessary to accurately identify operational units (terminal taxa) for phylogenetic studies. The failure to do so would endlessly bias such analyses, hampering the correct identification of the evolutionary patterns that serve as a framework for most kinds of macroevolutionary studies. Another challenge is the discovery of more complete and articulated early dinosauromorph skeletons. The burst of knowledge brought forth with the discoveries of the Chanãres dinosauromorphs in the mid-1970s and of *Silesaurus opolensis* early this century show the importance of such well-preserved fossils, and similar finds are needed from other Triassic deposits in order to take further steps forward. Finally, to go beyond taxonomic/phylogenetic studies, more modern approaches and techniques in the study of fossils, such as computed tomography (CT) scanning, osteohistology, biomechanic studies and phylogenetic bracket inferences, must be applied to non-dinosaur dinosauromorphs. Obviously, more precise dating/correlation of the deposits containing early dinosauromorph fossils is required to more securely calibrate their evolutionary patterns through time and space.

Appendix I

Institutional abbreviations

MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; UPLR, Universidad Provincial de La Rioja, La Rioja, Argentina; PVL, Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Appendix II

Anatomical abbreviations

4th, fourth trochanter; ac, acetabulum; act, acrocoracoid tuberosity; an, angular; aof, antorbital fenestra; apr, astragalar proximal ridge; at, antitrochanter; ati, atlas intercentrum; axi, axis intercentrum; bf, brevis fossa; bs, brevis shelf; bt, basal tubera; bpp, basipterygoid processes; c, coracoid; cacdl, caudal centrodiapophyseal lamina; cap, astragalar caudal ascending process; cc, cnemial crest; cp, cultriform process; crap, astragalar cranial ascending process; crcdl, cranial centrodiapophyseal lamina; crt, cranial tuber; ct, calcaneal tuber; d, dentary; dpc, deltopectoral crest; dtg, tibial distal groove; dig, dorsal ischial groove; dlt, dorsolateral trochanter; dpol, diapopostzygapophyseal lamina; dprl, diapoprezygapophyseal lamina; en, external naris; f, frontal; fa, fibular articulation; faa, facies articularis antitrochanterica; fc, fibular condyle; fcr, fibular crest; fi, fibula; fov, fenestra ovalis; iag, ischio-acetabular groove; icf, intercostal foramen; idf,

infradiapophyseal fossa; ifi, iliofemoral insertion on femur (lesser trochanter and trochanteric shelf); ilb, iliac blade; ipof, infrapostzapophyseal fossa; ipol, infrapostzapophyseal lamina; j, jugal; ldt, lateral distal tarsal; lm, outer malleolus; ltf, lower temporal fenestra; ltg, lateral tibial groove; mdt, medial distal tarsal; met, metotic foramen; mf, external mandibular fenestra; mt, medial tuber; msil, medial surface of ilium; mx, maxilla; n, nasal; no, ventral notch of the femoral head; ns, neural spine; o, orbit; oc, occipital condyle; of, obturator foramen; p, parietal; pa, parapophyses; padl, paradiapophyseal lamina; par, preacetabular ridge; pb, astragalar proximal basin; pbs, parabasisphenoid; pf, pelvic fenestra; pgf, preglenoid fossa; pgp, postglenoid process; pm, premaxilla; po, postorbital; poz, postzygapophysis; pp, paroccipital process; pr, prootic; prz, prezygapophysis; pt, pubic tubercle; qj, quadratojugal; qu, quadrate; sq, squamosal; sa, surangular; so, supraoccipital; sr, sacral rib; sr1, primordial sacral rib 1; sr2, primordial sacral rib 2; tp, transverse process; tp-sr, transverse process/sacral rib suture; ve, ventral emargination of the femoral head; V, foramen for cranial nerve V (trigeminal); VII, foramen for cranial nerve VII (facial); XII, foramen for cranial nerve XII (hypoglossal);

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