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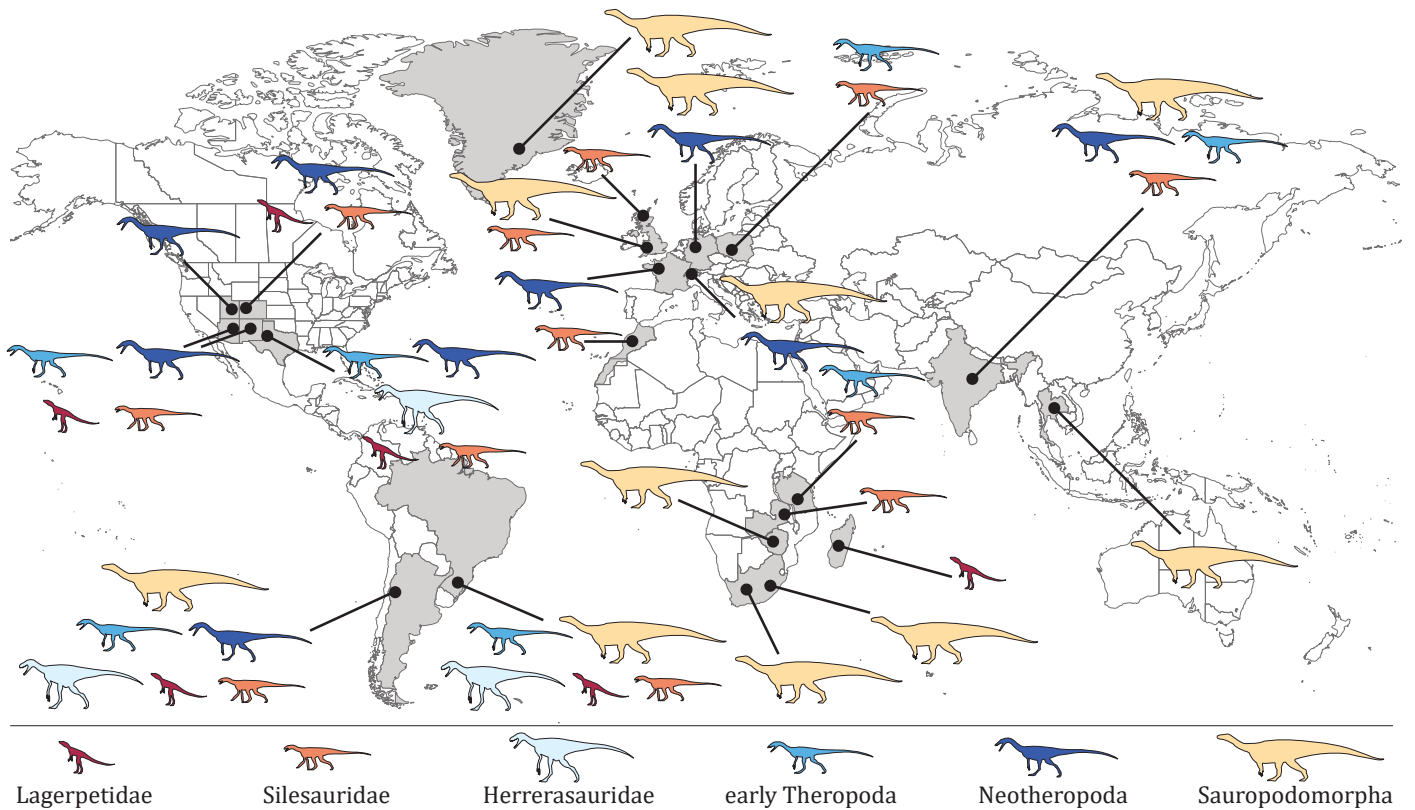
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# *PaleoBios*

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**Cover:** Global Triassic dinosauromorph occurrences known from body fossils. Maps modified from [[freevectormaps.com](https://www.freemaps.com/)] and silhouettes used from [[phylopic.org](https://www.phylopic.org/)]; see acknowledgements for full links.

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# New dinosauromorph specimens from Petrified Forest National Park and a global biostratigraphic review of Triassic dinosauromorph body fossils

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Dinosauromorph specimens from Petrified Forest National Park have been recovered from four major collecting efforts since 1982, including the most recent paleontological inventory of new park lands acquired in 2011. Additionally, an emphasis on understanding the stepwise acquisition of character traits along the dinosaurian lineage has helped identify previously collected specimens in museum collections. Here we briefly describe and use apomorphies to identify 32 additional dinosauromorph specimens found at Petrified Forest National Park, bringing the total number of dinosauromorph specimens presently known from the park to 50, a 600% increase since the year 2000. These specimens are all Norian in age and come from the Blue Mesa Member, Sonsela Member, and Petrified Forest Member of the Chinle Formation. These include the proximal end of a tibia that represents the oldest unambiguous dinosaur specimen from the Chinle Formation. We then contextualize these specimens with the dinosauromorph assemblages from the Norian of Utah, Colorado, New Mexico, and Texas, as well as the Carnian and Norian dinosauromorph assemblages from South America, Africa, and Europe. Despite increased sampling we still find no evidence for sauropodomorph and ornithischian dinosaurs in Western North America. An increase in sampling, combined with the use of apomorphies to identify collected specimens, will continue to improve the global dinosauromorph fossil record that can be used to answer questions on biochronology and the evolutionary history of the avian lineage.

**Keywords:** Dinosauromorpha, Dinosauria, Theropoda, Chinle Formation, Triassic

## INTRODUCTION

For most of the late 20<sup>th</sup> and early 21<sup>st</sup> centuries, the Late Triassic dinosauromorph record of the Chinle Formation across the American Southwest was thought to be relatively depauperate, outside of the notorious mass death assemblage of the neotheropod *Coelophysys bauri* Cope (1887) from Ghost Ranch, New Mexico (Colbert 1947, 1989). Among the numerous specimens of non-archosaur archosauromorphs, phytosaurs, and pseudosuchian archosaurs, dinosaurs themselves represented less than 5% of the Late Triassic tetrapod fossils collected in Arizona, Colorado, New Mexico, and Utah (Hunt et al. 1998). Regardless of the reasons behind the observed low number of dinosauromorph specimens in the area, be it taphonomic effects (Hunt et al. 1996, Therrien et al. 2000, Loughney et al. 2011) or geobiological exclusion (Irmis 2011, Whiteside et al. 2011, 2015), questions related to the timing of the origin and diversification

of dinosauromorphs are sensitive to the availability of reliably-identified body fossils (Irmis 2011). Thus, since 1921 when Charles Camp first began working in the Late Triassic of the Colorado Plateau, starting in the Petrified Forest area (Long and Murry 1995, Parker 2006) there has been a nearly constant effort to discover more fossils of dinosaurs and their closest relatives.

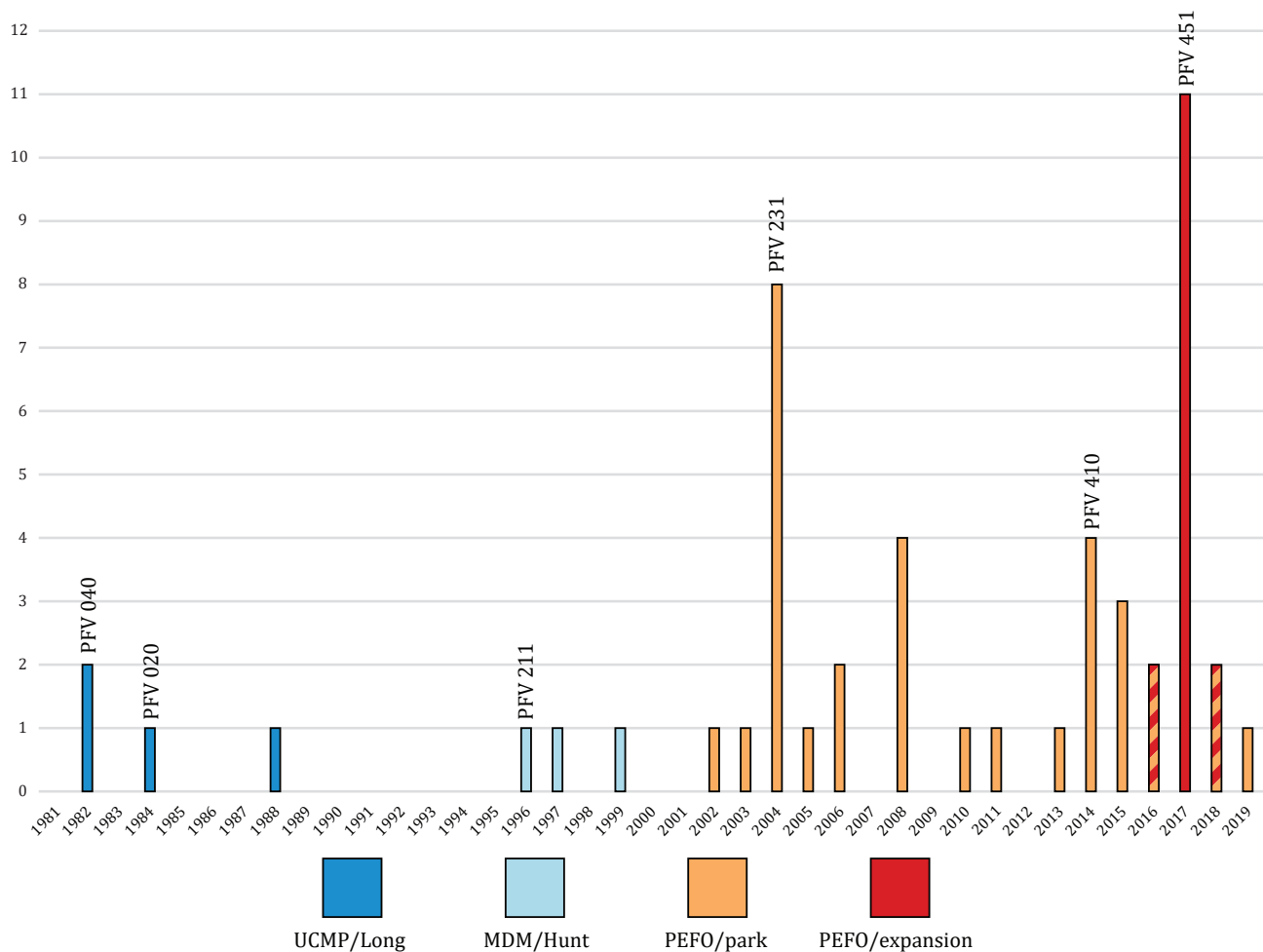
Since the early 1980s, there have been four distinct efforts to locate dinosauromorph fossil-bearing localities in the Chinle Formation at Petrified Forest National Park (PEFO). The first was led by the University of California Museum of Paleontology (UCMP) from 1981 to 1987 (Fig. 1). It culminated in the “Dawn of the Age of Dinosaurs in the American Southwest” field conference and symposium bulletin (Lucas and Hunt 1989). This synthesis of Late Triassic paleontology of the entire western United States (Long and Murry 1995) was the most-cited publication on Late Triassic vertebrate paleontology for nearly 20 years (Parker 2006). Kevin Padian and Robert ‘Rob’ Long visited PEFO in 1981 with Samuel Welles, Michael Parrish, Paul Olsen, John Bolt, and Will Downs (Parker

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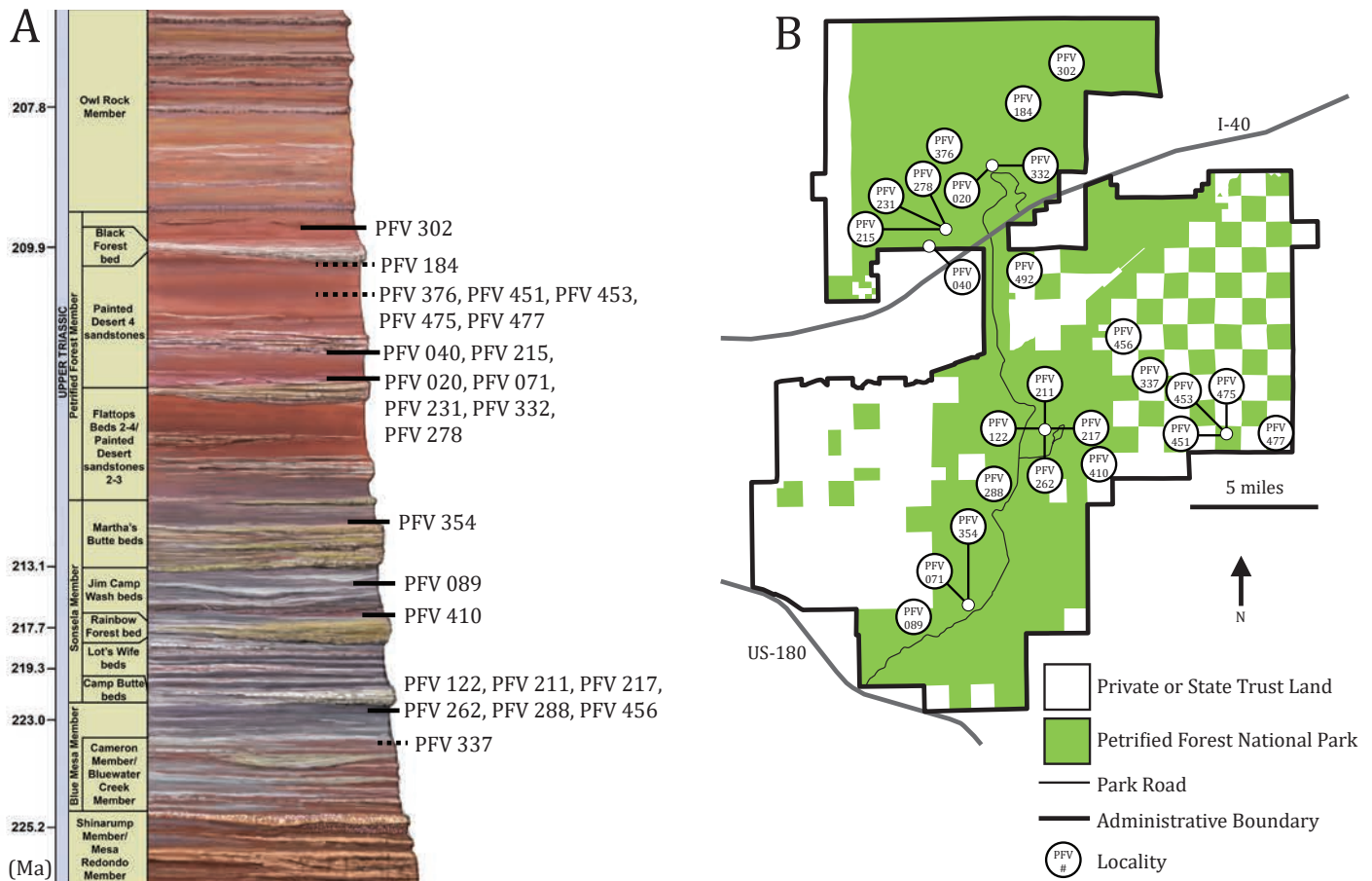
**Figure 1.** Number of dinosaur specimens found at Petrified Forest National Park by year, including the four major collecting efforts mentioned in the text.

2006) to relocate Camp’s PEFO sites. Padian’s work continued through 1983 (Long and Padian 1986) and Long subsequently worked with various UCMP crews in the park through 1987. During this period UCMP field crews discovered two of the most significant dinosaur localities in the Norian-age Petrified Forest Member of the Chinle Formation at PEFO (Long and Murry 1995): Anne Preston (an archaeologist) found PFV 040 (Dinosaur Hill) in 1982, which produced a partial skeleton of a coelophysid theropod (Padian 1986), and Bryan Small discovered PFV 020 (Dinosaur Hollow) in 1984, the type-locality of the early theropod *Chindesaurus bryansmalli* Long and Murry (1995) (Fig. 2).

The second dinosaur recovery effort at PEFO, led by Adrian Hunt from the Mesalands Dinosaur Museum (MDM), ran from 1996 to 1999 and was referred to as the “Dawn of the Dinosaurs Project” (Hunt 1998). Tom

Olson, an intern at the MDM, located the first purported dinosaur locality in the Blue Mesa Member of the Chinle Formation at PFV 211 (Dinosaur Ridge); (Hunt et al. 1996) (Fig. 2). The MDM group also reported a partially excavated theropod specimen from locality PFV 278 (Jeremiah’s Perch) from the Petrified Forest Member (Hunt and Wright 1999, Parker and Irmis 2005), which was recently returned and prepared at PEFO.

The third effort, initiated by William Parker in 2001 after the park hired a full-time paleontologist, concentrated on relocating historic localities and finding new ones and is ongoing as the park paleontology program continues under Adam Marsh (Parker 2002, Parker and Clements 2004, 2006, Parker and Irmis 2005) (Fig. 1). The discovery of locality PFV 297 (the *Revueletosaurus* Quarry) clarified that *Revueletosaurus callenderi* Hunt (1989) is actually a pseudosuchian archosaur and supported the



**Figure 2.** Stratigraphic position (A, modified from Martz et al. (2012)) and geographic location (B) of dinosauriform fossils at Petrified Forest National Park. Radiometric ages from Ramezani et al. (2011).

idea that ornithischian and sauropodomorph body fossils are absent in the Triassic of the American Southwest (Parker et al. 2005, Irmis et al. 2007a, Nesbitt et al. 2007). Thus, theropods became the sole emphasis of Late Triassic dinosaur paleontology in the area. Members of the PEFO paleontology program discovered PFV 231 (the Giving Site; Fig. 2), a fossil-rich locality that included both a *Chindesaurus*-like animal and a coelophysid (Stocker et al. 2004, Parker and Irmis 2005). During this time, dinosauriform fossils were also found for the first time in the Sonsela Member at PFV 089 (the Bowman Site), at the highest stratigraphic level in the Petrified Forest Member at the park at PFV 302 (Rabbit Foot Hills), and at the purported lowest stratigraphic level in the Blue Mesa Member at PFV 337 (Valley of the Dead) (Parker and Martz 2011). Importantly, it was also during this time that the most currently accepted lithostratigraphic framework of the Chinle Formation around PEFO was erected (Martz and Parker 2010, Martz et al. 2012), and high-resolution U-Pb detrital zircon geochronology provided age estimations for numerous fossil-bearing

horizons in the park and established that the entire Chinle Formation at PEFO is Norian in age (Ramezani et al. 2011, 2014, Atchley et al. 2013, Nordt et al. 2015).

In 2004, the United States Congress authorized a PEFO expansion of nearly 500 sq. km for the protection of paleontological and archaeological resources, and the fourth dinosauriform-collecting effort (2016–2018; Figs. 1, 2) occurred as part of a systematic inventory of these new lands within the increased park boundary. PEFO crews led by Charles Beightol, Adam Marsh, and Natalie Toth recovered numerous theropod and silesaurid femora and tibiae in the Sonsela Member and Petrified Forest Member of the former Paulsell Ranch on the eastern side of the park.

In the 1990s and early 2000s, the most common dinosaur remains found at PEFO, especially from sites in the Petrified Forest Member, were teeth of the purported ornithischian dinosaur *Revueltosaurus callenderi* (Padian 1990, Long and Murry 1995, Hunt 1998, Hunt and Wright 1999, Heckert 2002). Indeed, if one considers all of the taxa formerly attributed to *Ornithischia* Seeley (1887)

from Late Triassic rocks of North America (Hunt and Lucas 1994, Heckert 2002, 2004), including *R. callenderi*, *Galtonia gibbidens* Hunt and Lucas (1994), *Pekinosaurus olseni* Hunt and Lucas (1994), *Tecovasaurus murryi* Hunt and Lucas (1994), *Crosbysaurus harrisae* Heckert (2004), *Protecovasaurus lucasi* Heckert (2004), *Lucianosaurus wildi* Hunt and Lucas (1994), and *Krzyzanowskisaurus hunti* Heckert (2005), ornithischian dinosaurs would have been one of the most common vertebrate groups in the Late Triassic. In fact, none of the taxa that are known only from teeth can be assigned to the Ornithischia using unambiguous synapomorphies but rather come from a variety of archosauromorph taxa (Irmis et al. 2007a). Combined with the discovery of associated and semi-articulated skeletons of *R. callenderi* from PEFO and postcranial elements from the same horizon as the holotype from the Bull Canyon Formation in New Mexico (Hunt et al. 2005), it was recognized that *R. callenderi* is instead an armored pseudosuchian (Parker et al. 2005). Furthermore, the other putative Triassic ornithischians known from fossils other than teeth cannot be unambiguously assigned to Ornithischia or associated with Triassic rocks, e.g., *Pisanosaurus mertii* Casamiquela (1967) from the Ischigualasto Formation of Argentina has been hypothesized to be a silesaurid dinosauriform (Agnolín and Rozadilla 2017, Baron 2017; but see Desojo et al. 2020), and an unnamed heterodontosaurid from the Laguna Colorada Formation of Argentina (Báez and Marsicano 2001) and *Eocursor parvus* Butler et al. (2007) from the Upper Elliot Formation (previously thought to have been from the Lower Elliot Formation) of South Africa have been related to the Early Jurassic (Pol and Powell 2007, Olsen et al. 2011, McPhee et al. 2017, Sciscio et al. 2017, Bordy et al. 2020). Thus, there are no known unambiguous ornithischian dinosaurs in the Triassic around the world (Olsen et al. 2011, Padian 2013). Note that a recent phylogenetic analysis hypothesized that 'silesaurids' may be a paraphyletic Triassic group of the earliest ornithischians (Müller and Garcia 2020), but this hypothesis requires further testing and character state analysis.

Similarly, initial reports of sauropodomorph dinosaurs in the Chinle Formation at PEFO were misidentified and belong to other taxa. The teeth of 'anchisaurid' sauropodomorphs were reported from PFV 040 (Dinosaur Hill, Petrified Forest Member) (Murry and Long 1989), but were later assigned to the pseudosuchian archosaur *Revueltosaurus* (Hunt et al. 1998, Parker et al. 2005). Other fragmentary remains such as the proximal end of a femur from PFV 169 (=UCMP V82261, Battleship NW,

Sonsela Member) (Long and Murry 1995) and a cervical vertebra from PFV 279 (Dinosaur Wash E) lack dinosaur apomorphies (Hunt et al. 1996, 1998, Parker and Irmis 2005) and, in the case of PFV 279, belong to the non-archosaur archosauromorph group Azendohsauridae (Nesbitt et al. 2015, Marsh et al. 2017). Unlike the diverse Late Triassic sauropodomorph assemblages found in South America, Europe, and southern Africa (e.g., Yates 2003, McPhee et al. 2017, Langer et al. 2018, Müller et al. 2020), the first unambiguous sauropodomorphs in North America are Early Jurassic in age (Marsh and Rowe 2018).

The presence of Triassic theropod dinosaurs has been well-demonstrated from the Chinle Formation as early as the "Bone Wars" of the western United States (Cope 1887, 1889, Colbert 1964, Padian 1986). Perhaps the most well-known of these is *Coelophysis bauri*, represented by hundreds of individuals in a mass death assemblage in the uppermost 'siltstone member' of the Chinle Formation at Ghost Ranch, New Mexico (Colbert 1947, 1989). Ironically, Edwin 'Ned' Colbert planned to return to PEFO in 1947 to continue locating Camp's sites when he was waylaid by the discovery of the *Coelophysis* Quarry (Whitaker Quarry) at Ghost Ranch (Long and Murry 1995, Parker 2006).

Two theropod taxa are known from PEFO; the first is a large coelophysid collected by the UCMP in 1982 from PFV 040 (Dinosaur Hill) (Padian 1986), and the second is the non-neotheropod *Ch. bryansmalli* from PFV 020 (Dinosaur Hollow) (Long and Murry 1995, Marsh et al. 2019a). A smaller individual found with the holotype of *Ch. bryansmalli* was originally described as that of a juvenile theropod (Dunbar and Robson 1986), but has since been reported as belonging to a shuvosaurid pseudosuchian (Long and Murry 1995). In fact, many fossils from PEFO have been historically identified as belonging to theropods (e.g., Hunt 1998, Hunt et al. 1996), based on hollow centra and limb shafts, anteroposteriorly long caudal vertebrae, and sharp curved, serrated teeth, but these traits are either plesiomorphies in saurischians or are highly homoplastic among archosauromorphs (Hunt et al. 1998, Nesbitt 2011, Nesbitt et al. 2007, Ezcurra 2016). Similarly, theropod groups such as herrerasaurs (Long and Murry 1995, Hunt et al. 1998) or ceratosaurs (Kirby 1991, Long and Murry 1995, Hunt et al. 1998, Heckert et al. 2005) have been identified in the Chinle Formation, but the evolutionary relationships and diagnostic features of early saurischian groups has changed to the point that no theropod material from the formation can be unambiguously identified as being a herrerasaur or ceratosaur (Nesbitt et al. 2007, Marsh 2018a, Marsh

et al. 2019a; but see Baron and Williams 2018 for a putative herrerasaur interpreted as a dinosauriform from the Late Triassic of Texas). For example, coelophysids were thought to be early-diverging ceratosaurian theropods (*sensu* Rowe and Gauthier 1990, Tykoski and Rowe 2004), but are now recognized to be early-diverging stem-averostran neotheropods (e.g., Rauhut 2003, Carrano et al. 2012, Carrano and Sampson 2008).

Much of our current understanding of dinosaur groups and their closest relatives in the Chinle Formation has changed thanks to the discovery of a new fauna at the Hayden Quarry (Petrified Forest Member) (Irmis et al. 2007b) at Ghost Ranch, New Mexico, and the application of apomorphy-based identifications (Bell et al. 2004, 2010, Nesbitt and Stocker 2008, Martz et al. 2013, Lessner et al. 2018, Marsh 2018a), with respect to the ever-changing hypothetical evolutionary relationships of avemetatarsalian archosaurs (Nesbitt 2011, Cabreira et al. 2016, Nesbitt et al. 2017, Marsh et al. 2019a). The diverse assemblage containing a coelophysoid, non-neotheropod theropod, silesaurid dinosauriform, and lagerpetid dinosauriform from the Hayden Quarry demonstrated that dinosaurs and their closest non-dinosaur dinosauriform relatives co-occurred throughout most of the Late Triassic in the American Southwest (Irmis et al. 2007b, Nesbitt et al. 2009a, 2009b) and elsewhere around the world (Martínez et al. 2012, 2016, Cabreira et al. 2016, Garcia et al. 2019). Some putative theropods such as *Eucoelophysis baldwini* Sullivan and Lucas (1999) and putative ornithischians such as *Technosaurus smalli* Chatterjee (1984) were demonstrated to belong to these non-dinosaur dinosauriform groups thanks to the discovery of *Silesaurus opolensis* Dzik (2003) from the Late Triassic of Poland and redistribution of formerly dinosaurian apomorphies down the stem-dinosaur tree (Parker et al. 2006, Ezcurra 2006, Nesbitt et al. 2007, 2017, Nesbitt 2011, Müller et al. 2018a, Martz and Small 2019).

Here we provide an updated taxonomic and stratigraphic survey of dinosauriforms from the Chinle Formation of the American Southwest considering the ongoing reshuffling of the dinosauriform evolutionary tree, increased stratigraphic and geochronological controls on dinosauriform-bearing units around the Colorado Plateau, and new fossils from Petrified Forest National Park. We emphasize the continued use of an apomorphy-based approach to identify new fossils from PEFO, so that they can be used in future studies on dinosauriform evolutionary history and geobiology. We also discuss and compare the global record of Late

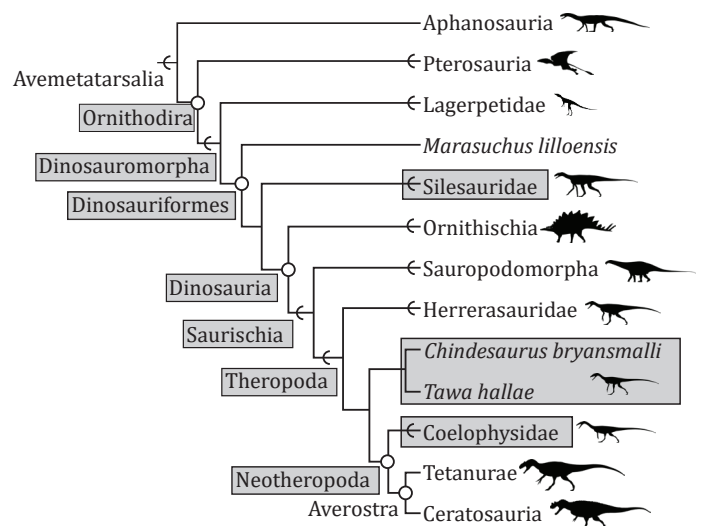
Triassic dinosauriforms.

## MATERIALS AND METHODS

### The available dinosauriform fossil record at PEFO

The material examined in this study includes both new PEFO specimens and those that have been mentioned or figured briefly elsewhere, either as catalogued or unnumbered specimens (Table 1). All the specimens were surface collected from the Blue Mesa Member (BMM), Sonsela Member (SM), or Petrified Forest Member (PFM) in the Chinle Formation without consolidant and adhesive, with the exception of PEFO 10395, PEFO 21373/UCMP 129618, and PEFO 33983, which were collected in field jackets. Similar to the study by Lessner et al. (2018), we identified each specimen to the least inclusive ornithodiran clade using discrete apomorphies (Bell et al. 2004, 2010, Nesbitt and Stocker 2008). Figure 3 displays the phylogenetic hypothesis used for Avemetatarsalia (Nesbitt et al. 2017, Marsh et al. 2019a), and Table 2 lists the literature from which apomorphies for specific groups were chosen. The apomorphies and character states are cited below as ‘Author, Year:character-state’. For example, character state 1 of character 565 in Ezcurra (2016) is cited as ‘(Ezcurra 2016:565-1)’. Note that we use Coelophysidae Nopsca (1923) when referring to the clade of neotheropods comprising *Coelophysis bauri* and its closest relatives instead of Coelophysoidea Nopsca (1928), because of the ambiguity

**Figure 3.** Hypothesized phylogenetic relationships of Avemetatarsalian archosaurs identified in this study (Nesbitt et al. 2017, Marsh et al. 2019a). Gray boxes highlight the clades represented by specimens described here. Silhouettes used from [phylopic.org]; see acknowledgements for full credit to artists.



**Table 1.** Previously published dinosaur morph specimens from Petrified Forest described in this study.

Specimen	References
PEFO 10395	Long and Murry 1995: p. 172–180, figs. 176–179, figs. 182–190, Marsh et al. 2019a: p. e1645682-2–13, figs. 2–4, figs. 6–9.
PEFO 21373/ UCMP 129618	Long and Murry 1995: p. 188, 238, Padian 1986: p. 48–55, figs. 5.1–5.8.
PEFO 21660/ UCMP 126751	Long and Murry 1995: p. 154, Parker and Irmis 2005: p. 52, fig. 5b, Parker and Martz 2011: p. 243.
PEFO 26678	Parrish and Carpenter 1986: p. 159, Hunt et al. 1998: p. 513.
PEFO 31187	Parker and Irmis 2005: p. 52, figs. 7i–j, Parker and Martz 2011: p. 243.
PEFO 33981	Stocker et al. 2004, Parker and Irmis 2005: p. 52, Nesbitt et al. 2007: p. 222, Parker and Martz 2011: p. 244.
PEFO 33982	Stocker et al. 2004; Parker and Irmis 2005: p. 52, fig. 7a, Nesbitt et al. 2007: p. 226 (incorrectly labelled for PEFO 10395 in fig. 4 and fig. 7), Parker and Martz 2011: p. 244; Stocker 2013: p. 108 (incorrectly labelled for PEFO 10395 in fig. 4 and fig. 7), Langer et al. 2017a (incorrectly labelled for PEFO 10395 supplementary information), Marsh et al. 2019a: p. e1645682-3, fig. 8a–e.
PEFO 33983	Stocker et al. 2004, Parker and Irmis 2005: p. 52, fig. 7f, Nesbitt et al. 2007: p. 222.
PEFO 33984	Parker and Irmis 2005: p. 52, figs. 7g–h (incorrectly labelled as PEFO 33987 in figure caption).
PEFO 34347	Parker et al. 2006: fig. 1a–c, Nesbitt et al. 2007: p. 214, fig. 2h–j, Parker and Martz 2011: p. 242.
PEFO 34562	Parker and Martz 2011: p. 245.
PEFO 34583	Marsh et al. 2019a: p. e1645682-3
PEFO 34605	Marsh et al. 2019a: p. e1645682-3, fig. 8f–j.
PEFO 34875	Marsh et al. 2019a: p. e1645682-3, fig. 8k–o
PEFO 35117	Parker and Martz 2011: p. 241.
PEFO 40753	Marsh et al. 2019a: fig. 8p–u.
PEFO 40754	Marsh et al. 2019a: p. e1645682-3
PEFO 43909	Hunt et al. 1996: p. 58, Hunt and Wright 1999: p. 97.

**Table 2.** Reference studies used for apomorphy-based identifications from relevant clades.

Clade	Element(s)	Reference study
Ornithodira	Metatarsal I	Nesbitt (2011), Ezcurra (2016)
Dinosauromorpha	Femur, tibia	Novas (1992), Nesbitt (2011)
Dinosauriformes	Scapula	Nesbitt (2011)
Silesauridae	Femur	Nesbitt (2011)
Dinosauria	Femur	Nesbitt (2011)
Saurischia	Femur	Nesbitt (2011)
Theropoda	Vertebrae, pubis	Nesbitt (2011)
<i>Chindesaurus</i> + <i>Tawa</i>	Femur, tibia, astragalus	Marsh et al. (2019a)
Neotheropoda	Femur, tibia, astragalus	Rauhut (2003), Nesbitt (2011)
Coelophysidae	Ilium, astragalus	Tykoski (2005), Marsh and Rowe (2020).

surrounding the membership of the latter clade. Taxa that were considered non-coelophysid coelophysoids such as *Dilophosaurus wetherilli* Welles (1954) and *Zupaysaurus rougieri* Arcucci and Coria (2003) (e.g., Carrano et al. 2005, Ezcurra and Novas 2007, Hendrickx and Mateus 2014) are hypothesized to be closer to averostran neotheropods (Ezcurra 2017, Zahner and Brinkmann 2019, Marsh and Rowe 2020). *Liliensternus liliensterni* Huene (1934) and *Lepidus praecisio* Nesbitt and Ezcurra (2015) are either recovered as coelophysoids or in a polytomy of neotheropods (Nesbitt and Ezcurra 2015, Martínez et al. 2017, Marsh and Rowe 2020). For the sake of this study, we consider Coelophysidae to include taxa such as *C. bauri*, *Megapnosaurus rhodesiensis* Raath (1969), ‘*Syntarsus*’ *kayentakatae* Rowe (1989), and *Camposaurus arizonensis* Hunt et al. (1998). We refrain from assigning any specimen described here to *Coelophysis*, because *C. bauri*, *M. rhodesiensis*, and ‘*Syntarsus*’ *kayentakatae* are all in need of thorough redescriptions and apomorphic diagnoses in light of the more recently-named coelophysid taxa (e.g., You et al. 2014, Ezcurra 2017, Martínez and Apaldetti



**Table 3.** List of Petrified Forest dinosaur morph specimens described in this study organized by clade and stratigraphic member. Abbreviations: **BMM**, Blue Mesa Member; **L**, left; **PFV**, Petrified Forest vertebrate locality; **PFM**, Petrified Forest Member; **R**, right; **SM**, Sonsela Member.

Apomorphy-based identification	Specimen	Element	PFV locality	Chinle Formation member	Figure
Ornithodira	PEFO 36741	Metatarsal I, II, L	215	PFM	4A–E
	PEFO 44217	Metatarsal I, R	217	BMM	4F–J
Dinosauromorpha	PEFO 44476	Tibia, R	456	BMM	4K–O
Dinosauriformes	PEFO 26678	Scapula, R	262	BMM	4P
	PEFO 46207	Scapulocoracoid, R	278	PFM	4Q
Silesauridae	PEFO 34347	Femur, R proximal end	122	BMM	5D–F
	PEFO 35117	Femur, L proximal end	337	BMM	5P–R
	PEFO 38279	Femur, R proximal	288	BMM	5G–I
	PEFO 39373/ UWBM 108379	Femur, L proximal	410	SM	5J–L
	PEFO 43474	Femur, L proximal end	345	SM	5M–O
	PEFO 44460	Femur, R proximal end	451	PFM	5A–C
Dinosauria	PEFO 34583	Femur, L proximal end	332	PFM	6E, 6F
	PEFO 34863	Femur, L proximal end	215	PFM	6G, 6H
	PEFO 44475	Femora, L and R proximal ends	376	PFM	6A–D
Saurischia	PEFO 21660/ UCMP 126751	Femur, R distal end	071	PFM	6I, 6J
	PEFO 33956	Femur, R distal end	231	PFM	6K, 6L
	PEFO 34562	Femur, L distal end	184	PFM	6O, 6P
	PEFO 42987/ UWBM 117640	Femur, L distal end	410	SM	6S, 6T
	PEFO 44469	Femur, R distal end	451	PFM	6M, N
	PEFO 44474	Femur, L distal end	492	PFM	6Q, R
Theropoda	PEFO 38710	Presacral and sacral vertebrae	302	PFM	7A–L
	PEFO 44470	Pubis, R distal end	453	PFM	7M–O
<i>Chindesaurus bryansmalli</i>	PEFO 10395	Partial skeleton	020	PFM	8A–C, 8M–O, 9M, 9N
<i>Chindesaurus</i> + <i>Tawa</i> clade	PEFO 35382	Tibia, R proximal end	231	PFM	9G, 9H
	PEFO 33982	Femur, L proximal end	231	PFM	8D–F
	PEFO 33988	Femur, L proximal end	231	PFM	8G–I
	PEFO 34085	Femur, R proximal end	231	PFM	8P–R
	PEFO 34605	Femur, R distal end, tibia, L proximal end and R distal end	231	PFM	9A–F
	PEFO 34875	Femur, R proximal end	089	SM	8S–U
	PEFO 39273/ UWBM 108212	Femur, L proximal end	410	SM	8J–L
	PEFO 39422/ UWBM 108882	Tibia, R proximal end	410	SM	9I, 9J
	PEFO 40753	Astragalus	089	SM	9K, 9L
	PEFO 40754	Femur, R proximal end	451	PFM	8V–X
Neotheropoda	PEFO 31187	Femur, R proximal end	089	SM	10A–C

**Table 3. (continued).** List of Petrified Forest dinosauriform specimens described in this study organized by clade and stratigraphic member. Abbreviations: **BMM**, Blue Mesa Member; **L**, left; **PFV**, Petrified Forest vertebrate locality; **PFM**, Petrified Forest Member; **R**, right; **SM**, Sonsela Member.

Apomorphy-based identification	Specimen	Element	PFV locality	Chinle Formation member	Figure
	PEFO 33984	Femur, L proximal end	231	PFM	11J-L
	PEFO 34079	Femur, L proximal end	231	PFM	11G-I
	PEFO 34080	Tibia, R proximal end	231	PFM	12E, 12F
	PEFO 34613	Femur, L proximal end	231	PFM	11D-F
	PEFO 38714	Femur, R proximal end	302	PFM	10G-I
	PEFO 39421/ UWBM 108881	Tibia, R proximal end	410	SM	12C, 12D
	PEFO 39563/ UWBM 109902	Femur, L proximal end	410	SM	11M-O
	PEFO 43506	Femur, L proximal end	475	PFM	11A-C
	PEFO 43550	Femur, R proximal end	475	PFM	10J-L
	PEFO 43909	Tibia, R proximal end	211	BMM	12A, 12B
	PEFO 44468	Tibia, L proximal end	451	PFM	12G, 12H
	PEFO 44472	Femur, R proximal end	475	PFM	10D-F
	PEFO 44473	Femur, R proximal end	477	PFM	10M-O
Coelophysidae	PEFO 21373/ UCMP 129618	Partial skeleton	040	PFM	13A-M
	PEFO 33981	Partial skeleton	231	PFM	14A-L
	PEFO 33983	Partial skeleton	231	PFM	15A-I

2017). The stratigraphic and geographic locations of the PEFO dinosauriform specimens described here from the Chinle Formation at PEFO are shown in Figure 2. Table 3 is a list of these dinosauriform specimens, and comparative linear measurements for each specimen are provided in [Supplemental Materials 1](#).

### Institutional abbreviations

**AMNH**, American Museum of Natural History, New York City, New York, U.S.A.; **BP**, Evolutionary Studies Institute (formerly the Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa; **CAPPA/UFSM**, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria, Santa Maria, Brazil; **DMNH**, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GPIM**, Geological-Palaeontological Institute and Museum of the University of Hamburg, Hamburg, Germany; **GR**, Ruth Hall Museum of Paleontology and Ghost Ranch, Abiquiu, New Mexico, U.S.A.; **GRCA**, Grand Canyon National Park, Arizona, U.S.A.; **MACN**, Museo Argentino de

Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; **MCN**, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sol, Porto Alegre, Brazil; **MCP**, Museo de Ciências e Tecnologia PUCRS, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **MWC**, Museum of Western Colorado, Fruita, Colorado, U.S.A.; **NHMUK**, Natural History Museum of London, London, United Kingdom; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania; **TTU-P**, Museum of Texas Tech University Paleontology, Lubbock, Texas, U.S.A.; **PEFO**, Petrified Forest National Park, Arizona, U.S.A.; **PULR**, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SAM-PK**, Iziko South African Museum, Cape Town, South Africa; **TMM**, Texas Memorial Museum collections, Vertebrate Paleontology Laboratory, University of Texas at

Austin, Austin, Texas, U.S.A.; **UCM**, University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah, U.S.A.; **UWBM**, University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, U.S.A.; **ULBRA**, Universidade Luterna do Brasil, Canoas, Brazil; **WTAMU**, West Texas A&M University, Canyon, Texas, U.S.A.; WUPA, Wupatki National Monument, Arizona, U.S.A.; **YPM**, Yale Peabody Museum, New Haven Connecticut, U.S.A.; **ZPAL**, Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland.

#### SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA COPE, 1869 *SENSU* NESBITT, 2011

AVEMETATARSALIA BENTON, 1999 *SENSU* NESBITT ET AL., 2017

ORNITHODIRA GAUTHIER, 1986 *SENSU* NESBITT ET AL., 2017

FIG. 4A–J

**Referred specimens and localities**—PEFO 36741 (Fig. 4A–E), left metatarsal I, PFV 215: Zuni Well Mound, PFM; PEFO 44217 (Fig. 4F–J), right metatarsal I, PFV 217: Dinosaur Wash, BMM.

**Description and rationale for assignment**—Metatarsals I of PEFO 36741 and PEFO 44217 are proportionally long and slender metapodials and, as observed by the crushing of PEFO 34741, hollow. The proximal end of PEFO 34371 is twisted with respect to the distal end. In proximal view, the medial surface is nearly straight where it would articulate with metatarsal II, and the lateral edge is rounded, making a subtriangular proximal outline (Fig. 4D, I). The proximal outline is mediolaterally narrow, which indicates that the metatarsus was compact, not splayed (Ezcurra 2016:565-1). A compact metatarsus is present in ornithodirans and some early crocodylomorphs (Nesbitt 2011, Ezcurra 2016). The proximal surface of PEFO 36741 and PEFO 44217 is flat, would articulate with the distal tarsals, and would reach the proximal extent of metatarsal II, unlike in neotheropods where metatarsal I is more distally placed along the back of the metatarsus (Rauhut 2003, Nesbitt 2011:385-1). The distal end is asymmetrical, such that the medial condyle is more prominent than the lateral (Fig. 4E, J). Both distal condyles have a collateral ligament fossa. In dorsal view, the medial condyle projects distally further than the lateral. The distal condyles of metatarsal I in the crocodylomorphs *Protosuchus richardsoni* Brown (1933) (AMNH FR 3024), Colbert and Mook 1951: fig. 20b) and *Terrestrisuchus gracilis* Crush (1984) are not

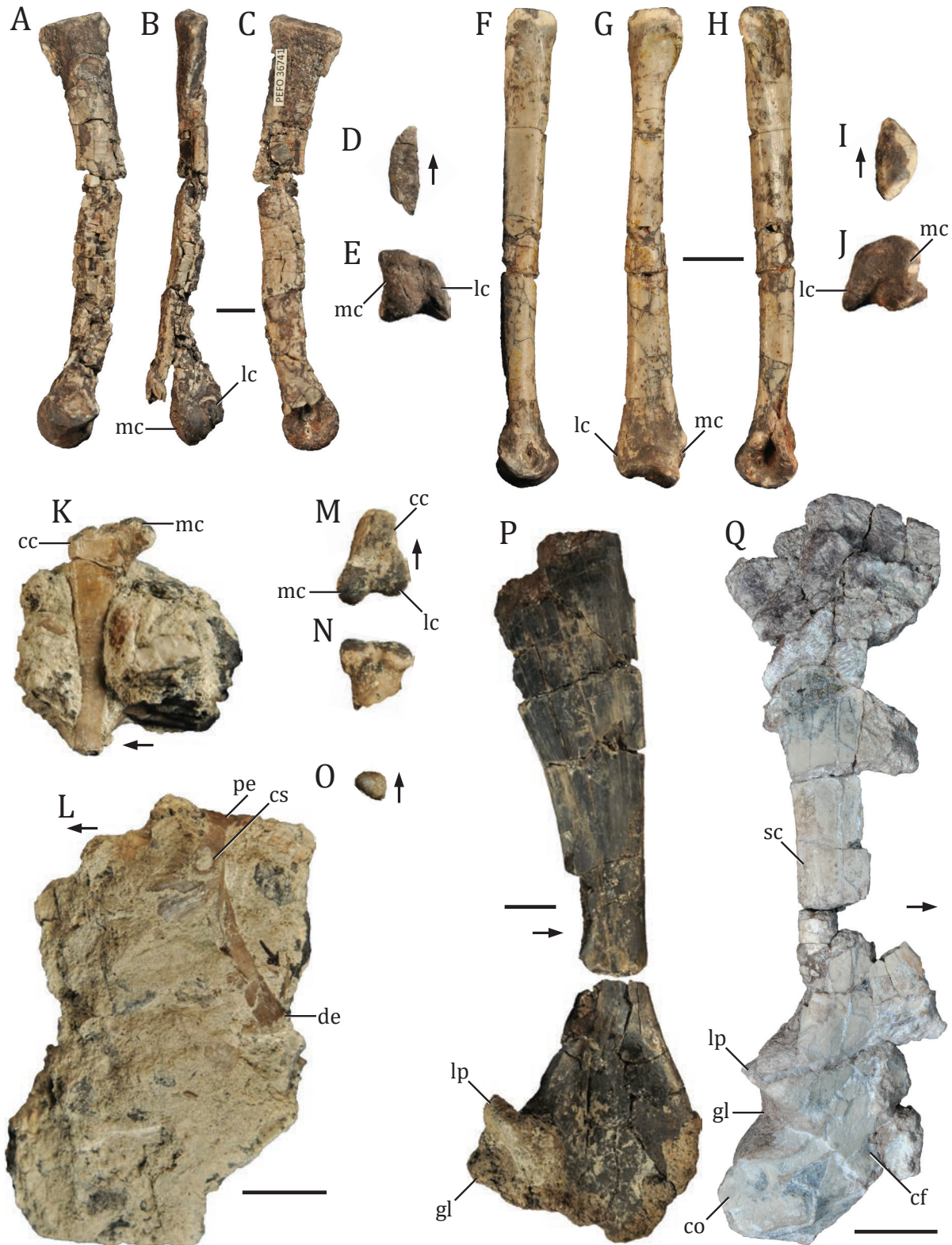
asymmetrical (Crush 1984: fig. 10e). Asymmetrical distal condyles of metatarsal I are found in *Heterodontosaurus tucki* Crompton and Charig (1962, SAM-PK-K1332) (Santa Lucas 1980: fig. 20b), *Eoraptor lunensis* Sereno et al. (1993, PVSJ 512) (Sereno et al. 2012: fig. 91b), *Saturnalia tupiniquim* Langer et al. (1999, MCP PV 3844) (Langer 2003: fig. 7e), *Herrerasaurus ischigualastensis* Reig (1963, PVSJ 373) (Novas 1993: fig. 9j) and *Coelophysis bauri* (MNA V3320, Nesbitt 2011: fig. 48f), but not in the non-dinosaur dinosauriform *Asilisaurus kongwe* Nesbitt et al. (2010, NMT RB159) (Nesbitt et al. 2019: fig. 53e). The PEFO specimens are identical to metatarsal I of GR 1033 (Nesbitt et al. 2009a: fig. 2j), a partial skeleton of *Tawa hallae* Nesbitt et al. (2009a). We assign PEFO 36741 and PEFO 44217 to non-neotheropod Ornithodira owing to the presence of a compact metatarsal I that is not distally positioned down the metatarsus.

DINOSAUROMORPHA BENTON, 1985 *SENSU* SERENO, 1991

FIG. 4K–O

**Referred specimen and locality**—PEFO 44476 (Fig. 4K–O), right tibia, PFV 456: Thunderstorm Ridge, BMM.

**Description and rationale for assignment**—PEFO 44476 is a small complete tibia, but broken at its midlength and the distal half makes a right angle with the proximal half (Fig. 4L). The shaft where broken is hollow and subcircular in cross section. The proximal end comprises two prominent posterior condyles and a short, rounded cnemial crest. The posterior condyles are rounded posteriorly and are divided by a wide, concave posterior intercondylar notch (Fig. 4M). The lateral condyle is offset anteriorly relative to the medial condyle as it is plesiomorphically in ornithodirans, as opposed to the condition in theropods in which the two condyles are in line with one another posteriorly (Nesbitt 2011:331-1). The proximal surface is crushed between the posterior condyles and cnemial crest. The cnemial crest projects straight anteriorly as it does in dinosauromorphs (Novas 1992:4-1, Nesbitt 2011:328-1) such as *Dromomeron romeri* Nesbitt et al. (2007, GR 220) (Nesbitt et al. 2009b: fig. 4c) and *D. gregorii* Nesbitt et al. (2009b, TMM 31100-278: fig. fc), *Marasuchus lilloensis* Sereno and Arcucci (1994, PVL 3871: fig. 10c, d), and *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 45a), not anterolaterally like that of dinosaurs (Nesbitt 2011:328-2) such as *Saturnalia tupiniquim* (MCP PV 3844, Langer 2003: fig. 5g), *Tawa hallae* (GR 242, Marsh et al. 2019a: fig. 5g), and *Dilophosaurus wetherilli* (UCMP 37302, Marsh and Rowe 2020: figs. 21.5, 21.11). The proximal end of the tibia compares favorably to that of



**Figure 4.** A-E. Left ornithodiran metatarsal I, PEFO 34741 in lateral (A), dorsal (B), medial (C), proximal (D), and distal (E) view. F-J. Right ornithodiran metatarsal I, PEFO 44217 in lateral (F), dorsal (G), medial (H), proximal (I), and distal (J) view. K-O. Right dinosauriform tibia, PEFO 44476 in medial (K), medial (L), proximal (M), posterior (N), and distal (O) view. P. Right dinosauriform scapula, PEFO 26678 in lateral view. Q. Right dinosauriform scapulocoracoid, PEFO 46207 in lateral view. Abbreviations: **cc**, cnemial crest; **cf**, coracoid foramen; **co**, coracoid; **cs**, cross-section; **de**, distal end; **gl**, glenoid; **lp**, lip; **mc**, medial condyle; **pe**, proximal end; **r**, ridge; **sc**, scapula. Scale bars=1 cm, arrows point in anterior direction (note that PEFO 44476 is broken in two pieces within the block, that those are perpendicular to one another in the block, and the written arrow on the matrix in L is a preparation mark and does not indicate direction).

the lagerpetid dinosauriform *Ixalerpeton polesinensis* Cabreira et al. (2016, ULBRA-PVT059: fig. s1f-h). The tibia (Fig. 4O) lacks a groove that separates the anterolateral and posterolateral processes of the distal end of the tibia in dinosauriforms (Nesbitt 2011:338-1). We assign PEFO 44476 to Dinosauriforma owing to its straight cnemial crest.

DINOSAURIFORMES NOVAS, 1992 *SENSU* NESBITT, 2011

FIG. 4P-Q

**Referred specimens and localities**—PEFO 26678 (Fig. 4P), right scapula, PFV 262: Blue Mesa Stump Field NE, BMM; PEFO 46207 (Fig. 4Q), right scapulocoracoid, PFV 278: Jeremiah's Perch, PFM.

**Description and rationale for assignment**—A scapula from the Bull Canyon Formation at Revuelto Creek, New Mexico reminiscent of PEFO 26678 was originally identified as that of a 'procompsognathid' (i.e., coelophysid) similar to *Lilliensternus lilliensterni* Huene (1934) (Parrish and Carpenter 1986). PEFO 26678 is mostly complete except for a small segment at the base of the blade, and the dorsal end of the blade is worn and incomplete. PEFO 46207 includes the posterodorsal portion of the coracoid, but the posterior part of the blade of the scapula is incomplete. In lateral view (Fig. 4P, Q) the anterior and posterior margins of the scapulae are concave. The scapular blade is mediolaterally flat and expands anteroposteriorly dorsally. Even given the missing segment of PEFO 26678, both specimens are relatively long; the blade is more than three times longer dorsoventrally than its dorsal anteroposterior width, which is a feature shared among Dinosauriformes (Nesbitt et al. 2009a, Nesbitt 2011:218-1). Also shared with the dinosauriforms *Marasuchus lilloensis* (PVL 3871, Bonaparte 1971: fig. 8), silesaurids, e.g., *Silesaurus opolensis* (ZPAL Ab III/361/23, Dzik 2003: fig. 9a), and *Lewisuchus admixtus* Romer (1972, PULR 01) (Bittencourt et al. 2014: fig. 10a-b), and dinosaurs, e.g., *Herrerasaurus ischigualastensis* (PVSJ 53, Sereno 1993: fig. 1a), *Saturnalia tupiniquim* (MCP PV 3844, Langer et al. 2007: fig. 4a), and 'Syntarsus' *kayentakatae* (MNA V2623, Rowe 1989: fig. 2) is a posteroventrally-oriented glenoid of the scapula (Nesbitt 2011:227-1). The glenoid itself is overlain by a lip of bone. The supraglenoid surface lacks the scar present in *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 30a, 30c) and *Saturnalia tupiniquim* (MCP PV 3844, Langer et al. 2007: fig. 4a). We assign PEFO 26678 and PEFO 46207 to Dinosauriformes owing to the relatively long scapular blade and posteroventrally-oriented glenoid.

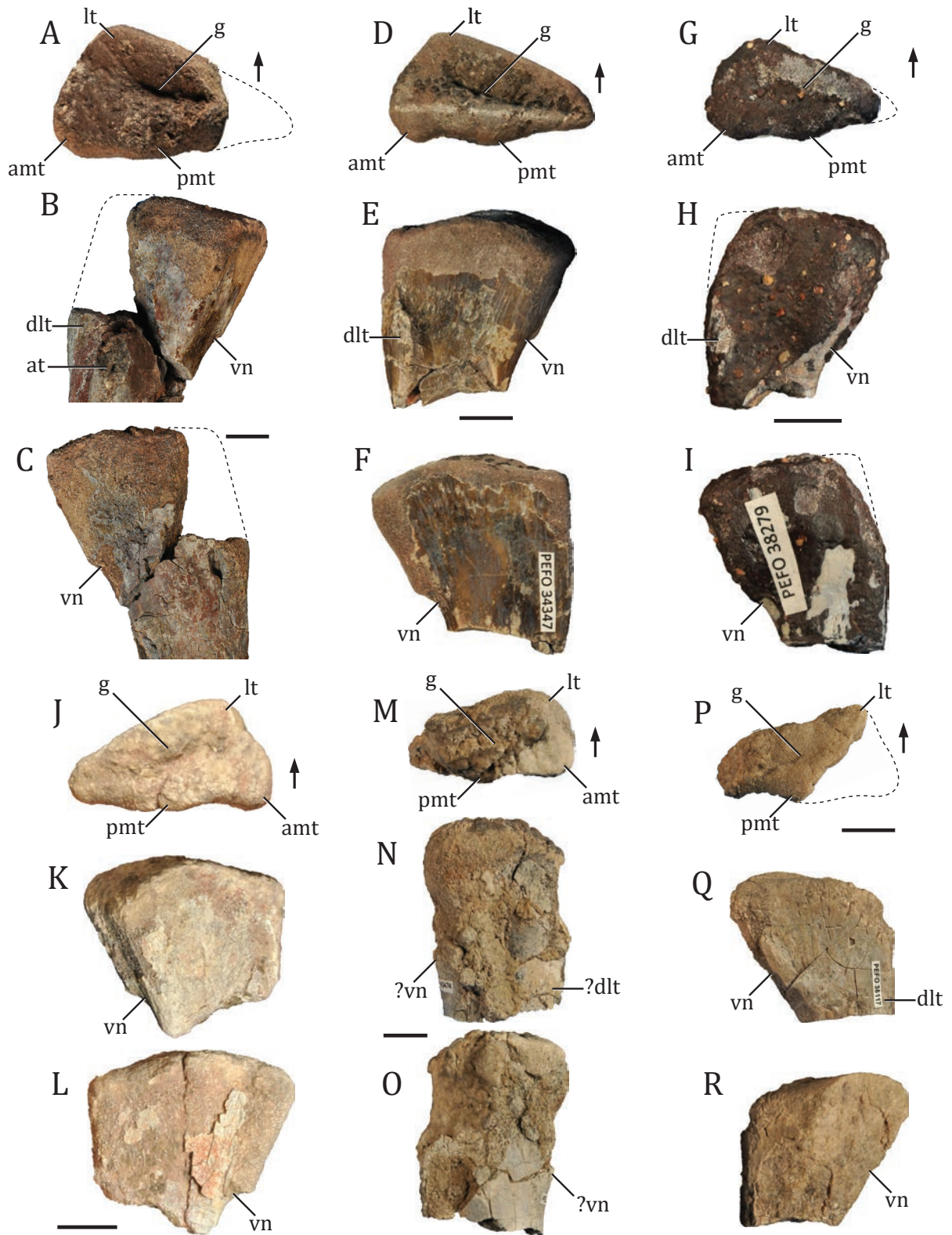
SILESAURIDAE NESBITT ET AL., 2010

FIG 5A-R

**Referred specimens and localities**—PEFO 44460 (Fig. 5A-C), proximal end of right femur, PFV 451: Black Knoll E, PFM; PEFO 34347 (Fig. 5D-F), proximal end of right femur, PFV 122: The Dying Grounds, UCMP V7038, BMM; PEFO 38279 (Fig. 5G-I), proximal end of right femur, PFV 288: Lot's Wife, BMM; PEFO 39373/UWBM 108379 (Fig. 5J-L), proximal end of left femur, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM; PEFO 43474 (Fig. 5M-O), proximal end of left femur, PFV 354: Flattops NE, Martha's Butte beds, SM; PEFO 35117 (Fig. 5P-R), proximal end of left femur, PFV 337: Valley of the Dead, BMM.

**Description and rationale for assignment**—All of these specimens represent proximal ends of femora. PEFO 44460 (Fig. 5A-C) is nearly the same size as the large silesaurid reported from the Middle Triassic of Tanzania (NHMUK R16303, Barrett et al. 2015). The PEFO femora have the three proximal condyles that are present plesiomorphically in ornithodirans (the lateral tuber, anteromedial tuber, and posteromedial tuber) (Nesbitt 2011), and the posteromedial tuber is small (Nesbitt 2011:301-0), unlike the relatively large posteromedial tuber found in lagerpetid dinosauriforms, e.g., *Dromomeron romeri* (GR 218) and *D. gregorii* (TMM 31100-1306, Nesbitt et al. 2009b: figs. 1C, 2c, respectively), and some suchian archosaurs such as *Revueltosaurus callenderi* (PEFO 34561), aetosaurs, e.g., *Typhothorax coccinarum* Cope (1875) (UCMP 34238, Nesbitt 2011: fig. 38a), and ornithosuchids, e.g., NHMUK PV R 3561 (Walker 1964: fig. 12d). The posteromedial tuber is so reduced (e.g., Fig. 5D) that it is identical to those that have been scored as 'absent' in *Silesaurus opolensis* (ZPAL Ab III/361/23, Dzik 2003: fig. 13a) and *Eucoelophysis baldwini* (NMMNH P-22298, Sullivan and Lucas 1999: fig. 6c), which is apomorphic for Silesauridae and creates a subtriangular proximal outline of the femur (Nesbitt 2011:301-2).

A straight transverse groove is present on the proximal surface of the femora (Nesbitt 2011:314-1) (Fig. 5D), similar to that of silesaurids, e.g., *Si. opolensis* (ZPAL Ab III/361/23, Dzik 2003: fig. 13a), and *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 42a), herrerasaurids, e.g., *Staurikosaurus pricei* Colbert (1970) (MCZ 1669, Bittencourt and Kellner 2009: fig. 26a), and early saurpodomorphs, e.g., *Saturnalia tupiniquim* (MCP PV 3844, Langer et al. 2003: fig. 4c) and *Buriolestes schultzzi* Cabreira et al. (2016, ULBRA-PVT280: fig. s2d). The development of this groove is owing to the presence of a cartilaginous cone on the proximal end of the femur in



**Figure 5.** A–C. Proximal end of right silesaurid femur, PEFO 44460 in proximal (A), anterior (B), and posterior (C) view. D–F. Proximal end of right silesaurid femur, PEFO 34347 in proximal (D), anterior (E), and proximal (F) view. G–I. Proximal end of right silesaurid femur, PEFO 39373/UWBM 108379 in proximal (G), anterior (H), and posterior (I) view. J–L. Proximal end of left silesaurid femur, PEFO 35117 in proximal (J), anterior (K), and posterior (L) view. M–O. Proximal end of left silesaurid femur, PEFO 43474 in proximal (M), anterior (N), and posterior (O) view. P–Q. Proximal end of left silesaurid femur, PEFO 35117 in proximal (P), anterior (Q), and posterior (R) view. Abbreviations: **amt**, anteromedial tuber; **at**, anterior trochanter; **dlt**, dorsolateral trochanter; **g**, groove; **lt**, lateral tuber; **pmt**, posteromedial tuber; **vn**, ventral notch. Scale bars=1 cm, arrows point in anterior direction, and dashed lines indicate inferred outlines.

archosaurs (Tsai et al. 2018), which is ontogenetically variable (Griffin 2018). All PEFO specimens except PEFO 43474 and PEFO 39373/UWBM 108379 preserve a sharp ridge-like dorsolateral trochanter, or attachment for the *m. ischiotrochantericus* (Piechowski et al. 2020), on the anterolateral surface of the femur (Nesbitt 2011:307-1) (Fig. 5E), which is found in silesaurids, e.g., *E. baldwini* (NMMNH P-22298, Sullivan and Lucas 1999: fig. 6a), *Kwanasaurus williamparkeri* Martz and Small (2019, DMNH EPV.54828: fig. 17e), and *Si. opolensis* (ZPAL Ab III/361/21, Piechowski et al. 2020: fig. 19b), and some early ornithischian dinosaurs, e.g., *Lesothosaurus diagnosticus* Galton (1978, NHMUK RU B17) (Baron et al. 2017a: fig. 14a), *Eocursor parvus* (SAM-PK-K8025, Butler 2009: fig. 15e), and *Scutellosaurus lawleri* Colbert (1981, MNA V1752: fig. 25). The development of this feature is also ontogenetically variable (Piechowski et al. 2014, Griffin and Nesbitt 2016).

Perhaps the most obvious apomorphy of Silesauridae present in the PEFO femora, excluding the heavily weathered PEFO 43474, is the notch presented ventromedial to the femoral head (Nesbitt 2011:304-1) (Fig. 5F), which is present in early silesaurids such as *As. kongwe* (NMT RB19, Nesbitt et al. 2010: fig. 2k), as well as later-diverging silesaurids such as *K. williamparkeri* (DMNH EPV 54828, Martz and Small 2019: fig. 17b) and *E. baldwini* (NMMNH P-22298, Sullivan and Lucas 1999: fig. 6a). The only PEFO specimen complete enough to preserve the anterior trochanter is PEFO 44460 (Fig. 5B). In that specimen, that trochanter is a raised, rounded knob. We assign these femora to the Silesauridae owing to the presence of a ventral notch under the femoral head when preserved and a highly reduced posteromedial proximal tuber that forms a subtriangular proximal outline.

DINOSAURIA OWEN, 1842 *SENSU* PADIAN AND MAY, 1993

FIG. 6A–H

**Referred specimens and localities**—PEFO 44475 (Fig. 6A–D), proximal ends of left and right femora, PFV 376: Scour Sandstone, PFM; PEFO 34583 (Fig. 6E, F), proximal end of left femur, PFV 332: Chinde Valley Pinnacle, PFM; PEFO 34863 (Fig. 6G, H), proximal end of left femur, PFV 215: Zuni Well Mound, PFM.

**Description and rationale for assignment**—These proximal ends of femora are highly fragmentary and weathered; each of them is broken proximal to the fourth trochanter. Each preserves a mound-like anterior trochanter that remains attached to the shaft proximally (Nesbitt 2011:308-1) (Fig. 6D), which is a feature present in Dinosauriformes, e.g., *Marasuchus lilloensis* (PVL

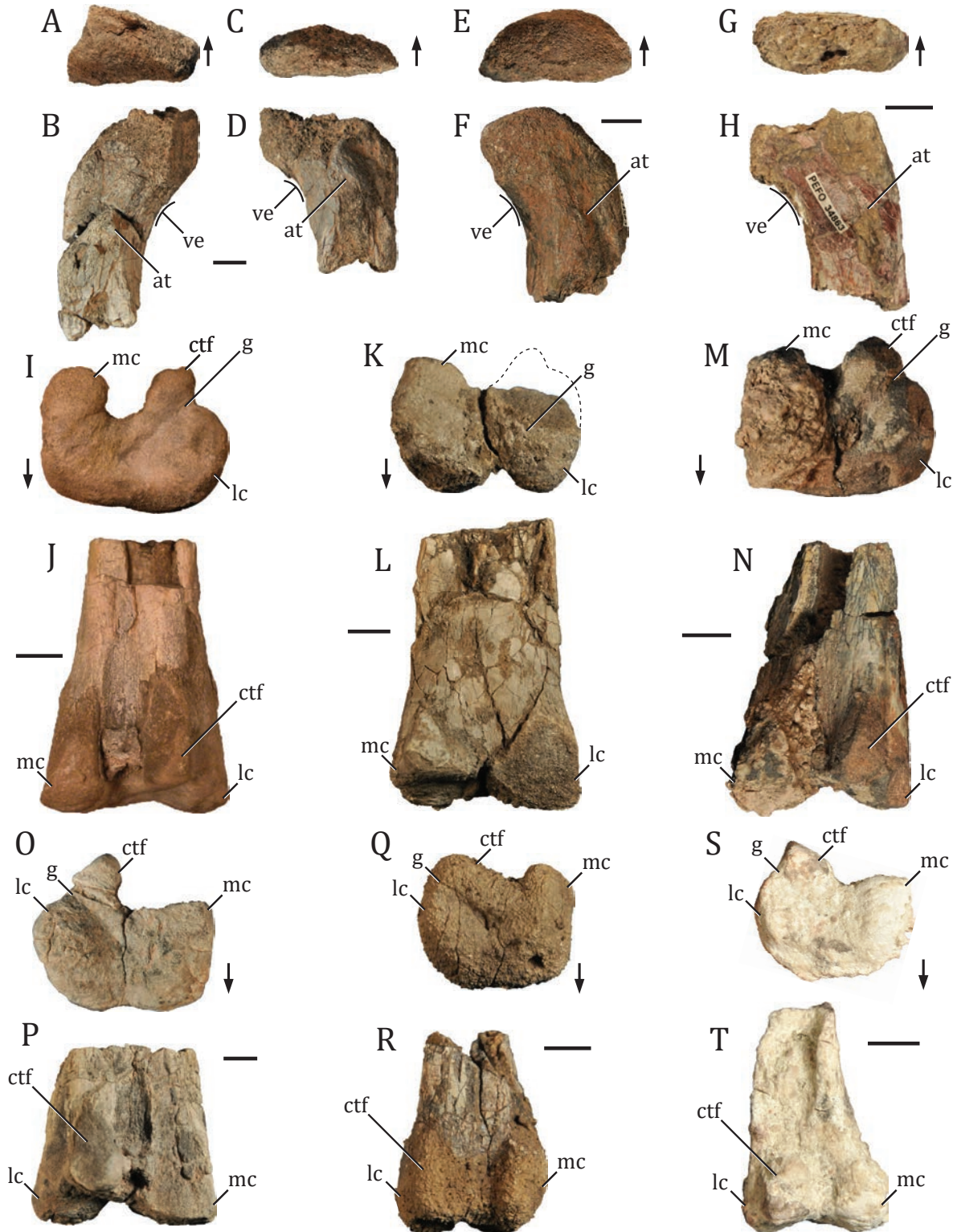
3871, Sereno and Arcucci 1994: fig. 8b), *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 42d), and *Buriolestes schultzi* (ULBRA-PVT280, Cabreira et al. 2016: fig. 1n). Unlike the smooth transition between the ventromedial margin of the femoral head and the shaft (Nesbitt 2011:304-0) found in early dinosauromorphs, e.g., *Lagerpeton chanarensis* Romer (1971, PVL 4619) (Nesbitt et al. 2009b: fig. 3a), and *Dromomeron romeri* (GR 218, Nesbitt et al. 2009b: fig. 1a) and the ventral notch (Nesbitt 2011:304-1) present on silesaurid femora (see above), these femora exhibit a concave emargination ventral to the femoral head (Nesbitt 2011:304-2) (Fig. 6H), which is apomorphic for dinosaurs, e.g., *Eocursor parvus* (SAM-PK-K8025, Butler 2009: fig. 15d), *Eodromaes murphi* Martínez et al. (2011, PVSJ 562: fig. 2k), and *Herrerasaurus ischigualastensis* (PVSJ 373, Novas 1993: fig. 7c). Thus, we assign these fragmentary proximal ends of femora to Dinosauria.

SAURISCHIA SEELEY, 1887 *SENSU* GAUTHIER, 1986 (=EUSAURISCHIA PADIAN ET AL., 1999)

FIG. 6I–T

**Referred specimens and localities**—PEFO 21660/UCMP 126751 (Fig. 6I, J), distal end of right femur, PFV 071: Flattops W, UCMP V82259, PFM; PEFO 33956 (Fig. 6K–L), distal end of right femur, PFV 231: The Giving Site, PFM; PEFO 44469 (Fig. 6M, N), distal end of right femur, PFV 451: Black Knoll E, PFM; PEFO 34562 (Fig. 6O, P), distal end of left femur, PFV 184: Clambake Amphitheater, PFM; PEFO 44474 (Fig. 6Q, R), distal end of left femur, PFV 492: Dead Wash NW2, PFM; PEFO 42987/UWBM 117640 (Fig. 6S, T), distal end of left femur, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM.

**Description and rationale for assignment**—These distal ends of femora are all broken distal to the fourth trochanter, but they all preserve the distal medial and lateral condyles and *crista tibiofibularis*, except PEFO 33956 (Fig. 6K), which is lacking most of the *crista tibiofibularis*. In all of the specimens, a groove divides the lateral condyle and *crista tibiofibularis* in distal view (Nesbitt 2011:322-1) (Fig. 6I), which is a synapomorphy of Saurischia, e.g., *Herrerasaurus ischigualastensis* (PVSJ 373, Novas 1993: fig. 7f), *Saturnalia tupiniquim* (MCP PV 3844, Langer 2003: fig. 4d), and '*Syntarsus kayentakatae*' (MNA V2623). Furthermore, this groove opens posterolaterally in an obtuse angle in distal view in all these specimens. Shuvosaurid pseudosuchians have a similar morphology in the distal end of the femur but can be differentiated as their groove opens at a 90° angle (Parker and Irmis 2005). A similar groove is also



**Figure 6.** A–D. Proximal ends of right and left dinosaur femora, PEFO 44475 in proximal (A, C) and anterior view (B, D). E, F. Proximal end of left dinosaur femur, PEFO 34863 in proximal (E) and anterior (F) view. G, H. Proximal end of left dinosaur femur, PEFO 34863 in proximal (G) and anterior (H) view. I, J. Distal end of right saurischian femur, PEFO 21660/UCMP 126751 in distal (I) and posterior (J) view. K, L. Distal end of right saurischian femur, PEFO 33956 in distal (K) and posterior (L) view. M, N. Distal end of right saurischian femur, PEFO 44469 in distal (M) and posterior (N) view. O, P. Distal end of left saurischian femur, PEFO 34562 in distal (O) and posterior (P) view. Q, R. Distal end of left saurischian femur, PEFO 44474 in distal (Q) and posterior (R) view. S, T. Distal end of left saurischian femur, PEFO 42987/UWBM 117640 in distal (S) and posterior (T) view. Abbreviations: at, anterior trochanter; ctf, crista tibiofibularis; g, groove; lc, lateral condyle; mc, medial condyle; ve, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.



present convergently in lagerpetids (Garcia et al. 2019: fig. 7a–h), but in that group the *crista tibiofibularis* is greatly enlarged and is larger than the medial condyle in distal view (Nesbitt 2011:326-1), e.g., *Dromomeron romeri* (GR 218, Nesbitt et al. 2009b: fig. 1d).

In distal view, the posterior margin of the medial condyle is rounded in PEFO 21660/UCMP 126751 (Fig. 6I), PEFO 44469 (Fig. 6M), and PEFO 44474 (Fig. 6Q), and pointed in PEFO 33956 (Fig. 6K), PEFO 34562 (Fig. 6O), and PEFO 42987/UWBM 117640 (Fig. 6S). A round medial condyle is present in most early dinosaur groups, including ornithischians, e.g., *Eocursor parvus* (SAM-PK-K8025, Butler 2009: fig. 15f), and *Scutellosaurus lawleri* (MNA V175), early sauropodomorphs, e.g., *Buriolestes schultzi* (ULBRA-PVT280, Cabrera et al. 2016: fig. s2e), and *Sa. tupiniquim* (MCP PV 3844, Langer 2003: fig. 4d), early theropods, e.g., *Tawa hallae* (GR 244, Nesbitt 2011: fig. 39b), and *H. ischigualastensis* (PVSJ 373, Novas 1993: fig. 7f), and stem-averostrans, e.g., *Dilophosaurus wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 20.6), and *Cryolophosaurus ellioti* Hammer and Hickey (1994, FMNH PR 4923). A pointed medial condyle is present in the large-bodied coelophysid specimens from PEFO (PEFO 21373/UCMP 129618 and PEFO 33981). In distal view, the *crista tibiofibularis* and lateral condyle are not well separated from one another in PEFO 44474 (Fig. 6Q), much like the condition found in *Chindesaurus bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 7f) and *T. hallae* (GR 244, Nesbitt 2011: fig. 39b). In the other specimens (Fig. 6O), the *crista tibiofibularis* and lateral condyle are distinctly separate structures and resemble the distal outline of theropods such as coelophysids and stem-averostran (Ezcurra 2017: figs. 4.1, 4.3, 4.4, 4.6, 4.7). We assign these distal femora to Saurischia owing to the presence of a groove between the lateral condyle and *crista tibiofibularis* that opens at an obtuse angle in distal view.

THEROPODA MARSH, 1881 *SENSU* GAUTHIER, 1986

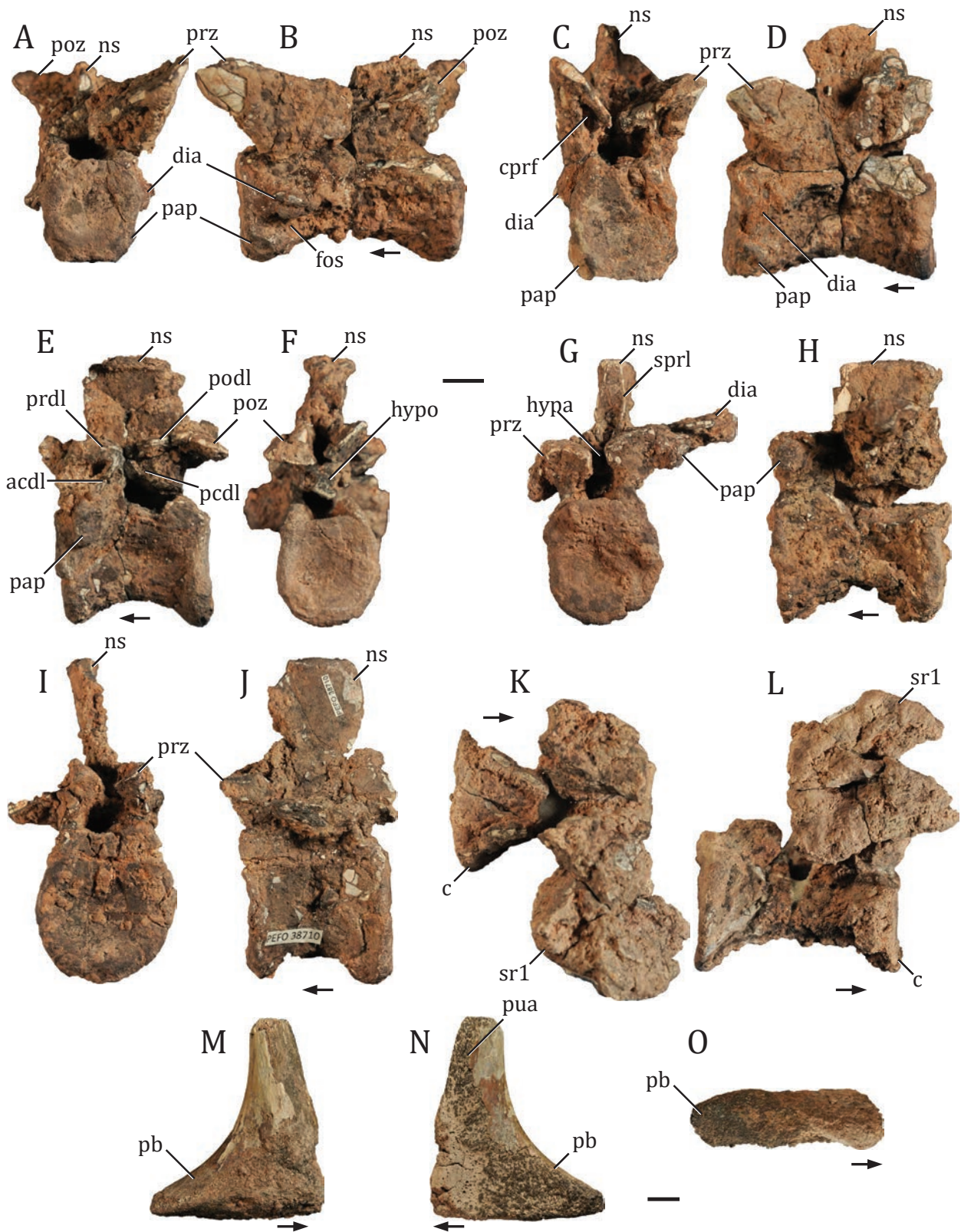
FIG. 7A–O

**Referred specimens and localities**—PEFO 38710 (Fig. 7A–L), presacral and sacral vertebrae, PFV 302: Rabbit Foot Hills, PFM; PEFO 44470 (Fig. 7M–O), distal end of right pubis, PFV 453: Puerco Ridge N, PFM.

**Description and rationale for assignment**—The presacral and sacral vertebrae (PEFO 38710) belong to a single individual and were collected as float; the fossils are covered in carbonate mineralization that obscures some details. The anterior cervical vertebrae (Fig. 7A–D) are relatively more anteroposteriorly elongate than the

more posterior vertebrae. The prezygapophysis of the anterior cervical vertebra is triangular in lateral outline and projects anteriorly past the centrum face. In proximal view the centroprezygapophyseal fossa is present dorsolateral to the neural canal. The diapophysis and parapophysis frame the anterior margin of an anterior pneumatic fossa (Nesbitt 2011:188-1; Fig. 7B); such a fossa is apomorphic for theropod dinosaurs, e.g., *Chindesaurus bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 2a); *Coelophysis bauri* (AMNH FR 2701, Nesbitt 2011: fig. 28a), and *Dilophosaurus wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 7.1). The posterior pneumatic fossa (Nesbitt 2011:129-1) found in coelophysids, e.g., *Coelophysis bauri* (AMNH FR 2701, Nesbitt 2011: fig. 28a), ‘*Syntarsus*’ *kayentakatae* (MNA V2623, Tykoski 1998: fig. 16c–d), and *Lucianovenator bonoi* Martínez and Apaldetti (2017, PVSJ 906: fig. 4) is not present in PEFO 38710. The neural spine of the more posterior cervical vertebra (Fig. 7E, F) is complete and preserves a transverse dorsal expansion, which is also present in several pseudosuchian archosaurs (see discussion in Nesbitt 2011: p. 113), *Eoraptor lunensis* (PVSJ 512, Sereno et al. 2012: fig. 47b), *Herrerasaurus ischigualastensis* (PVL 2566, Novas 1993: fig. 1c), *Ch. bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 2s, t). This vertebra also has a hyposphene ventral to the postzygapophyses, but it is broken at its base. A hypantrum is clearly present on the anterior trunk vertebra (Fig. 7G). The presence of hyposphene-hypantrum articulations in the posterior cervical vertebrae and trunk vertebrae (Nesbitt 2011:195-1) is apomorphic for saurischian dinosaurs, e.g., *Saturnalia tupiniquim* (MCP PV 3845), *Tawa hallae* (GR 241), and *Di. wetherilli* (UCMP 37302), but they are also found in some aetosaurs, ctenosaurischid poposauroids, ‘rauisuchian’ loricatans, *Teleocrater rhadinus* Nesbitt et al., 2017, and some silesaurids (Stefanic and Nesbitt 2019). The first sacral rib (Fig. 7K–L) is located on the anterior half of the first sacral vertebra, and it is C-shaped in lateral view (Langer and Benton 2006, Nesbitt 2011:209-1). This condition is found in saurischian dinosaurs such as *Sa. tupiniquim* (MCP PV 3844, Langer 2003: fig. 1b) and *Ch. bryansmalli* (PEFO 10395, Marsh et al., 2019a: fig. 2w–x). We assign this partial vertebral column to the Theropoda owing to the presence of an anterior pneumatic fossa on the centrum.

PEFO 44470 is an isolated distal end of a right pubis that preserves the base of the pubic apron in medial view and a distinct posterior ‘boot’. The distal end of the shaft and the posterior boot form a right angle anteroventrally (Fig. 7M), and the posterodorsal surface between them



**Figure 7.** A–F. Theropod cervical vertebrae, PEFO 38710 in anterior (A, C), lateral (B, D, E), and posterior (F) view. G–J. Theropod trunk vertebrae, PEFO 38710 in anterior (G, I) and lateral (H, J) view. K, L. Theropod first sacral vertebra, PEFO 38710 in dorsal (K) and lateral (L) view. M–O. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **c**, centrum; **cprf**, centroprezygapophyseal fossa; **dia**, diapophysis; **fos**, fossa; **hypa**, hypantrum; **hypo**, hyposphene; **ns**, neural spine; **pap**, parapophysis; **pb**, pubic boot; **pcdl**, posterior centrodiapophyseal lamina; **podl**, postzygodiapophyseal lamina; **poz**, postzygapophysis; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **pua**, pubic apron; **sprl**, spinoprezygapophyseal lamina; **sr1**, first sacral rib. Scale bars=1 cm, arrows point in anterior direction.

is gently concave. A pubic boot is present in theropod dinosaurs (Nesbitt 2011:283-1) such as *H. ischigualastensis* (PVL 2566, Novas 1993: fig. 5a), *Staurikosaurus pricei* (MCZ 1669, Colbert 1970: fig. 8b), *Gnathovorax cabreirai* Pacheco et al. (2019, CAPP/UFMS 0009: fig. 7a), and *T. hallae* (GR 155, Nesbitt et al. 2009a: fig. 2h), but is also found in some ‘rauisuchian’ (Nesbitt 2011: fig. 35a, c) and poposauroid suchians (Nesbitt 2011: fig. 35e). The ventral margin of the pubic boot of PEFO 44470 and theropods (e.g., *T. hallae*) is fairly straight, but it is greatly concave in pseudosuchian archosaurs such that the pubic boot curves posterodorsally, e.g., *Poposaurus gracilis* Mehl (1915, YPM 57100) (Schachner et al. 2019: fig. 28a), and *Effigia okeeffeae* Nesbitt and Norell (2006, AMNH FR 30587) (Nesbitt 2007: fig. 42). We assign PEFO 44470 to the Theropoda owing to the presence of a posteriorly-straight and relatively short pubic boot. However, if herrerasaurids and *T. hallae* are in fact not theropods but rather earlier-diverging saurischians (Nesbitt and Sues 2020; Müller and Garcia 2020), then PEFO 44470 would also belong to an earlier-diverging dinosaur group.

*CHINDESAURUS BRYANSMALLI + TAWA HALLAE CLADE SENSU MARSH ET AL., 2019A*

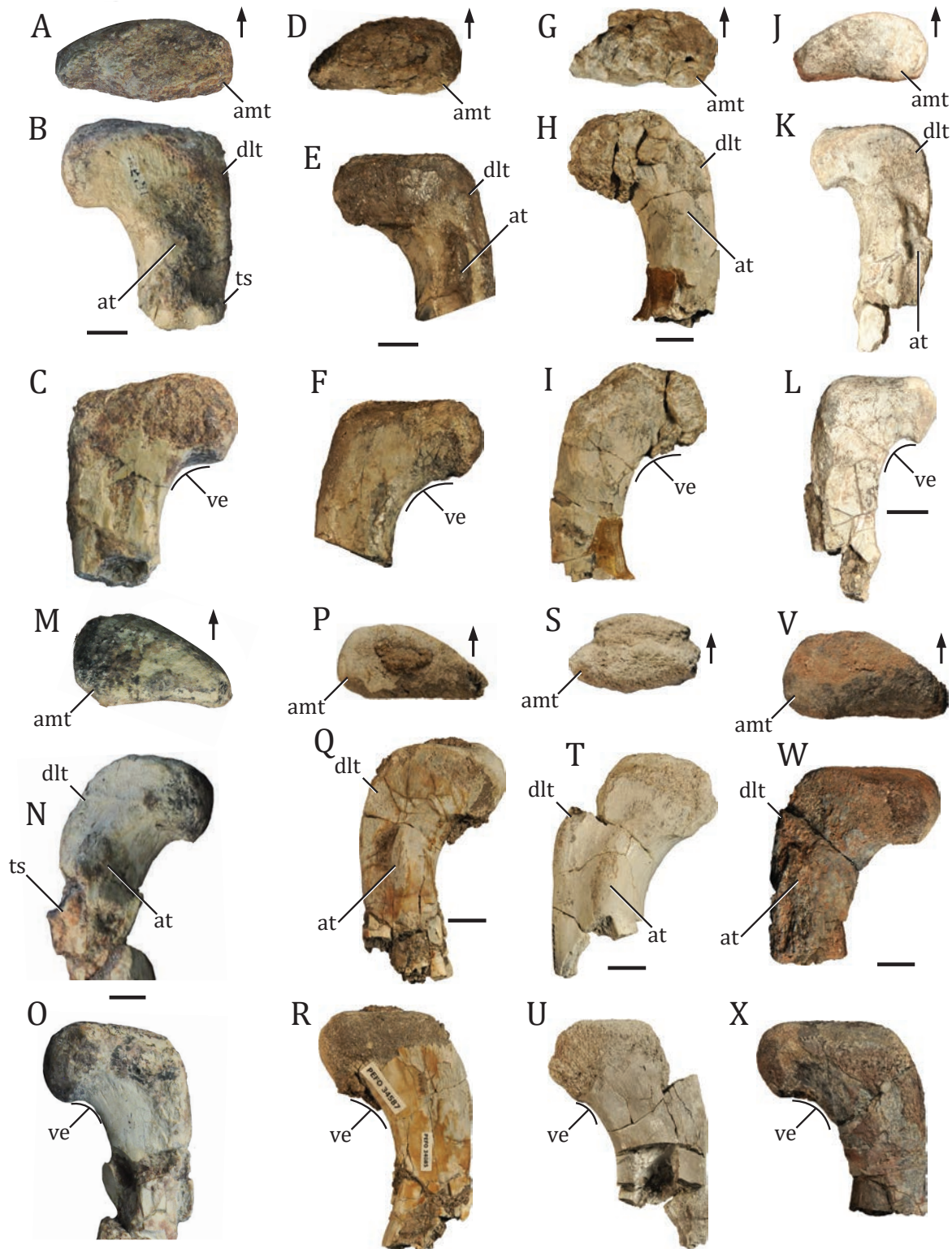
FIGS. 8A–X, 9A–N

**Referred specimens and localities**—PEFO 10395 (Fig. 8A–C, 8M–O, 9M, 9N), proximal ends of left and right femora and right astragalus, PFV 020: Dinosaur Hollow, PFM; PEFO 33982 (Fig. 8D–F), proximal end of left femur and vertebrae, PFV 231: The Giving Site, PFM; PEFO 33988 (Fig. 8G–I), proximal end of left femur, PFV 231: The Giving Site, PFM; PEFO 39273/UWBM 108212 (Fig. 8J–L), proximal end of left femur, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM; PEFO 34085 (Fig. 8P–R), proximal end of right femur, PFV 231: The Giving Site, PFM; PEFO 34875 (Fig. 8S–U), proximal end of right femur, PFV 089: The Bowman Site, UCMP V84127, Jim Camp Wash beds, SM; PEFO 40754 (Fig. 8V–X), proximal end of right femur, PFV 451: Black Knoll E, PFM; PEFO 34605 (Fig. 9A–F), distal end of right femur, proximal end of right tibia, and distal end of left tibia, PFV 231: The Giving Site, PFM; PEFO 35382 (Fig. 9G, H), proximal end of right tibia, PFV 231: The Giving Site, PFM; PEFO 39422/UWBM 108882 (Fig. 9I, J), proximal end of right tibia, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM; PEFO 40753 (Fig. 9K, L), right astragalus, PFV 089: The Bowman Site, UCMP V84127, Jim Camp Wash beds, SM.

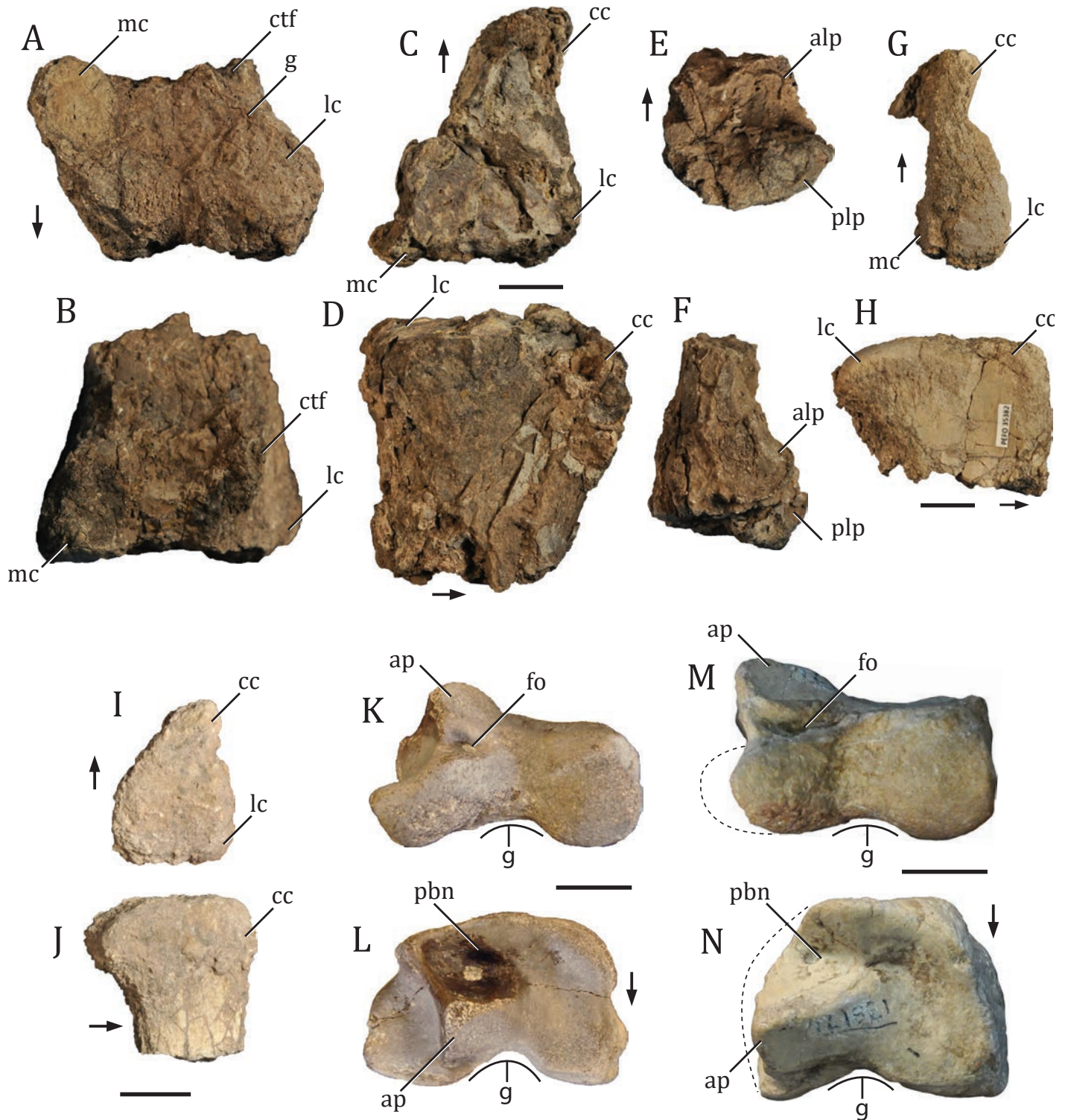
**Description and rationale for assignment**—The proximal ends of femora described here are all broken

proximal to the fourth trochanter. They each have a proportionally proximodistally-long anterior trochanter that is connected to the shaft proximally, as seen in all dinosauriforms (Nesbitt 2011:308-1) (Fig. 8Q). These femora lack the trochanteric shelf found in the holotype specimen of *Chindesaurus bryansmalli* (PEFO 10395) (Fig. 8B, N), but the development of that feature is ontogenetically variable in dinosauriforms (Tykoski 2005, Griffin and Nesbitt 2016, Griffin 2018). The proximal ends of the PEFO femora preserve the ventral emargination beneath the femoral head found in early dinosaurs (Nesbitt 2011:304-2). In proximal view, the proximal tubers found plesiomorphically in avemetatarsalians are fairly reduced (e.g., Fig. 8D); the posteromedial tuber is small as in all dinosauriforms (Nesbitt 2011:308-1) and the femora lack the prominent posteriorly-projecting anteromedial process found in neotheropods (Rauhut 2003, Nesbitt 2011). These femora preserve the unique combination of characters found in the *Ch. bryansmalli* + *Tawa hallae* clade recovered in a recent analysis (Marsh et al. 2019a), including the lack of a transverse groove on the proximal surface (Marsh et al. 2019a:236-0), the presence of a rounded dorsolateral trochanter (Marsh et al. 2019a: 230-2; as opposed to the sharp ridge it forms in silesaurids and some other early dinosaurs, see above), and the absence of the oblique ligament sulcus on the posterior surface of the femoral head (Marsh et al. 2019a:344-0).

The fragmentary skeleton of another specimen assigned here to the *Ch. bryansmalli* + *T. hallae* clade (PEFO 34605) preserves the distal end of a femur with a groove between the *crista tibiofibularis* and lateral condyle (Nesbitt 2011:322-1) present in lagerpetids and saurischian dinosaurs (Fig. 9A), and the proximal and distal ends of tibiae (Fig. 9C–F). Like the isolated proximal ends of tibiae PEFO 35382 and PEFO 39422/UWBM 108882, PEFO 34605 preserves an anterolaterally-directed cnemial crest (Nesbitt 2011: 328-2) (Fig. 9C), which is apomorphic for Dinosauria, as can be observed in *Scutellosaurus lawleri* (MNA V175), *Saturnalia tupiniquim* (MCP PV 3844, Langer 2003: fig. 5g), and ‘*Syntarsus*’ *kayentakatae* (MNA V2623). The cnemial crest of these three PEFO specimens is relatively short (Marsh et al. 2019a:349-1), which is unique to *Ch. bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 9a), *T. hallae* (GR 242, Marsh et al. 2019a: fig. 5g), and *Guaibasaurus candelariensis* Bonaparte et al. (1999) (MCN PV 2356, Langer et al. 2011: fig. 13f). Unfortunately, poor preservation precludes the observation of the second posterior notch in the proximal end of the tibia unique to the *Ch. bryansmalli* + *T. hallae*



**Figure 8.** Proximal ends of theropod femora belonging to the *Chindesaurus bryansmalli* + *Tawa hallae* clade. A–C, M–O. Left and right femora of the holotype specimen of *Chindesaurus bryansmalli*, PEFO 10395 in proximal (A, M), anterior (B, N), and posterior (C, O) view. D–F. Left femur, PEFO 33982 in proximal (D), anterior (E), and posterior (F) view. G–I. Left femur, PEFO 33988 in proximal (G), anterior (H), and posterior (I) view. J–L. Left femur, PEFO 39273/UWBM 108212 in proximal (J), anterior (K), and posterior (L) view. P–R. Right femur, PEFO 34085 in proximal (P), anterior (Q), and posterior (R) view. S–U. Right femur, PEFO 34875 in proximal (S), anterior (T), and posterior (U) view. V–W. Right femur, PEFO 40754 in proximal (V), anterior (W), and posterior (X) view. Abbreviations: **amt**, anteromedial tubercle; **at**, anterior trochanter; **dlt**, dorsolateral trochanter; **ts**, trochanteric shelf; **ve**, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.



**Figure 9.** Hindlimb elements of theropods belonging to the *Chindesaurus bryansmalli* + *Tawa hallae* clade. **A, B.** Distal end of right femur, PEFO 34605 in distal (**A**) and posterior (**B**) view. **C, D.** Proximal end of right tibia, PEFO 34605 in proximal (**C**) and lateral (**D**) view. Distal end of left tibia, PEFO 34605 in distal (**E**) and anterior (**F**) view. **G, H.** Proximal end of right tibia, PEFO 35382 in proximal (**G**), and lateral (**H**) view. **I, J.** Proximal end of right tibia, PEFO 39422/UWBM 108882 in proximal (**I**), and lateral (**J**) view. **K, L.** Right astragalus, PEFO 40753 in anterior (**K**) and dorsal (**L**) view. **N, O.** Holotype right astragalus of *Chindesaurus bryansmalli*, PEFO 10395 in anterior (**N**) and dorsal (**O**) view. Abbreviations: **alp**, anterolateral process; **ap**, ascending process; **cc**, cnemial crest; **ctf**, crista tibiofibularis; **fo**, foramen; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle; **pbn**, posterior basin; **plp**, posterolateral process. Scale bars=1 cm, arrows point in anterior or dorsal direction.

clade (Marsh et al. 2019a:348-1). These tibiae lack the fibular crest on the lateral surface of the proximal end (Fig. 9H) that is found in some silesaurids, e.g., *Silesaurus opolensis* (ZPAL Ab III/361/23, Dzik 2003: fig. 13b) and *Sacisaurus agudoensis* Ferigolo and Langer (2007, MCN PV 10020) (Langer and Ferigolo 2013: fig. 18c), *Heterodontosaurus tucki* (SAM-PK-K1332, Santa Luca 1980: fig. 20a), *Sa. tupiniquim* (MCP PV 3844, Langer 2003: fig. 5b), and neotheropods (Nesbitt 2011:333-1), but unlike in silesaurids, the lateral proximal condyle is not offset anteriorly relative to the medial condyle (Nesbitt 2011:331-1) (Fig. 9I), which is a trait found in theropods, e.g., *Herrerasaurus ischigualastensis* (PVSJ 373, Novas 1993: fig. 8c), and *Dilophosaurus wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 21.5). Additionally, the distal outline is round and not subrectangular like that of neotheropods (Fig. 9E), and in anterior view (Fig. 9F) the posterolateral process tapers distally and projects laterodistally (Marsh et al. 2019a:342-2) like it does in *Ch. bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 9g), *T. hallae* (GR 242), and *G. candelariensis* (MCN PV 2356, Langer et al. 2011: fig. 13c).

The isolated astragalus PEFO 40753 (Fig. 9K, L) compares favorably to that of the broken holotype specimen of *Ch. bryansmalli* (PEFO 10395) (Fig. 9M, N). It preserves the anterior ascending process found in dinosauriforms, e.g., *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 51a), and *Sa. tupiniquim* (MCP PV 3844, Langer 2003: fig. 6b), and the articular basin posterior to that ascending process (Nesbitt 2011:359-1) of early non-neotheropod saurischian dinosaurs such as *Sa. tupiniquim* (MCP PV 3844, Langer 2003: fig. 6a), *Eoraptor lunensis* (PVSJ 599, Sereno et al. 2012: fig. 88g), and *H. ischigualastensis* (PVSJ 373). We assign PEFO 40753 to the *Ch. bryansmalli* + *T. hallae* clade because it is relatively mediolaterally short (Marsh et al. 2019a:352-1) compared to the relatively wider astragalus of *H. ischigualastensis* (PVSJ 373) and neotheropods, e.g., *Coelophysis bauri* (AMNH FR 30576, Nesbitt 2011: fig. 46e) and *Di. wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 23.3), and it preserves the anterior and ventral cleft or groove (Marsh et al. 2019a:336-2) apomorphic for *Ch. bryansmalli* (PEFO 10395) (Fig. 9M, N) and *T. hallae* (GR 242, Marsh et al. 2019a: fig. 5h-k).

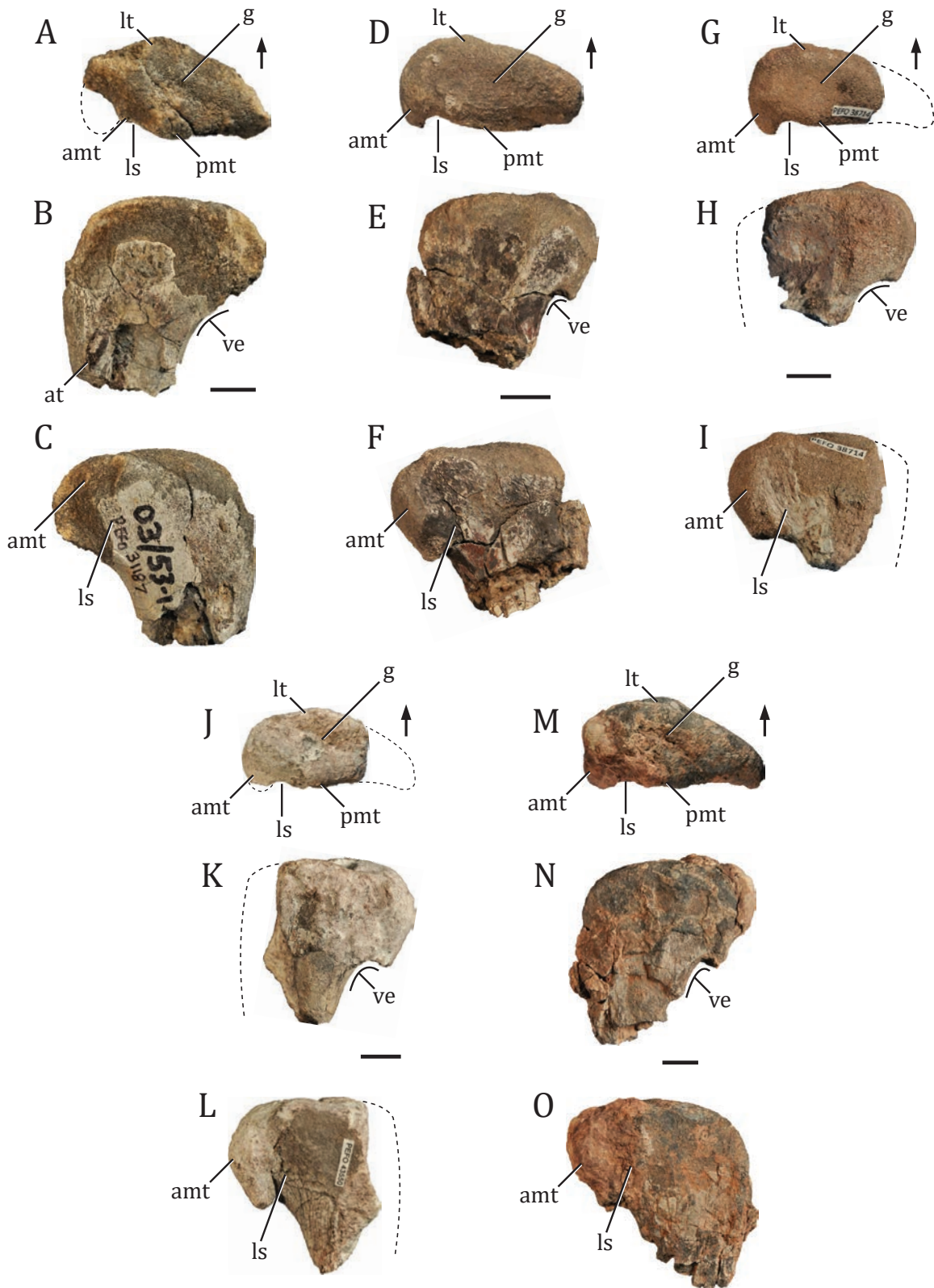
NEOTHEROPODA BAKKER, 1986 *SENSU* SERENO, 1998

FIGS. 10A-O, 11A-O, 12A-H

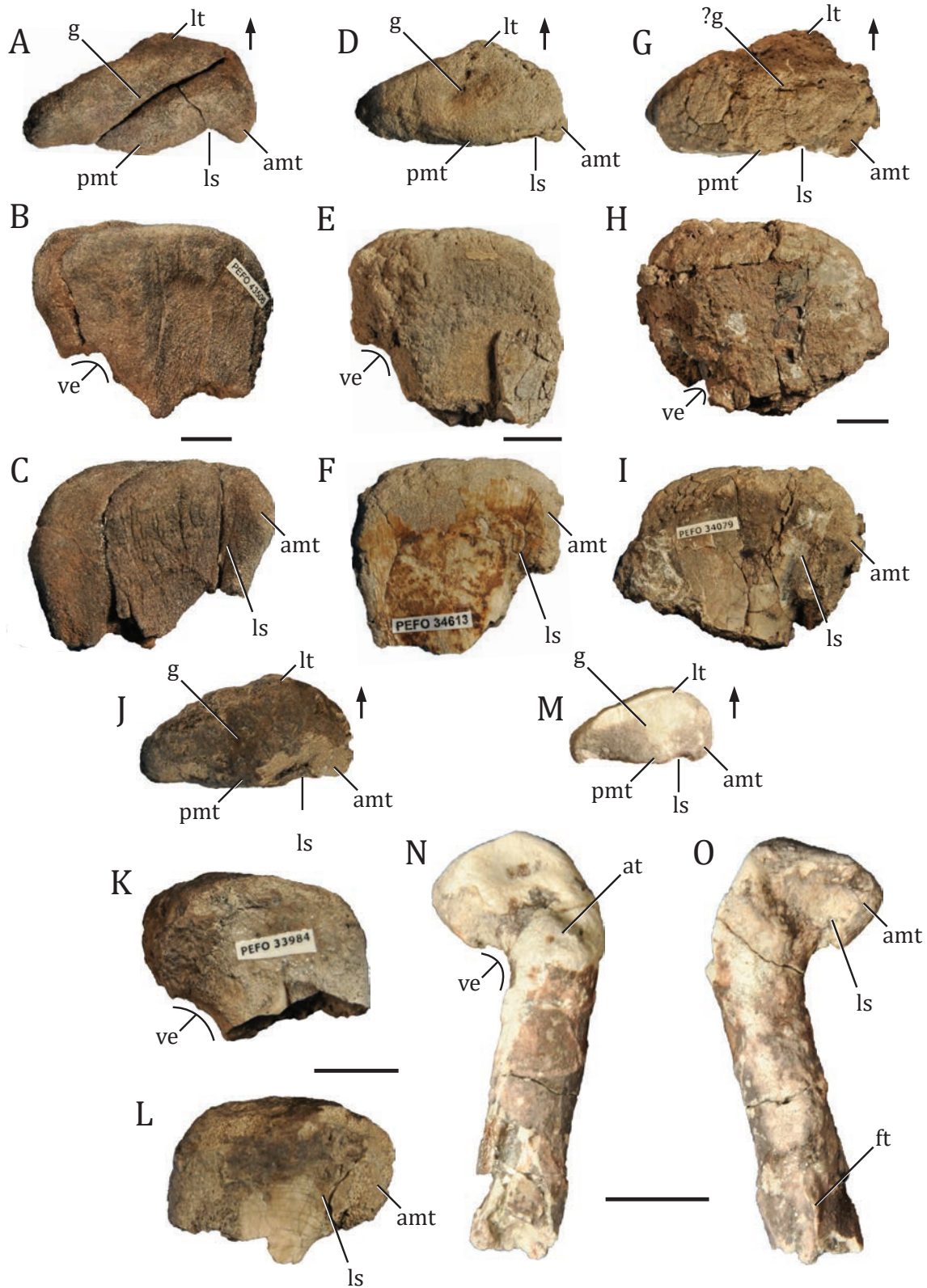
**Referred specimens and localities**—PEFO 31187 (Fig. 10A-C), proximal end of right femur, PFV 089: The Bowman Site, UCMP V84127, Jim Camp Wash beds, SM;

PEFO 44472 (Fig. 10D-F), proximal end of right femur, PFV 475: Sorrel Horse Mesa SE, PFM; PEFO 38714 (Fig. 10G-I), proximal end of right femur, PFV 302: Rabbit Foot Hills, PFM; PEFO 43550 (Fig. 10J-L), proximal end of right femur, PFV 475: Sorrel Horse Mesa SE, PFM; PEFO 44473 (Fig. 10M-O), proximal end of right femur, PFV 477: The Corner, PFM; PEFO 43506 (Fig. 11A-C), proximal end of left femur, PFV 475: Sorrel Horse Mesa SE, PFM; PEFO 34613 (Fig. 11D-F), proximal end of left femur, PFV 231: The Giving Site, PFM; PEFO 34079 (Fig. 11G-I), proximal end of left femur, PFV 231: The Giving Site, PFM; PEFO 33984 (Fig. 11J-L), proximal end of left femur, PFV 231: The Giving Site, PFM; PEFO 39563/UWBM 109902 (Fig. 11M-O), proximal end of left femur, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM; PEFO 43909 (Fig. 12A, B), proximal end of right tibia, PFV 211: Dinosaur Ridge, BMM; PEFO 39421/UWBM 108881 (Fig. 12C, D), proximal end of left tibia, PFV 410: Kaye Quarry, UWBM C2226, Jim Camp Wash beds, SM; PEFO 34080, proximal end of right tibia (Fig. 12E, F), PFV 231: The Giving Site, PFM; PEFO 44468 (Fig. 12G, H), proximal end of left tibia, PFV 451: Black Knoll E, PFM.

**Description and rationale for assignment**—All of the femora described here are broken proximal to the anterior trochanter, except for PEFO 31187, which is broken distal to the anterior trochanter (Fig. 10B) and PEFO 39563/UWBM 109902, broken distal to the fourth trochanter (Fig. 11O). Each femur preserves the emargination on the ventromedial surface of the femoral head that is found in early dinosaurs (Nesbitt 2011:304-2). The curved transverse groove on the proximal surface of the femoral head (Nesbitt 2011:314-2) found in neotheropods, e.g., *Coelophysis bauri* (AMNH FR 30816), *Dilophosaurus wetherilli* (TMM 43646-1.61, Marsh and Rowe 2020: fig. 52.9), and *Cryolophosaurus ellioti* (FMNH PR 1821, Smith et al. 2007: fig. 16c) is variably present in these specimens; it is more prominent in PEFO 31187 (Fig. 10A), more subtle in PEFO 39563/UWBM 109902 (Fig. 11M), and partially obscured by matrix in PEFO 34079 (Fig. 11G). In proximal view, the posteromedial tuber is small as in all dinosauriforms (Nesbitt 2011:308-1). The anteromedial tuber projects prominently posteriorly and is enlarged perpendicular to the long axis of the proximal surface of the femoral head (Nesbitt 2011; e.g., Fig. 11A, C), and in posterior view an oblique ligament sulcus extends from the proximal edge to the ventral emargination of the femoral head lateral to the anteromedial tuber (Rauhut 2003:197-1). The anteromedial tuber of PEFO 31187 (Fig. 10A) is broken but its size is evident from its broken base. An enlarged anteromedial

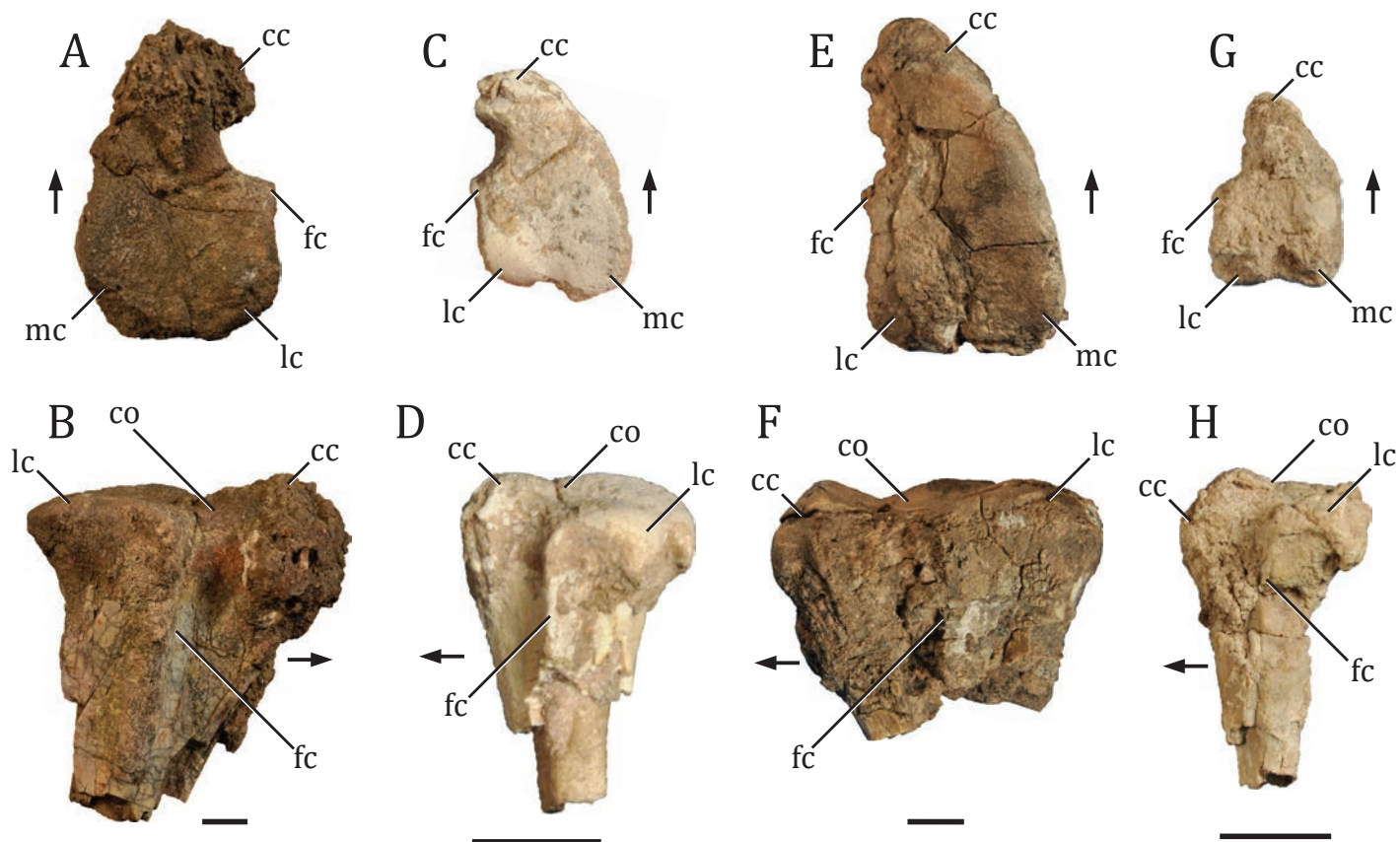


**Figure 10.** A–C. Proximal end of right neotheropod femur, PEFO 31187 in proximal (A), anterior (B), and posterior (C) view. D–F. Proximal end of right neotheropod femur, PEFO 44472 in proximal (D), anterior (E), and posterior (F) view. G–I. Proximal end of right neotheropod femur, PEFO 43550 in proximal (G), anterior (H), and posterior (I) view. J–L. Proximal end of right neotheropod femur, PEFO 44473 in proximal (J), anterior (K), and posterior (L) view. M–O. Proximal end of right neotheropod femur, PEFO 44473 in proximal (M), anterior (N), and posterior (O) view. Abbreviations: **at**, anterior trochanter; **amt**, anteromedial tuber; **g**, groove; **ls**, ligament sulcus; **lt**, lateral tuber; **pmt**, posteromedial tuber; **ve**, ventral emargination. Scale bars=1 cm, arrows point in anterior direction, and dashed lines indicate inferred outlines.



**Figure 11.** A–C. Proximal end of left neotheropod femur, PEFO 43506 in proximal (A), anterior (B), and posterior (C) view. D–F. Proximal end of left neotheropod femur, PEFO 34613 in proximal (D), anterior (E), and posterior (F) view. G–I. Proximal end of left neotheropod femur, PEFO 34079 in proximal (G), anterior (H), and posterior (I) view. J–L. Proximal end of left neotheropod femur, PEFO 33984 (J), anterior (K), and posterior (L) view. M–O. Proximal end of left neotheropod femur, PEFO 39563/UWBM 109902 in proximal (M), anterior (N), and posterior (O) view. Abbreviations: **amt**, anteromedial tuber; **ft**, fourth trochanter; **g**, groove; **ls**, ligament sulcus; **lt**, lateral tuber; **pmt**, posteromedial tuber; **ve**, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.





**Figure 12.** A, B. Proximal end of right neotheropod tibia, PEFO 43909 in proximal (A) and lateral (B) view. C, D. Proximal end of left neotheropod tibia, PEFO 39421/UWBM 108881 in proximal (C) and lateral (D) view. E, F. Proximal end of left tibia, PEFO 34080 in proximal (E) and lateral (F) view. G, H. Proximal end of left tibia, PEFO 44468 in proximal (G) and lateral (H) view. Abbreviations: cc, cnemial crest; co, concavity; fc, fibular crest; lc, lateral condyle; mc, medial condyle. Scale bars equal 1 cm, arrows point in anterior direction.

tuber and corresponding ligament sulcus is apomorphic for the Neotheropoda and can be observed in coelophysids, e.g., ‘*Syntarsus*’ *kayentakatae* (MNA V2623, Rowe 1989: fig. 4c, e), *Di. wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 20.4, 20.5), and *C. ellioti* (FMNH PR 1821, Smith et al. 2007: fig. 16b, 16c). The fourth trochanter present in PEFO 39563/UWBM 109902 is symmetrical and blade-like as in other theropod dinosaurs (Nesbitt 2011:316-1 and 317-0).

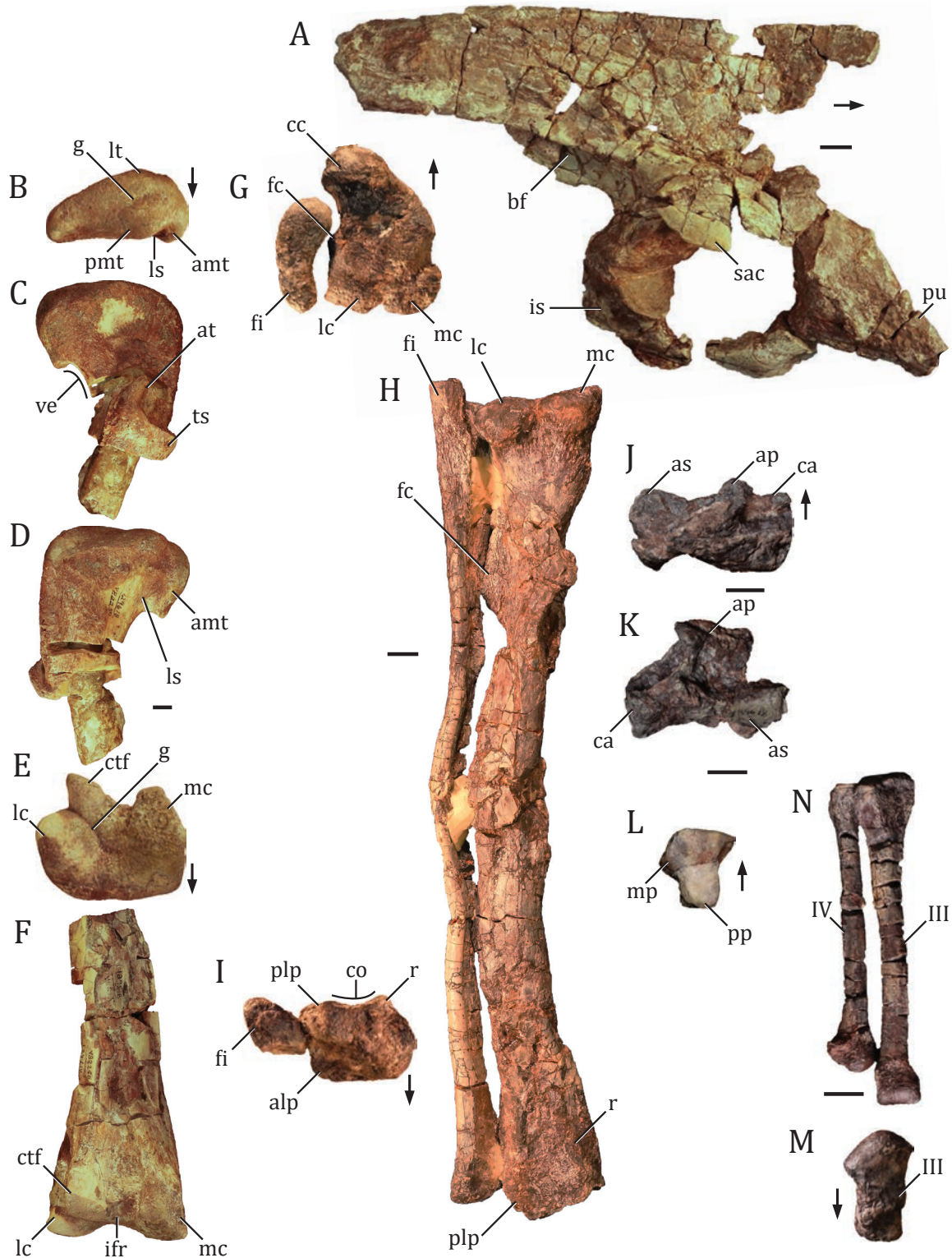
The proximal ends of the tibiae preserve a relatively long cnemial crest that arcs strongly anterolaterally (Nesbitt 2011:328-2) (Fig. 12A) as in other dinosaurs. Like the proximal ends of the other theropod tibiae described above, the medial and lateral proximal condyles are level with one another posteriorly. In lateral view, the proximal surface between the cnemial crest and posterior condyles is concave (Fig. 12F) as apomorphic for neotheropods, e.g., ‘*S.*’ *kayentakatae* (MNA V2623, Tykoski 1998: fig. 26a), and *Di. wetherilli* (TMM 43646-1.78, Marsh and Rowe 2020: 53.1) and unlike the flat area seen in non-neotheropod dinosauriforms, e.g., *Dromomeron gregorii*

(TMM 31100-278, Nesbitt et al. 2009b: fig. 5a), *Silesaurus opolensis* (ZPAL Ab III/361/22, Nesbitt 2011: fig. 40e), and *Chindesaurus bryansmalli* (PEFO 10395, Marsh et al. 2019a: fig. 9a). Similarly, a fibular crest is present on the lateral surface of these tibia (Rauhut 2003, Nesbitt 2011:333-1) (Fig. 12D), which is a structure unique to neotheropods, e.g., *Liliensternus liliensterni* (HMN MB R 2175, Huene 1934: pl. 15.15a), and *Tachiraptor admirabilis* Langer et al. (2014, IVIC-P-2867: fig. 3c) and convergently present in some silesaurids (ZPAL Ab III/361/23), *Heterodontosaurus tucki* (SAM-PK-K1332), and *Saturnalia tupiniquim* (MCP PV 3844). We assign these tibiae to the Neotheropoda owing to the presence of the fibular crest and a concave proximal surface between the cnemial crest and posterior condyles.

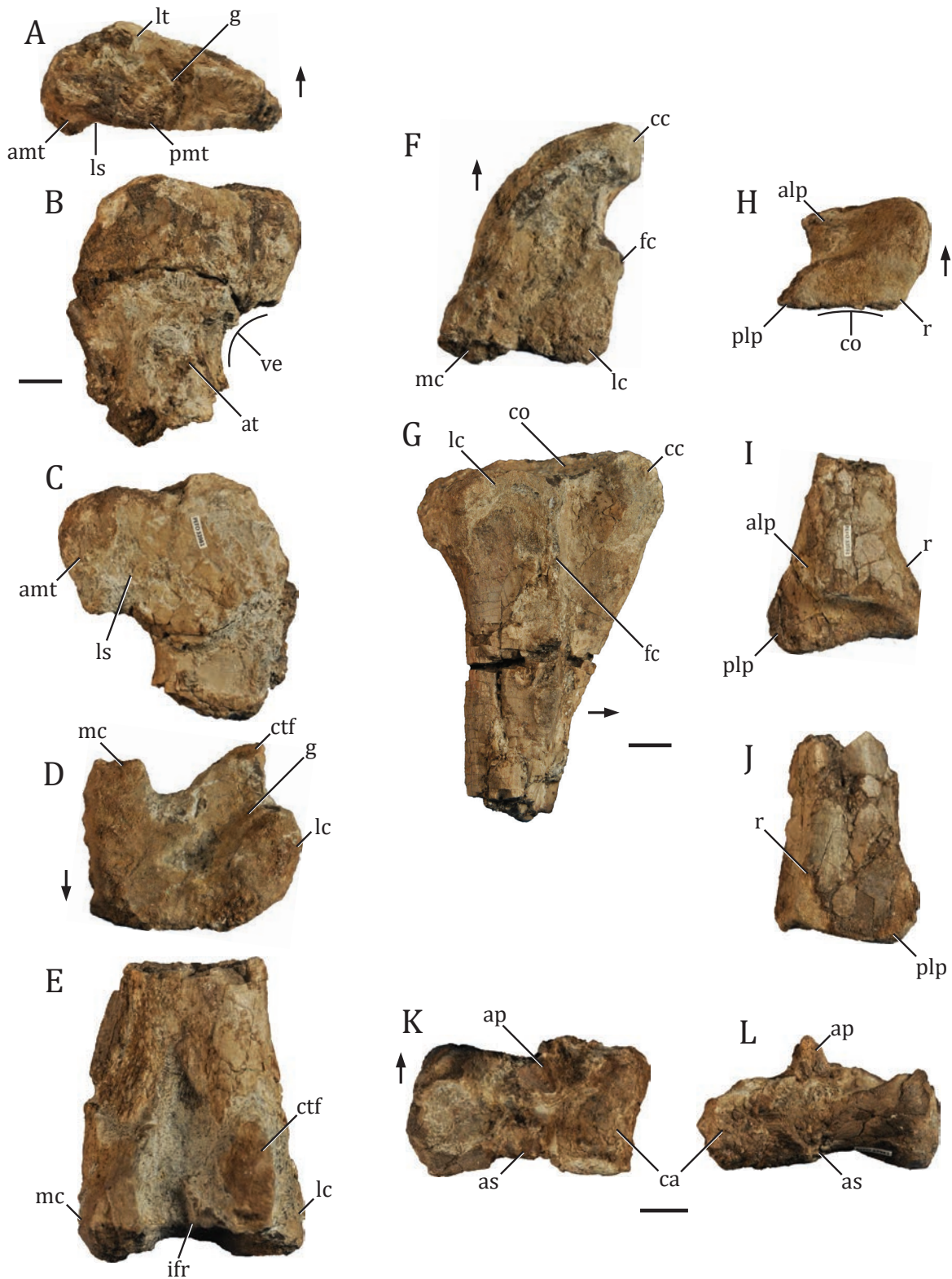
#### COELOPHYSIDAE NOPSICA, 1923 SENSU TYKOSKI, 2005

FIGS. 13A–N, 14A–L, 15A–I

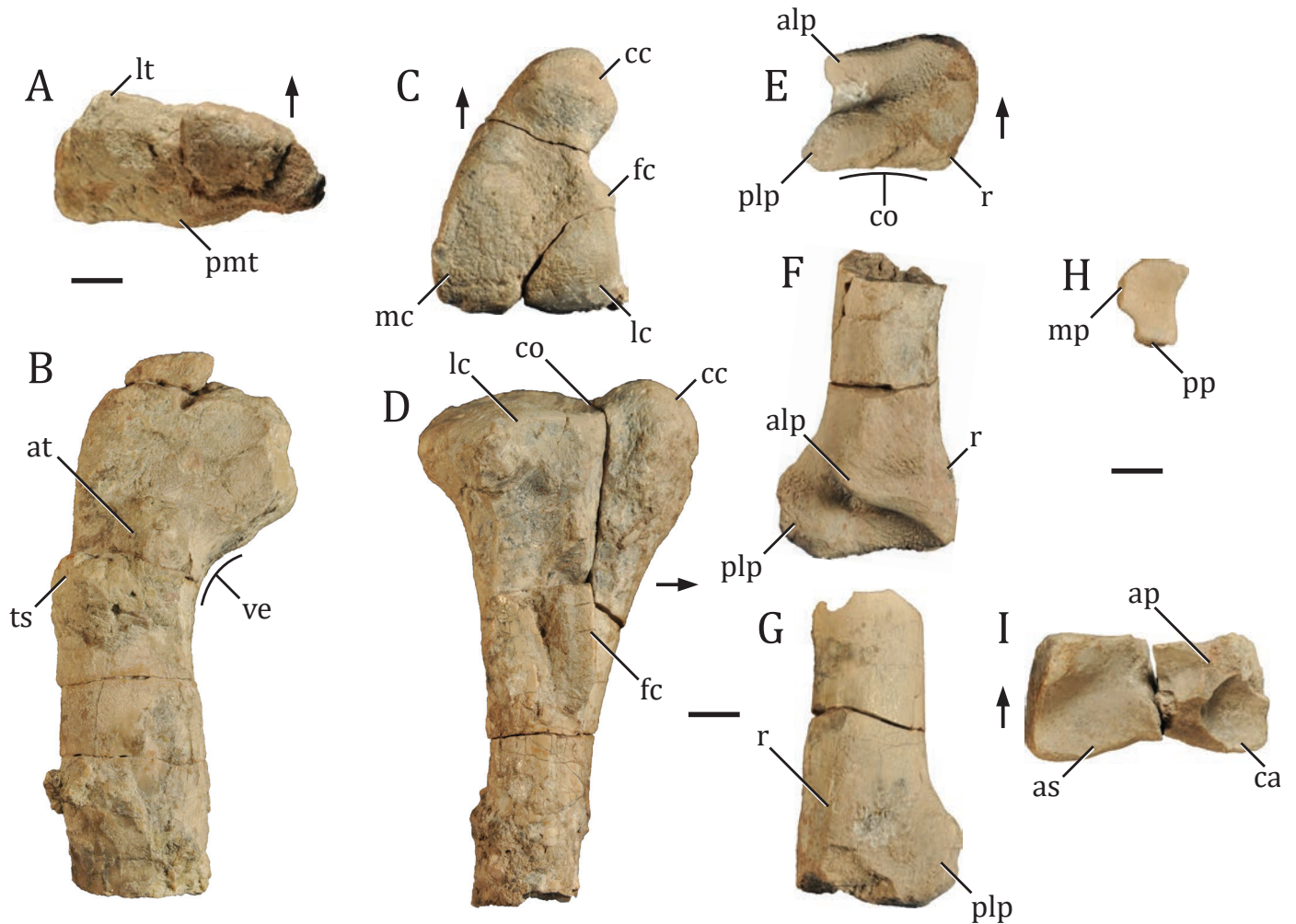
**Referred specimens and localities**—PEFO 21373/UWBM 129618 (Fig. 13), partial skeleton including a right ilium (Fig. 13A), right astragalocalcaneum (Fig. 13J–K),



**Figure 13.** A–M. Partial coelophysid skeleton, PEFO 21373/UCMP 129618. A. Right ilium and partial ischium and pubis in lateral view. B–D. Proximal end of left femur in proximal (B), anterior (C), and posterior (D) view. E, F. Distal end of left femur in distal (E) and posterior (F) view. G–I. Left tibia and fibula in proximal (G), posterior (H), and distal (I) view. J, K. Left astragalocalcaneum in dorsal (J), and anterior (K) view. L. Right distal tarsal 4. N, M. Right metatarsal III and metatarsal IV in dorsal (N) and proximal (M) view. Abbreviations: III, metatarsal III; IV, metatarsal IV; alp, anterolateral process; amt, anteromedial tuber; ap, ascending process; as, astragalus; at, anterior trochanter; bf, brevis fossa; ca, calcaneum; cc, cnemial crest; co, concavity; ctf, crista tibiofibularis; fc, fibular crest; fi, fibula; g, groove; ifr, infrapopliteal ridge; is, ischium; lc, lateral condyle; ls, ligament sulcus; lt, lateral tuber; mc, medial condyle; mp, medial process; plp, posterolateral process; pmt, posteromedial tuber; pp, posterior process; pu, pubis; r, ridge; sac, supraacetabular crest; ts, trochanteric shelf; ve, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.



**Figure 14.** A–L. Partial coelophysid skeleton, PEFO 33981. A–C. Proximal end of right femur in proximal (A), anterior (B), and posterior (C) view. D, E. Distal end of right femur in distal (D) and posterior (E) view. F, G. Proximal end of right tibia in proximal (F) and lateral (G) view. H–J. Distal end of right tibia in distal (H), anterior (I), and posterior (J) view. K, L. Left astragalocalcaneum in dorsal (K) and anterior (L) view. Abbreviations: alp, anterolateral process; amt, anteromedial tubercle; ap, ascending process; as, astragalus; at, anterior trochanter; ca, calcaneum; cc, cnemial crest; co, concavity; ctf, *crista tibiofibularis*; fc, fibular crest; g, groove; ifr, infrapopliteal ridge; lc, lateral condyle; ls, ligament sulcus; lt, lateral tubercle; mc, medial condyle; plp, posterolateral process; pmt, posteromedial tubercle; r, ridge; ve, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.



**Figure 15.** A–I. Partial coelophysid skeleton, PEFO 33983. A, B. Proximal end of right femur in proximal (A) and anterior (B) view. C, D. Proximal end of right tibia in proximal (C) and lateral (D) view. E–G. Distal end of right tibia in distal (E), anterior (F), and posterior (G) view. H. Left distal tarsal 4. I. Left astragalocalcaneum in dorsal view. Abbreviations: **alp**, anterolateral process; **ap**, ascending process; **as**, astragalus; **at**, anterior trochanter; **ca**, calcaneum; **cc**, cnemial crest; **co**, concavity; **fc**, fibular crest; **lc**, lateral condyle; **lt**, lateral tuber; **mc**, medial condyle; **mp**, medial process; **plp**, posterolateral process; **pmt**, posteromedial tuber; **pp**, posterior process; **r**, ridge; **ts**, trochanteric shelf; **ve**, ventral emargination. Scale bars=1 cm, arrows point in anterior direction.

left femur (Fig. 13B–F), left tibia and fibula (Fig. 13G–I), and partial right pes (Fig. 13L–N), PFV 040: Dinosaur Hill, UCMP V82250, PFM; PEFO 33981 (Fig. 14), partial skeleton including left (Fig. 14A–C) and right femora (Fig. 14D–E), right (Fig. 14F–J) tibia, and left astragalocalcaneum (Fig. 14K–L), PFV 231: The Giving Site, PFM; PEFO 33983 (Fig. 15), partial skeleton including proximal end of right femur (Fig. 15A–B), right tibia (Fig. 15C–G), right astragalocalcaneum (Fig. 15I), and distal tarsal 4 (Fig. 15H), PFV 231: The Giving Site, PFM).

**Description and rationale for assignment**—The three partial skeletons have preserved elements in common that aid in identifying the specimens, namely the proximal ends of femora, distal ends of femora (except for PEFO 33983), proximal and distal ends of tibiae, astragalocalcanea, and distal tarsal 4 (except for PEFO

33981). Three additional apomorphies of Neotheropoda are present on the distal end of the tibiae of these specimens: a subrectangular distal outline (Rauhut 2003:208-1) (Fig. 15E) that has a concave posterolateral margin (Nesbitt 2011:335-1) and a proximodistal ridge on the posteromedial surface (Langer and Benton 2006; Nesbitt 2011:336-1). A concave posterolateral margin of the tibia in distal view is also present in some early sauropodomorphs, e.g., *Saturnalia tupiniquim* (MCP PV 3844, Langer 2003: fig. 5h), and the posteromedial ridge is variably present in other early dinosaurs such as *Lesothosaurus diagnosticus* (NHMUK PV RU B17, Baron et al. 2017a: fig. 15c), *Eodromaeus murphii* (PSVJ 562, Ezcurra 2017), and *Sarhsaurus aurifontanalis* Rowe et al., 2010 (TMM 43646-2.173, Marsh and Rowe, 2018: fig. 37b). Distal tarsal 4 is preserved in PEFO 21373/UCMP

129618 and PEFO 33983; the medial process found in saurischian dinosaurs, e.g., *Sa. tupiniquim*, (MCN PV 3844, Nesbitt 2011: fig. 42g) is present but rounded (Nesbitt 2011:235-1) (Fig. 13L), and like the fourth distal tarsal of other neotheropods, e.g., *Dilophosaurus wetherilli* (UCMP 37302, Marsh and Rowe, 2020: fig. 24.48), the posterior process is has a straight posterior margin (Nesbitt 2011:350-0, reversal).

These specimens also preserve apomorphies of the Coelophysidae. The partial skeleton PEFO 21373/UCMP 129618 (Padian 1986) includes a nearly complete right ilium with a prominent supraacetabular crest that projects ventrally (Gauthier 1986, Nesbitt 2011:264-1) (Fig. 13A). This condition is best seen in the coelophysids *Coelophysis bauri* (MNA V3318) and *Megapnosaurus rhodesiensis* (BP/1/5246, Munyikwa and Raath 1999: fig. 2b), as well as the stem-averostran *Di. wetherilli* (TMM 43646-1.60, Marsh and Rowe 2020: fig. 49.1) and some poposauroid pseudosuchians such as *Poposaurus gracilis* (YPM 57100, Schachner et al. 2019: fig. 26e) and *Effigia okeeffeae* (AMNH FR 30588, Nesbitt 2007: fig. 32). Additionally, PEFO 21373/UCMP 129618 (Fig. 13F) and PEFO 33981 (Fig. 14E) preserve the infrapopliteal ridge on the femur that connects the *crista tibiofibularis* and medial condyle posteriorly (Tykoski 2005, Marsh and Rowe 2020:240-1), which is best exemplified in ‘*Syntarsus*’ *kayentakatae* (MNA V2623, Rowe 1989: fig. 4f) and *C. bauri* (TMM 45559-12), but is also convergently present in ceratosaurs such as *Ceratopsaurus nasicornis* Marsh (1884) (UMNH VP 5278, Madsen and Welles 2000: pl. 21c) and *Carnotaurus sastrei* Bonaparte (1985) (MACN-CH 894, Bonaparte 1990: fig. 32c).

As in other neotheropods, e.g., *C. bauri* (AMNH FR 30576, Nesbitt 2011: fig. 46e, and *Di. wetherilli* (UCMP 37302, Marsh and Rowe 2020: fig. 23.3), the astragalus lacks the basin posterior to the ascending process found in most early saurischians (Nesbitt 2011:359-0) (Fig. 15I). Unlike non-dinosaur avemetatarsalians and early dinosaurs, e.g., *Teleocrater rhadinus* (NMT RB490, Nesbitt et al. 2017: fig. 2n), *Asilisaurus kongwe* (NMT RB159, Nesbitt et al. 2019: fig. 50), *Eoraptor lunensis* (PVSJ 559, Sereno et al. 2012: fig. 88g), and *Scutellosaurus lawleri* (MNA V175, Colbert 1981: fig. 30c), the proximal tarsals of these three PEFO specimens (Fig. 13J, 14K, 15I) are co-ossified to form an astragalocalcaneum (Tykoski 2005:149, Nesbitt 2011:370-1). Coossified proximal tarsals are apomorphic for pterosaurs, e.g., *Dimorphodon macronyx* Buckland (1829) (YPM 9182, Padian 1983: fig. 18c), lagerpetids, e.g., *Dromomeron romeri* (GR 223, Nesbitt et al. 2009b: fig. 7a), *Heterodontosaurus tucki*

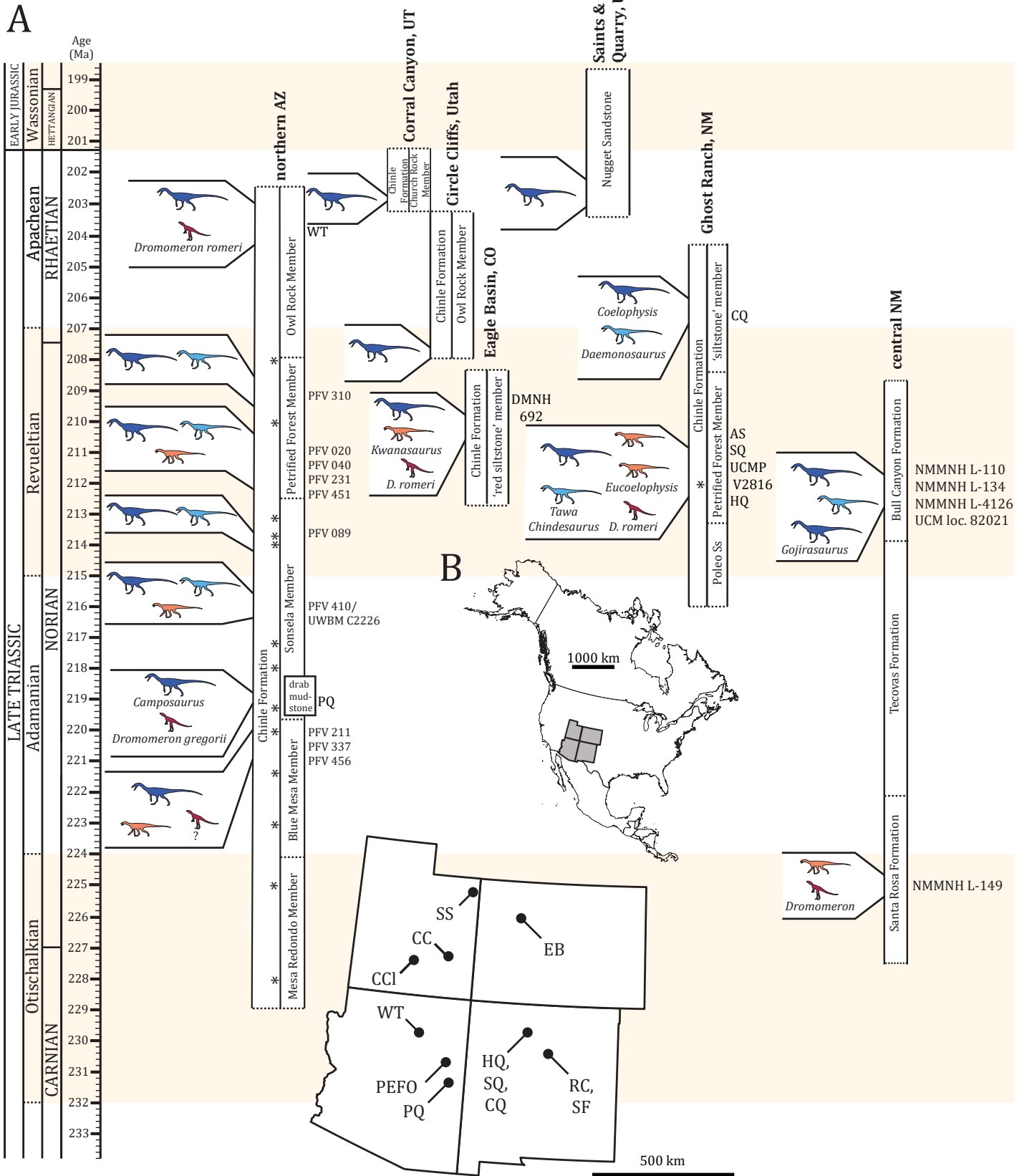
(SAM-PK-K1332, Santa Luca 1980: fig. 19), coelophysids, e.g., *C. bauri* (AMNH FR 30576, Nesbitt 2011: fig. 46e) and ‘*S.*’ *kayentakatae* (MNA V2623, Rowe 1989: fig. 6a), and ceratosaurs, e.g., *Ce. nasicornis* (UMNH VP 5278, Madsen and Welles 2000: pl. 22a), and *Majungasaurus crenatissimus* Depéret (1896) (FMNH FR 2278, Carrano 2007: fig. 9d). In some of these taxa, e.g., pterosaurs, *Heterodontosaurus tucki*, and ‘*S.*’ *kayentakatae*, the distal tarsals are also co-ossified to the distal ends of the tibia and fibula to form a tibiotarsus; at least in coelophysids the degree of coossification between the astragalocalcaneum, tibia, and fibula is ontogenetically variable (Tykoski 2005, Griffin 2018). We assign these three partial skeletons to the Coelophysidae owing to the presence of the infrapopliteal ridge on the distal end of the femur and the coossified proximal tarsals.

## DISCUSSION

### PEFO dinosaur morph biostratigraphy

As mentioned above, recent collection efforts at PEFO focusing on especially fossiliferous sites and sites in newly acquired areas have provided a significant increase in dinosaur morph fossils. The PEFO dinosaur morph record (as identified here) increased by more than 600% after 2000, and it increased by 85% after 2013 (Fig. 1). These new finds represent new highest and lowest occurrences for certain dinosaur morph groups in the park.

There are five main dinosaur morph assemblages preserved at PEFO (Fig. 16A). The lowest occurs in the upper part of the Blue Mesa Member of the Chinle Formation at localities such as PFV 211, PFV 337, and PFV 456. The localities comprised in this assemblage are bracketed between two stratigraphic levels with associated radiometric ages (U-Pb zircon data), from  $223.036 \pm 0.059$  Ma and  $220.123 \pm 0.068$  Ma (Ramezani et al. 2011, Atchley et al. 2013); the estimated age of a stratigraphically-equivalent mudstone is 221.946 Ma (early-middle Norian; Adamanian holochronozone) (Nordt et al. 2015, Martz and Parker 2017) and a more recent single crystal age from a similar horizon in a research core is  $220.5 \pm 0.96$  Ma (Rasmussen et al. 2020). The proximal end of an *Ixalerpeton*-like dinosaur morph tibia (PEFO 44476) may be the earliest record of a lagerpetid at PEFO, silesaurids are represented by proximal ends of femora (PEFO 34347, PEFO 35117, and PEFO 38279), and the proximal end of a neotheropod tibia (PEFO 43909) represents the stratigraphically oldest known dinosaur element in the Chinle Formation of Arizona and New Mexico. Prior to the geochronological framework now established at PEFO



**Figure 16. A (pg. 28).** Triassic dinosaur morph biostratigraphy of Arizona, Colorado, New Mexico, and Utah. **B.** Maps of localities discussed in the text. Shaded states (**B**) contain Triassic dinosaur morphs. Maps modified from [freevectormaps.com] and silhouettes and colors correspond to those used in Figure 21; see acknowledgements for full links. Timescale and radiometric dates (\*) modified from Lucas 2010, Irmis et al. 2011, Ramezani et al. 2011, 2014, Atchley et al. 2013, Nordt et al. 2015, Kent et al., 2017, 2018. Abbreviations: **AS**, Arroyo Seco; **EB**, Eagle Basin; **CC**, Corral Canyon; **CCI**, Circle Cliffs; **CQ**, *Coelophysis* Quarry; **HQ**, Hayden Quarry; **PQ**, *Placerias* Quarry; **RC**, Revuelto Creek; **SF**, Santa Fe; **SQ**, Snyder Quarry; **SS**, Saints and Sinners Quarry; **WT**, Ward Terrace.

and nearby localities, the *Placerias* Quarry (UCMP A269) was thought to preserve the oldest dinosaur fossils in the Chinle Formation (Long and Murry, 1995; Irmis, 2011), but that locality is now believed to be correlated with younger strata in the Sonsela Member. Similarly, PEFO 35117 was at one time thought to be the oldest dinosaur from PEFO (Parker and Martz 2011, Sarigül 2017b), because it was collected from PFV 337 just above the Newspaper Rock bed in the upper part of the Blue Mesa Member, lower than ‘classic’ upper Blue Mesa Member localities such as the Dying Grounds (PFV 122). However, PFV 337 is in the eastern expansion of the park and in that area there are more than one ‘Newspaper Rock bed’ facies, so that in a given outcrop it cannot be determined which (if any) of these are equal to the Newspaper Rock bed at Newspaper Rock, making precise stratigraphic determinations with the other Blue Mesa Member sites impossible at this time. Here, we assign PEFO 35117 to the Silesauridae.

The two dinosaur morph assemblages from the Sonsela Member at PEFO (Fig. 16A) come from above and below the ‘persistent red silcrete’ interval that is thought to coincide with the Adamanian-Revueltian boundary (Parker and Martz 2011, Martz and Parker 2010, 2017). The Adamanian locality in the lower part of the Jim Camp Wash beds of the Sonsela Member, supported by its vertebrate fossils (Goncalves and Sidor 2019) is PFV 410, a multidominant bonebed of drepanosaurs, allokotosaurs, shuvosaurid pseudosuchians, and dinosaur morphs (Sidor et al. 2018, Goncalves et al. 2019) that preserves silesaurids (PEFO 39373/UWBM 108379), a theropod in the *Chindesaurus bryansmalli* + *Tawa hallae* clade (PEFO 39422/UWBM 10882, PEFO 39273/UWBM 108212), and a neotheropod (PEFO 39563/UWBM 109902, PEFO 39421/UWBM 108881). The higher, Revueltian assemblage occurs in the upper part of the Jim Camp Wash beds at PFV 089 and includes isolated elements of an early theropod the *Ch. bryansmalli* + *T. hallae* clade (PEFO 34875, PEFO 40753) and a neotheropod (PEFO 31187). Both of these sites are constrained by radiometric ages (U-Pb zircon data) between  $218.017 \pm 0.088$  Ma and  $213.870 \pm 0.078$  Ma (Ramezani et al. 2011), and a sample from a horizon stratigraphically equivalent to that of PFV 089 in a drill core is  $214.08 \pm 0.20$  Ma in age (Kent et al. 2018).

The uppermost dinosaur morph assemblages at PEFO

(Fig. 16A) occur throughout the Petrified Forest Member of the Chinle Formation and are between  $213.124 \pm 0.069$  Ma and  $210.08 \pm 0.22$  Ma in age (late Norian, Revueltian holochronozone, Ramezani et al. 2011, Martz and Parker 2017). This includes the holotype specimen of *Ch. bryansmalli* (PEFO 10395) from PFV 020, the coelophysid neotheropods from PFV 231 (PEFO 33981, PEFO 33983) and PFV 040/UCMP V82250 (PEFO 21373/UCMP 129618), and the proximal end of a silesaurid femur from PFV 451 on the eastern expansion of the park. A partial theropod vertebral column (PEFO 38710) and proximal end of a neotheropod femur (PEFO 38714) are from PFV 310, which is slightly higher in section above the Black Forest bed of the Petrified Forest Member. The age of that locality is constrained to between  $210.08 \pm 0.22$  Ma and  $\sim 208$  Ma (U-Pb zircon data, Ramezani et al. 2011), making these the youngest dinosaurs in the park.

#### A review of global Triassic dinosaur morph body fossil biostratigraphy

*Arizona*—The *Placerias* Quarry (UCMP A269) occurs in the ‘drab mudstone’ overlying the Blue Mesa Member near St. John’s, Arizona (Ramezani et al. 2014, Parker 2018, Marsh et al. 2019b) and radiometric dates indicate it is  $219.39 \pm 0.16$  Ma in age (U-Pb zircon data, Ramezani et al. 2014) and correlates with the Lot’s Wife beds of the Sonsela Member at PEFO (Fig. 16). The diverse dinosaur morph assemblage from the *Placerias* Quarry includes the distal end of a femur from the lagerpetid *Dromomeron gregorii* (UCMP 25815, Nesbitt et al. 2009b), the distal end of a dinosauriform femur (UCMP 25793, Nesbitt et al. 2007), the distal ends of a saurischian dinosaur femur (UCMP 139662, Irmis 2005) and tibia (UCMP 25820, Irmis 2005, Nesbitt et al. 2007), and the distal end of the tibiotarsus from the coelophysid neotheropod *Camposaurus arizonensis* (UCMP 34498, Hunt et al. 1998, Ezcurra and Brusatte 2011).

The youngest Triassic dinosaur morph assemblage from Arizona comes from Ward Terrace on the Navajo Nation near Tuba City (Fig. 16). This material comes from the upper part of the Owl Rock Member (late Norian–Rhaetian, Apachean holochronozone) of the Chinle Formation; the base of the Owl Rock Member is at most  $\sim 208$  Ma in age at PEFO (U-Pb zircon data; Ramezani et al. 2011, Martz and Parker 2017). The Ward

Terrace MNA localities preserve isolated elements of the lagerpetid *D. romeri* (MNA V7237, MNA loc. 795, [Marsh 2018a](#)) and a putative neotheropod (MNA V7240, MNA loc. 853, [Kirby 1991](#): pl. 15h–l; [Spielmann et al. 2007](#): fig. 3i–k). Of course, neotheropods persist through the end-Triassic extinction event in western North America and are known from the Glen Canyon Group of northern Arizona. A coelophysid is known from two specimens (MNA V2588 and MNA V1968) in the Dinosaur Canyon Member of the Moenave Formation (MNA loc. 854-1, [Lucas and Heckert, 2001](#)), in which the Triassic-Jurassic boundary is found ([Suarez et al. 2017](#)). Unambiguous Early Jurassic dinosaur assemblages include the ‘silty facies’ of the Kayenta Formation, which preserves the coelophysids ‘*Syntarsus kayentakatae*’ ([Rowe 1989](#)) and the ‘Shake-N-Bake’ taxon ([Tykoski 1998, 2005](#)), as well as the stem-averostran *Dilophosaurus wetherilli* ([Welles 1954](#)); the fossiliferous interval of the Kayenta Formation on the Navajo Nation may be as young as ~183 Ma (U-Pb zircon data, [Marsh et al. 2014](#)). Finally, the Navajo Sandstone preserves the coelophysid *Segisaurus halli* ([Camp 1936, Carrano et al. 2005](#)). The Navajo Sandstone may be Toarcian in age ([Marsh 2018b](#)), but recent U-Pb ages from carbonates in the unit near Moab, Utah, suggest it could be older than that ([Parrish et al. 2019](#)).

*Utah*—The Chinle Formation of Utah is relatively depauperate of dinosauromorph body fossils; like in other areas, fragmentary elements that had been described as dinosaur fossils (e.g., [Parrish and Good 1987, Parrish 1999](#) and references therein) lack the apomorphies unique to the group. The proximal end of an ornithodiran tibia (YPM 57231) from the Chinle Formation in the Circle Cliffs area was briefly mentioned by [Martz et al. \(2017\)](#). This specimen is from either the top of the Petrified Forest Member or the base of the overlying Owl Rock Member; in any case, it is Revueltian in age. The element is poorly preserved, missing much of the cortical bone, but is clearly mediolaterally narrow and anteroposteriorly elongate with a pronounced cnemial crest. The cnemial crest curves strongly anterolaterally, and the proximal surface between the cnemial crest and posterior condyles is concave, allowing us to assign this element to Neotheropoda. A second documented record of a dinosaur from the Chinle Formation of Utah is known from Corral Canyon north of Moab in the base of the Church Rock Member ([Jenkins et al. 2017](#)), which is likely Rhaetian in age (Apachean holochronozone, [Martz and Parker 2017](#)) (Fig. 16), as it overlies the Owl Rock Member in southeastern Utah (<208 Ma, U-Pb zircon data, [Ramezani et al. 2011, Martz et al. 2017](#)). The

specimen (MWC 5627) comprises the partial pelvis of a neotheropod dinosaur, and is likely a coelophysid owing to the co-ossification of the sacral centra ([Marsh and Rowe 2020:139-1](#)).

Associated and semi-articulated skeletons of coelophysid theropods are present at the Saints & Sinners Quarry in the Nugget Sandstone of northeastern Utah ([Shumway et al. 2016, Britt et al. 2018](#)) (Fig. 16A) along with a dimorphodontid pterosaur, sphenosuchian crocodylomorph, drepanosaurs, and a procolophonid. The Nugget Sandstone in that part of Utah overlies informally named members of the Chinle Formation ([Irmis et al. 2015](#)), but it is hypothesized that the Nugget Sandstone is correlated with some or all of the Late Triassic-Early Jurassic Glen Canyon Group of northern Arizona and southern Utah ([Sprinkel et al. 2011](#)). The presence of drepanosaurs and procolophonids in the Saints & Sinners Quarry suggests that it is latest Triassic in age (late Norian–Rhaetian, [Britt et al. 2018](#)).

*Colorado*—The geographically-isolated Eagle Basin of northwestern Colorado ([Dubiel 1992](#)) preserves an abbreviated section of the Chinle Formation (Fig. 16A). Localities from the fossiliferous interval within the middle of the ‘red siltstone member’ (the uppermost part of the ‘course facies’; [Martz and Small 2019](#)) preserve isolated lagerpetid fossils, some of which can be identified as *Dromomeron romeri* ([Small and Martz 2013](#)), as well as numerous silesaurid remains, including *Kwanasaurus williamparkeri* and undescribed coelophysoid theropods ([Martz and Small 2019](#)). Vertebrate biostratigraphy suggests that the ‘red siltstone member’ is at least partially located within the Revueltian holochronozone (~213–207 Ma, [Small and Martz 2013, Martz and Parker 2017](#)) and in part may correlate with the Petrified Forest Member of the Chinle Formation in Arizona ([Martz and Small 2019](#)).

*New Mexico*—The Late Triassic strata of east-central New Mexico preserve a dinosauromorph locality in the Los Esteros Member of the Santa Rosa Formation ([Beyl et al. 2019, 2020](#)) (Fig. 16). This site (NMMNH L-149) preserves the lagerpetid *Dromomeron* and an unnamed silesaurid. Its Otischalkian age can only be estimated on the presence of non-phytosaurid phytosaurs ([Martz and Parker 2017, Beyl et al. 2020](#)), but correlations with other Otischalkian and early Norian Triassic localities in the western United States suggests that the site is ~225 Ma in age ([Ramezani et al. 2011, Long and Lehman 1993, 1994, 2009](#)). Dinosauromorphs in central New Mexico occur at Bull Canyon and Revuelto Creek (Fig. 16) at NMMNH L-110 and UCM locality 82021, respectively,



within the Bull Canyon Formation (Griffin, 2019). The only dinosauromorphs identified using unambiguous apomorphies from the Bull Canyon Formation are two theropods. The first, *Gojirasaurus quayi* Carpenter (1997) was recently re-analyzed and is thought to be a neotheropod (Griffin 2019). The second, NMMNH P-4569, was first hypothesized to be a sauropodomorph (Long and Murry 1995) and later a herrerasaurid (Hunt et al. 1998), but actually represents a neotheropod (Griffin 2019). Other theropod specimens (i.e., proximal ends of femora) from the Bull Canyon Formation include the neotheropod NMMNH P-4126 and the early-diverging theropod NMMNH P-4415 (Heckert et al. 2000b). Lacking radiometric age constraints, the Bull Canyon Formation in this part of New Mexico includes the type area for the Revueltian holochronozone, which ranges from 215 Ma to 207 Ma (Martz and Parker 2017). Given that the lower part of the overlying Redonda Formation is also considered to be Revueltian (Martz and Parker 2017), the Revuelto Creek and Bull Canyon localities are likely to be mid-late Norian in age (~212 Ma).

Of course, the most famous Triassic dinosauromorph assemblages in North America are known from the Chinle Formation at the Ghost Ranch area in northern New Mexico (Colbert 1947, Zeigler et al. 2003, Irmis et al. 2007b, Nesbitt and Stocker 2008) (Fig. 16). The lower of its two assemblages is in the Petrified Forest Member of the Chinle Formation. The lower assemblage includes the Hayden Quarry (actually four distinct quarries that are in the lower half of member,  $211.9 \pm 0.7$  Ma in age, Irmis et al. 2007b, 2011, Whiteside et al. 2015), and the Snyder (NMMNH L-3845) and Canjilon (UCMP V2816) quarries, which are slightly higher, closer to the middle of the member (Irmis et al. 2007b). Baldwin's original 'Arroyo Seco' localities (including Cope's type '*Coelophysis*' material; Cope 1887) and the type *Eucoelophysis* locality are also from this same stratigraphic interval (Padian 1986, Colbert 1989, Sullivan et al. 1996, Sullivan and Lucas 1999, Nesbitt et al. 2007). The dinosauromorph assemblage from these quarries includes limb bones and partial skeletons of the lagerpetid *D. romeri* (Irmis et al. 2007b, Smith et al. 2018), *Eucoelophysis baldwini* (Sullivan and Lucas 1999, Ezcurra 2006) and an unnamed *Silesaurus*-like silesaurid (Irmis et al. 2007b, Breeden et al. 2017), the early theropods *Tawa hallae* and *Chindesaurus bryansmalli* (Irmis et al. 2007b, Nesbitt et al. 2009a), and coelophysid neotheropods (Heckert et al. 2003, Irmis et al. 2007b, Nesbitt and Stocker 2008). Note that the Hayden Quarry is purportedly the only place where *Ch. bryansmalli* and *T. hallae* co-occur; and ongoing

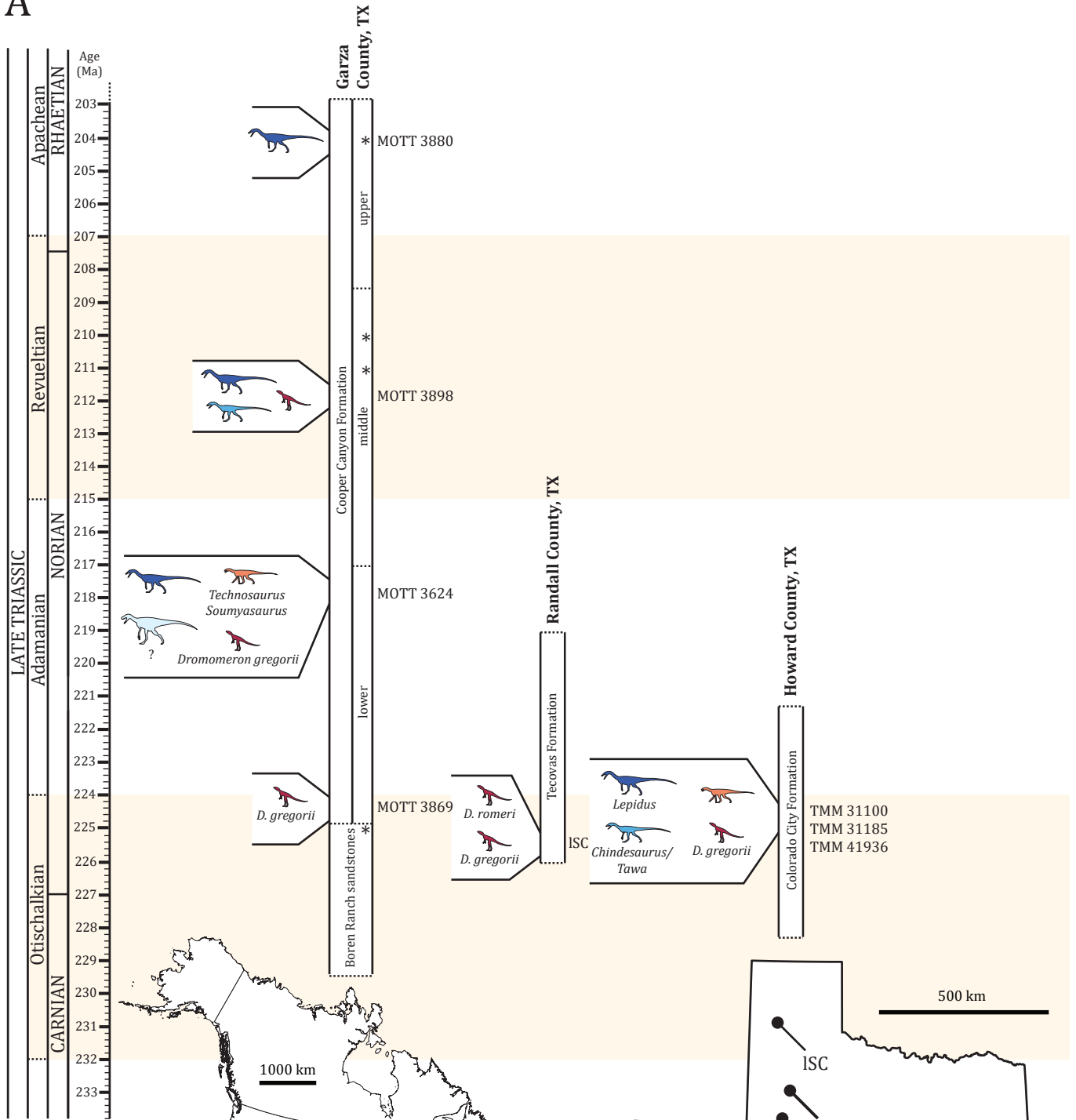
histological studies are testing the ontogenetic status of these specimens at Ghost Ranch (Evans et al. 2018).

The *Coelophysis* Quarry (Whitaker Quarry, NMMNH L-3115) is higher in section and therefore younger than ~212 Ma; this locality is from the middle of the 'siltstone member' of the Chinle Formation and delineates the base of the Apachean holochronozone (Irmis et al. 2007b, Whiteside et al. 2015, Martz and Parker 2017). Other Apachean localities such as those in the Owl Rock Member of the Chinle Formation at PEFO are younger than ~208 Ma in age (Ramezani et al. 2011, Marsh 2018a). The *Coelophysis* Quarry lacks non-dinosaur dinosauromorphs, but preserves the early theropod *Daemonosaurus chauliodus* Sues et al. (2011) (see Nesbitt and Sues 2020 for an interpretation of this taxon as an indeterminate saurischian) and articulated skeletons representing a growth series of the coelophysid neotheropod *Coelophysis bauri* (Colbert 1989, Rinehart et al. 2009); indeed, it is the neotype locality of *C. bauri* (Colbert et al. 1992, ICZN 1996).

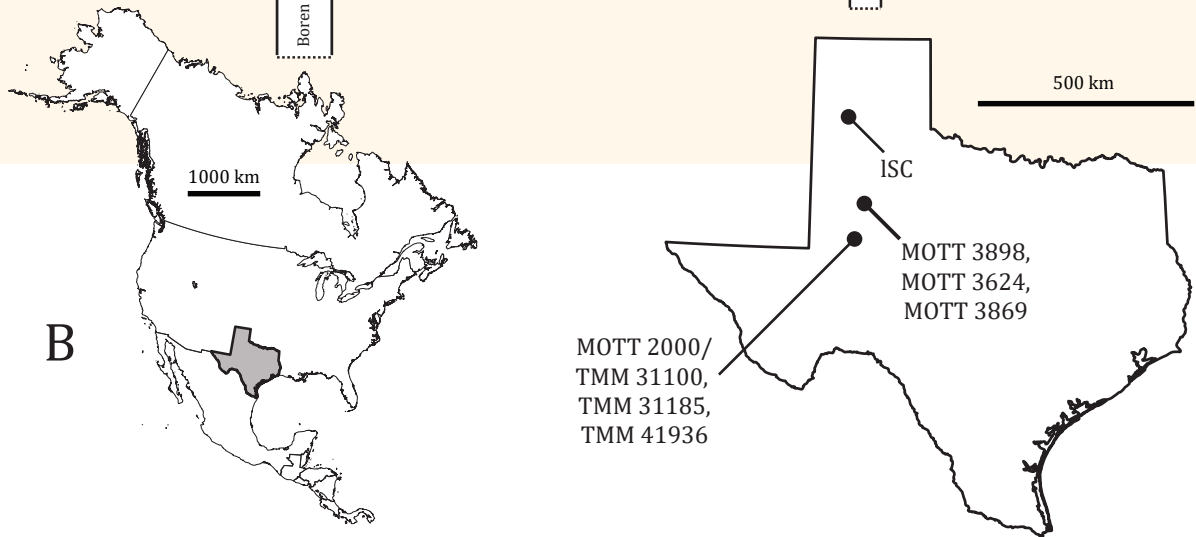
Older dinosaur records have been hypothesized from the Otischalkian (Salitral Formation, NMMNH L-913; Los Esteros Member of the Santa Rosa Formation, NMMNH L-149 and NMMNH L-588) and the Adamanian (Bluewater Creek Member of the Chinle Formation, NMMNH L-530; Garita Creek Formation, Lamy Quarry) in New Mexico (Heckert 1997, Heckert et al. 1994, 2000a), but these specimens lack unambiguous apomorphies to assign them to any dinosauromorph group.

Texas—All of the Triassic dinosauromorph assemblages in the western United States are Norian in age. In the Dockum Group of western Texas there are three early Norian assemblages (Otischalkian holochronozone, Martz et al. 2013, Martz and Parker 2017) (Fig. 17): the Boren Quarry (MOTT 3869) in the lower unit of the Cooper Canyon Formation in Garza County (<225 Ma, Rb-Sr mica data, Long and Lehman [1993, 1994, 2009]); the Otis Chalk Quarry 3 (TMM 31100 and TMM 31185) and the stratigraphic equivalent Dockum Site 7 General (TMM 41936) in the Colorado City Formation of Howard County; and the 'lower Sunday Canyon' site in the lower part of the Tecovas Formation in Randall County. Lagerpetids are present in all three Otischalkian sites in the Dockum Group. *Dromomeron gregorii* is found in TMM 31100, MOTT 3869, and the 'lower Sunday Canyon' site (Nesbitt et al. 2009b, Sarigül 2016, Lessner et al. 2018), and *D. romeri* is reported from the 'lower Sunday Canyon' site (i.e., WTAMU-V-8301 (Sarigül 2016), making that locality the only known co-occurrence of two named lagerpetid taxa. The only silesaurid specimens known from the Otischalkian sites in the Dockum Group come

A



B



**Figure 17. A. (pg. 32).** Triassic dinosauriform biostratigraphy of west Texas. **B.** Map of Texas showing localities discussed in the text. Maps modified from [freevectormaps.com] and silhouettes and colors correspond to those used in Figure 21; see acknowledgements for full links. Timescale and radiometric dates (\*) modified from Long and Lehman (1993, 1994, 2009), Lucas (2010), Kent et al. (2017). Abbreviations: ISC, 'lower Sunday Canyon'.

from TMM 31100 and include partial femora and tibiae (Nesbitt et al. 2010, Stocker 2013). Dinosaurs from the Otischalkian sites include limb bones of an early theropod (TMM 31100-545 and TMM 31100-1324, Stocker 2013, Nesbitt and Ezcurra 2015), the proximal end of a femur from a theropod probably belonging to the *Chindesaurus bryansmalli* + *Tawa hallae* clade (TMM 31100-523, Nesbitt et al. 2007, Stocker 2013, Marsh et al. 2019a), and the neotheropod *Lepidus praecisio* (TMM 41936-1.3, Nesbitt and Ezcurra 2015). Isolated dentaries originally identified as those of saurischian dinosaurs (TTU-P10514 and TTU-P10515, Sarigül 2017b) are actually those of an azendohsaurid allokotosaur (non-archosaur archosauriforms, Lessner et al. 2018).

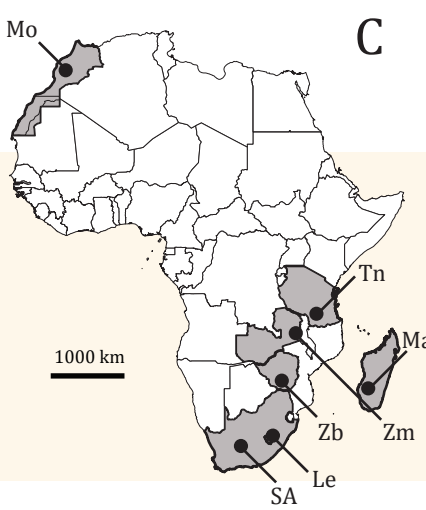
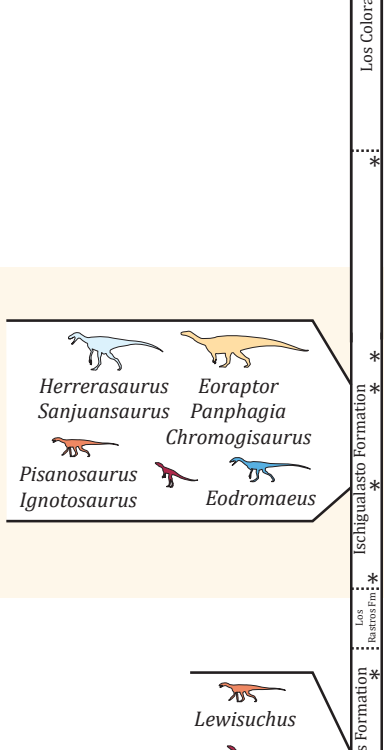
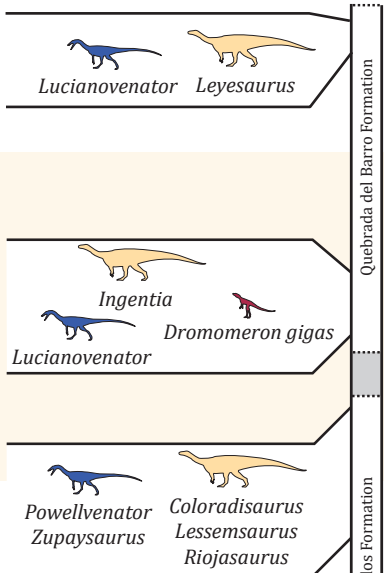
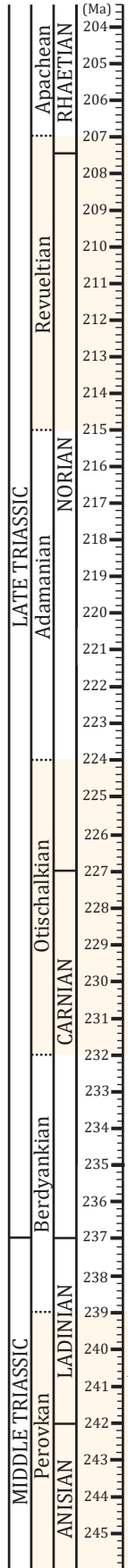
Two west Texas Dockum Group dinosauriform assemblages are mid-Norian in age (Fig. 17); the Post Quarry (MOTT 3624) is from the top of the lower unit of the Cooper Canyon Formation in Garza County (Adamanian holochronozone, Martz et al. 2013), and Headquarters South (MOTT 3898) is from the middle unit of the Cooper Canyon Formation (Revueltian holochronozone, >211 Ma, Rb-Sr mica data, Long and Lehman 1993, 1994, 2009, Lessner et al. 2018). *D. gregorii* (TTU-P 11282) and an unnamed lagerpetid (TTU-P10866) are present at the Post Quarry and Headquarters South, respectively (Martz et al. 2013, Lessner et al. 2018). The fragmentary silesaurids *Technosaurus smalli* (Nesbitt et al. 2007, Martz et al. 2013) and *Soumyasaurus aenigmaticus* Sarigül et al., 2018 are known from the Post Quarry; there are no unambiguous silesaurid elements from Revueltian sites in the Dockum Group. The purported herrerasaurid pelvis (TTU-P10082) from the Post Quarry (Martz et al. 2013, Sarigül 2017a) may represent the only member of the Herrerasauridae in North America, as *Ch. bryansmalli* is hypothesized to be a non-neotheropod theropod closely related to *T. hallae* (Marsh et al. 2019a), *Caseosaurus crosbyensis* Hunt et al. (1998, UMMP 8870 and the referred specimen from the Snyder Quarry of New Mexico NMMNH P-35995) cannot be identified using apomorphies beyond Dinosauriformes (Nesbitt et al. 2007; see Baron and William 2018 with a different interpretation and phylogenetic hypothesis of saurischian paraphyly), and the 'herrerasaurids' from the Bull Canyon Formation of New Mexico (e.g., NMMNH P-4569, Hunt 1994, Hunt 2001, Hunt et al. 1998) cannot be assigned to that clade using discrete apomorphies (Nesbitt et al. 2007, Griffin 2019). The proximal ends of tibiae from non-neotheropod theropods are reported from MOTT

3898 (TTU-P11404A, TTU-P11397A). Neotheropods are present from both the Post Quarry and Headquarters South, represented by an ilium (TTU-P10071) and tibia (TTU-P11044, Chatterjee and Nesbitt 2008, Martz et al. 2013), and a distal end of a tibia (TTU-P14786, Sarigül 2017a), respectively. The Patty East site (MOTT 3880) is from the upper unit of the Cooper Canyon Formation in Garza County (Apachean holochronozone) and is potentially Rhaetian in age (~204 Ma, Rb-Sr mica data, Long and Lehman 1993, 1994, 2009). As such, the youngest dinosauriform from the Dockum Group of west Texas is a neotheropod represented by a complete left tibia (TTU-P10534).

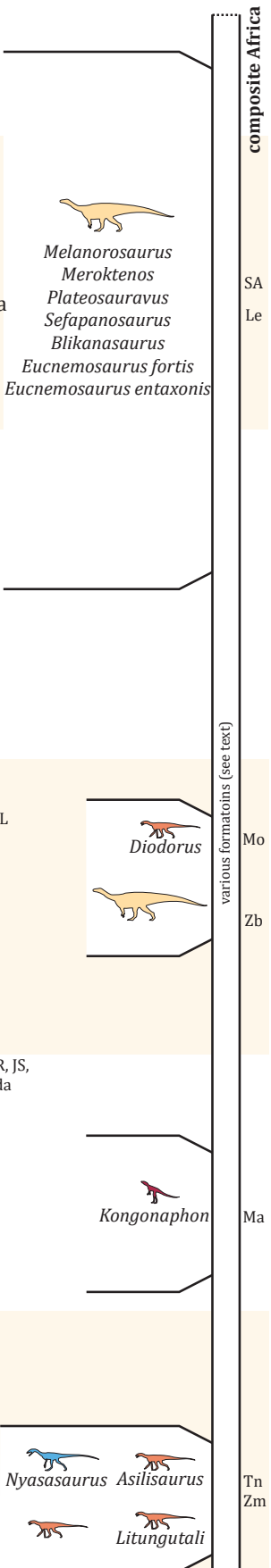
**Brazil**—There are two main dinosauriform assemblages from the southern region of Brazil. The first is a Carnian assemblage from the upper part of the Santa Maria Formation (Fig. 18). At  $233.23 \pm 0.73$  Ma (U-PB zircon data, Langer et al. 2018), the Cerro da Alemoa site is the oldest known assemblage to include both dinosaurs and non-dinosaur dinosauriforms (Garcia et al. 2019). That site and similar localities in the area from the upper part of the Santa Maria Formation (Fig. 18) have produced *Ixalerpeton polesinensis* Cabreira et al. (2016) and an unnamed lagerpetid (Garcia et al. 2019), an unnamed silesaurid (Langer et al. 2017b, Garcia et al. 2019), the putative theropod *Nhandumirim waldsangae* Marsola et al. (2019), the early sauropodomorphs *Buriolestes schultzi* Cabreira et al. (2016), *Pampadromaeus barberenai* Cabreira et al. (2011), *Bagualosaurus agudoensis* Pretto et al. (2018), and *Saturnalia tupiniquim* Langer et al. (1999), and the herrerasaurids *Staurikosaurus pricei* Colbert (1970) and *Gnathovorax cabreirai* Pacheco et al. (2019).

The second Brazilian dinosauriform assemblage is early Norian and is found within the Caturrita Formation at localities such as the Linha São Luiz site (Fig. 18), which is  $225.42 \pm 0.37$  Ma in age (U-Pb zircon data, Langer et al. 2018). This younger assemblage includes the silesaurid *Sacisaurus agudoensis* Ferigolo and Langer (2007) (Müller et al. 2016), the early theropod *Guaibasaurus candelariensis* Bonaparte (1999) (Bonaparte et al. 2007, Langer et al. 2011), and the unaysaurid sauropodomorphs *Unaysaurus toletinoi* Leal et al. (2004) and *Macrocollum itaquii* Müller et al. (2018b) (Bittencourt et al. 2012, Müller et al. 2016, 2020). An isolated distal end of a femur (MMACR 039 T) was identified as that of a neotheropod (Pinheiro 2016), but no unambiguous

A



C



**Figure 18. A (pg. 34).** Triassic dinosaur morph biostratigraphy of South America and Africa **B, C.** Maps of localities discussed in the text. Shaded countries (**B, C**) contain Triassic dinosaur morphs. Maps modified from [freevectormaps.com] and silhouettes and colors correspond to those used in Figure 21; see acknowledgements for full links. Timescale and radiometric dates (\*) modified from Lucas (2010), Martínez et al. (2011), Mariscano et al. (2015), Kent et al. (2017), Langer et al. (2018), Bordy et al. (2020), and Desojo et al. (2020). Abbreviations: **ASRH**, A.S.R. Hill; **BR**, Buriol Ridge; **Cda**, Linha São Luiz; **CIC**, Cerro las Lajas; **JS**, Janner Site; **LSL**, Linha São Luiz; **Le**, Lesotho; **Ma**, Madagascar; **Mo**, Argana Basin, Morocco; **QdP**, Quebrada del Puma; **SA**, South Africa; **Tn**, Ruhuhu Basin, Tanzania; **VP**, Valle Pintado; **Zb**, Zimbabwe; **Zm**, Zambia.

apomorphies of Neotheropoda were used in that identification. It resembles the distal ends of femora described from PEFO above and preserves those apomorphies that would assign it to Saurischia.

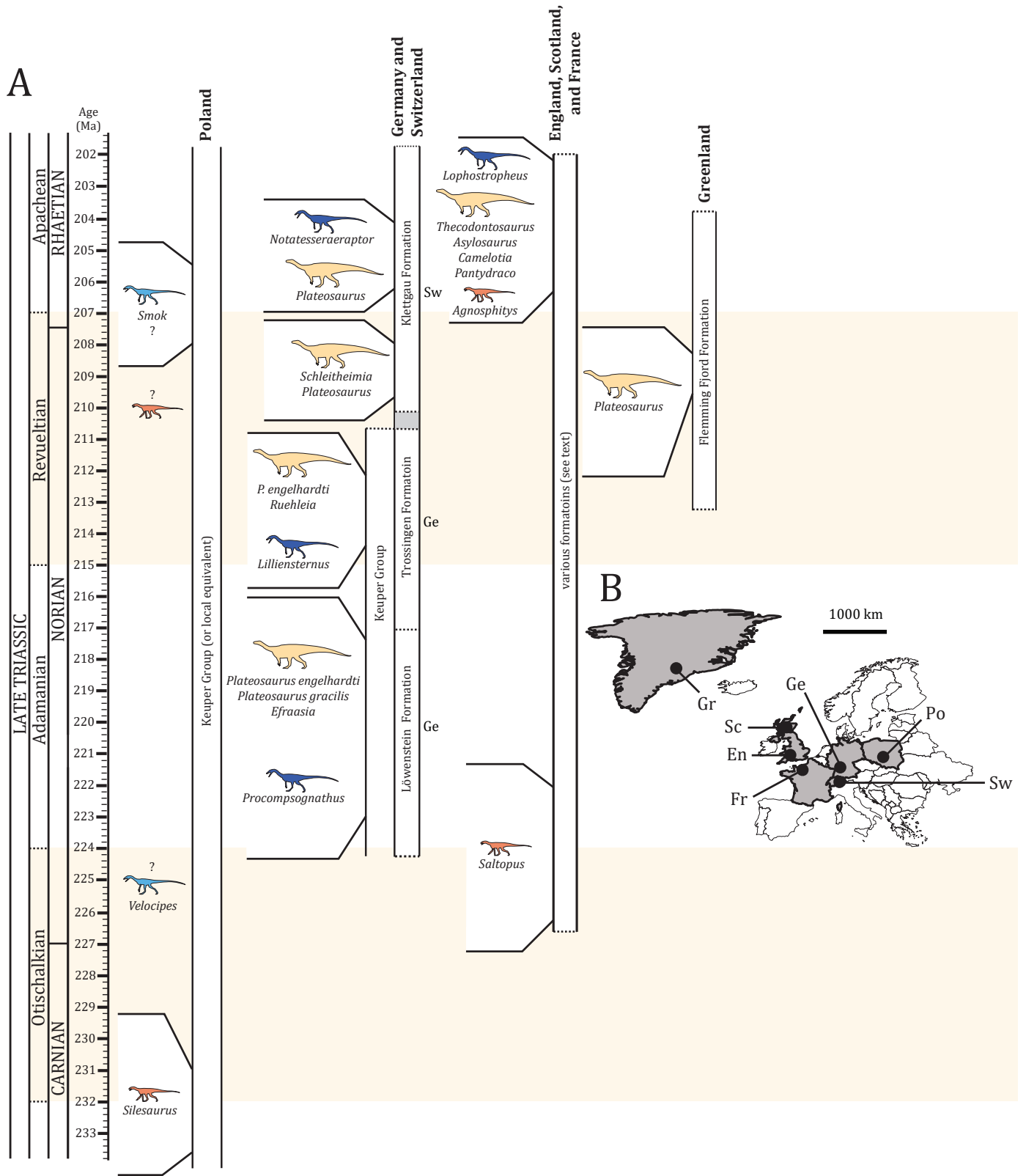
**Argentina**—The Triassic dinosaur morph record in Argentina includes two Carnian and two Norian assemblages. The lower Carnian assemblage is from the Chañares Formation (Fig. 18); the vertebrate-bearing horizon near the base of the formation is  $236.1 \pm 0.6$ – $233.7 \pm 0.4$  Ma in age (U-Pb zircon data, Mariscano et al. 2015, Ezcurra et al. 2017). That horizon preserves the lagerpetid *Lagerpeton chanarensis* (Romer 1971), the dinosauriform *Marasuchus lilloensis* (Serenó and Arcucci 1994) which is considered a senior synonym of *Lagosuchus talampayensis* Romer (1971) (Agnolín and Ezcurra 2019), and the silesaurid *Lewisuchus admixtus* (a proposed senior synonym of *Pseudolagosuchus major* Arcucci (1987) (Romer 1972, Ezcurra et al. 2019). The late Carnian assemblage is from the base of the Ischigualasto Formation (Fig. 18), which is  $231.4 \pm 0.3$  Ma in age (Ar-Ar sanidine data, Rogers et al. 1993, Martínez et al. 2011), but the vertebrate-bearing interval is between  $\sim 229.20$  Ma and  $\sim 226.85$  Ma (U-Pb zircon data, Desojo et al. 2020). The Ischigualasto Formation at Valle Pintado and nearby localities preserves an unnamed lagerpetid (Martínez et al. 2012), the silesaurid *Ignotosaurus fragilis* Martínez et al. (2012), the sauropodomorphs *Eoraptor lunensis* (Serenó et al. 1993), *Panphagia protos* Martínez and Alcober (2009), and *Chromogisaurus novasi* Ezcurra (2010), the herrerasaurids *Herrerasaurus ischigualastensis* (Reig 1963) and *Sanjuansaurus gordilloi* Alcober and Martínez (2010), and the early theropod *Eodromaeus murphi* (Martínez et al. 2011). *Pisanosaurus mertii* (Bonaparte 1976) comes from the Ischigualasto Formation at Cerro Las Lajas, La Rioja ( $\sim 229.20$  Ma) and has been alternatively assigned to Silesauridae or Ornithischia (Desojo et al. 2020).

The lower of the two Norian dinosaur morph assemblages in Argentina is found in the Los Colorados Formation (Fig. 18). The Los Colorados Formation lacks non-dinosaur dinosaur morphs, but preserves the sauropodomorphs *Coloradisaurus brevis* Bonaparte (1978), *Lessemsaurus sauropoides* Bonaparte (1999), and *Riojasaurus incertus* Bonaparte (1969), the coelophysid *Powellvenator podocitus* Ezcurra (2017), and the

stem-averostran *Zupaysaurus rougieri* (Arcucci and Coria 2003). No radiometric ages have been proposed from the unit, but magnetostratigraphy constrains its age to between 227 Ma and 213 Ma (middle Norian, Kent et al. 2014). All of the dinosaur fossils are from the uppermost part of the formation, so they are likely  $\sim 213$  Ma in age (Groeber and Stipanovic 1953, Caselli et al. 2001).

The late Norian assemblage comes from the Quebrada del Barro Formation and includes two major intervals of vertebrate remains in its  $\sim 200$  m section (Fig. 18). The lower part of the formation has produced the lagerpetid *Dromomeron gigas* Martínez et al. (2016) and the lessemsaurid sauropodomorph *Ingentia prima* Apaldetti et al. (2018). The massospondylid sauropodomorph *Leyesaurus marayensis* Apaldetti et al. (2011) was recovered from the upper part of the formation, and the coelophysid neotheropod *Lucianovenator bonoi* Martínez and Apaldetti (2017) has been found throughout the section. Early vertebrate biostratigraphic estimations for the age of the Quebrada del Barro Formation found it to be Norian in age owing to the similarities of a sauropodomorph referred to *Riojasaurus incertus*, which is found in the Norian Los Colorados Formation (Bossi and Bonaparte 1978). Apaldetti et al. (2011) questioned that referral and suggested that *Leyesaurus marayensis* from relatively high in the Quebrada del Barro Formation is more closely related to the Early Jurassic sauropodomorphs *Massospondylus carinatus* Owen (1854) and *Adeopapposaurus mognai* Martínez (2009). The coeval cynodont, archosaur, and lepidosauromorph taxa were used to suggest a late Norian to Rhaetian age for the formation (Martínez et al. 2015).

**Africa**—There are dinosaur morphs known from several Triassic stages and various stratigraphic units in northern and southern Africa. The earliest assemblage is from the Lifua Member of the Manda beds in the Ruhuhu Basin, Tanzania (Fig. 18), and age-equivalent strata in Zambia (Sidor and Nesbitt 2018). Silesaurids are relatively diverse; *Asilisaurus kongwe* (Nesbitt et al. 2010) and a large unnamed taxon (Barrett et al. 2015) are known from the Manda beds and *Lutungutali sitwensis* Peacock et al. (2013) is known from the upper part of the Ntawere Formation of Zambia. These units in southern Africa are hypothesized to be Middle Triassic (Anisian) in age (Nesbitt et al. 2010), but precise age determinations



**Figure 19. A.** Triassic dinosaur biostratigraphy of Europe and Greenland. **B.** Maps of localities discussed in the text. Shaded countries (**B**) contain Triassic dinosauriforms. Maps modified from [freevectormaps.com] and silhouettes and colors correspond to those used in Figure 21; see acknowledgements for full links. Note that the stratigraphic context for *Velocipes* in the Lisów Breccia and indeterminate dinosauriforms of the Keuper Group of Poland is unknown beyond Middle Triassic to Upper Triassic and Norian to Rhaetian, respectively. Timescale modified from Lucas (2010) and Kent et al. (2017). Abbreviations: **En**, England; **Fr**, France; **Ge**, Germany; **Gr**, Greenland; **Sc**, Scotland; **Sw**, Switzerland.

are difficult because of a lack of independent radiometric data from the *Cynognathus* Assemblage Zone (Sidor and Nesbitt 2018). The dinosauriform *Nyasasaurus paringtoni* Nesbitt et al. (2013) is also known from the Lifua Member of the Manda beds, and may represent an early dinosaur, theropod, or sauropodomorph depending on which referred specimens are included in a given phylogenetic analysis (Nesbitt et al. 2013, Baron et al. 2017b, Langer et al. 2017a). *Kongonaphon kely* Kammerer et al. (2020) is the only known lagerpetid from what is now Africa and comes from the basal Isalo II beds in the Morondava Basin of Madagascar. The age of these beds are not well-constrained radiometrically, but they may be correlated to the *Santacruzodon* Assemblage Zone in Brazil (Ezcurra et al. 2017, Schmitt et al. 2019), and depending on if the Isalo II deposits are Middle or Late Triassic (Flynn et al. 2000), *K. kelyi* may be the oldest known lagerpetid (Kammerer et al. 2020).

Two early Late Triassic African dinosauromorphs may or may not be contemporaneous in time but come from opposite sides of the continent. The locality that may be slightly older (late Carnian) is in Zimbabwe (Fig. 18C), where recent fieldwork reported the presence of a *Saturnalia*-like dinosaur from the ‘Pebble Arkose Formation’ (Griffin et al. 2018). The silesaurid *Diodorus scytobrachion* Kammerer et al. (2012) is present at the base of the Irohalene Mudstone Member (t5) of the Timezgadiouine Formation in Morocco (Fig. 18), which is hypothesized to be Otischalkian in age (Kammerer et al. 2012). Unfortunately, more precise chronological constraints for most African terrestrial Triassic units is not available at this time, with the exception of the Norian–Rhaetian Lower Elliot Formation (219.6 Ma to 204.9 Ma, Bordy et al. 2020) (Fig. 18). The sauropodomorph assemblage of the Lower Elliot Formation in South Africa and Lesotho is the youngest Triassic dinosauromorph assemblage in Africa; it is incredibly diverse and includes *Melanorosaurus readi* Haughton (1924), *Meroktenos thabanensis* (Gauffre, 1993) de Fabrègues and Allain (2016), *Plateosaurus cullingworthi* Haughton (1924), *Sefapanosaurus zastronensis* Otero et al. (2015), *Blikanasaurus cromptoni* Galton and van Heerden (1985), *Eucnemosaurus fortis* Hoepen (1920), and *E. entaxonis* McPhee et al. (2015).

**Europe**—The oldest dinosauromorph in Europe is the silesaurid *Silesaurus opolensis* from a clay pit in the lower part of the Keuper Group (late Carnian) at Krasiejów, Poland (Dzik 2003, Dzik and Sulej 2007, Bodzioch and Kowal-Linka 2012) (Fig. 19). There are two Norian dinosauromorph assemblages in central Europe, namely in Germany and Switzerland. The early Norian assemblage

includes the coelophysoid neotheropod *Procompsognathus triassicus* Fraas (1913) from the Middle Stubensandstein Member of the Löwenstein Formation (Keuper Group, Fraas 1907, Rauhut and Hungerbühler 1998, Havlik et al. 2013) of Germany (Fig. 19). The putative theropod *Halticosaurus longotarsus* Huene (1907/1908) is also from that unit, but that taxon was considered a nomen dubium (Rauhut and Hungerbühler 1998). Also from the Löwenstein Formation of Germany are the sauropodomorphs *Efraasia minor* von Huene (1907/1908), *Plateosaurus gracilis* von Huene (1907/1908), and *P. engelhardti* von Meyer (1837) (Galton 2001b, Yates 2003). *P. engelhardti* is also present in the overlying (late Norian) Trossingen Formation in Germany (Galton 2001b, Yates 2003) (Fig. 19) along with the sauropodomorph *Ruehleia bedheimensis* Galton (2001a) and the neotheropod *Lilliensternus lilliensterni* (Huene 1934, Rauhut and Hungerbühler 1998). Dinosaurs are known from two horizons in the Gruhalde Member of the Klettgau Formation of Switzerland (Zahner and Brinkmann 2019, Rauhut et al. 2020). The late Norian sites (Jordan et al. 2016) in Canton Schaffhausen include *Plateosaurus* sp., the sauropodiform *Schleitheimia schutzi* Rauhut et al. (2020), and potentially a third sauropodomorph taxon (Rauhut et al. 2020). The second and youngest dinosauromorph assemblage from central Europe is from a clay pit in Frick (Sander 1992). This site is the uppermost part of the Gruhalde Member (Norian–?Rhaetian; Jordan et al. 2016, Zahner and Brinkmann 2019) and preserves *Plateosaurus* (Sander 1992, Foelix et al. 2011) and the stem-averostran neotheropod *Notatesseraeraptor frickensis* Zahner and Brinkmann (2019), which was found ~1 m below the Triassic–Jurassic boundary (Fig. 19). Incidentally, plateosaurid material (e.g., NHMD 164741) has also been found from the Norian–Rhaetian-aged Malmros Klint Member of the Fleming Fjord Formation in eastern Greenland (Jenkins et al. 1993, 1994, Marzola et al. 2018) (Fig. 19).

There have been a variety of theropod and sauropodomorph taxa described from other Triassic sites in southwestern Poland, but few are still considered valid (see the extensive discussion in Skawiński et al. 2016). *Velocipes guerichi* Huene (1932, GPIM UH No. 252) probably represents the proximal end of a fibula belonging to an early theropod from a clay pit in the ‘Lisów Breccia’ (Middle Triassic to Upper Triassic) (Fig. 19) near Kocury, and an unnumbered proximal end of a fibula from the Keuper Group (Norian to Rhaetian) near Ostrowiec Świętokrzyski is referred to Dinosauriformes (Skawiński et al. 2016). Additionally, the taxon *Smok wawelski*

Niedźwiedzki et al. (2012, ZPAL V.33/15) is known from the Lisowice (Lipie Śląskie) clay pit and at Marciszów in southern Poland (Dzik et al. 2008, Niedźwiedzki et al. 2012, Niedźwiedzki and Budziszewska-Karwowska 2018). *S. wawelsi* has been referred to the Theropoda (Dzik et al. 2008), but it may also represent a non-crocodylomorph loricatan pseudosuchian (Niedźwiedzki et al. 2012, Niedźwiedzki and Budziszewska-Karwowska 2018). The strata at Lisowice are latest Norian to early Rhaetian in age and correlate with the upper part of the Keuper Group in eastern Germany (Niedźwiedzki et al. 2012).

The dinosauromorphs from western Europe are all found in Rhaetian-aged rocks (Fig. 19) with the exception of *Saltopus elginensis* Huene (1910), a dinosauriform from the Lossiemouth Sandstone Formation (early Norian) from Scotland (Benton and Walker 2011, Baron et al. 2017b). Some of those are from fissure fill deposits, such as the small sauropodomorphs *Thecodontosaurus antiquus* Morris (1843) and *Asylosaurus yalensis* Galton (2007a) near Bristol, England (Benton et al. 2000, Galton 2007a, Ballell et al. 2020) and *Pantydraco caducus* Galton et al. (2007b) from South Wales. The larger melanorosaurid sauropodomorph *Camelotia borealis* Galton (1985) is known from the Wedmore Stone near the base of the Westbury Formation (Penarth Group), in Somerset, England (Galton 1985, 1998). The neotheropod *Lophostropheus airelensis* Cuny and Galton (1993) is from the Moon-Airel Formation (late Rhaetian–early Hettangian) of Normandy, France (Rauhut and Hungerbühler 1998, Ezcurra and Cuny 2007). *Agnosphitys cromhallensis* Fraser et al. (2002), is a taxon known from the holotype ilium and referred maxilla, astragalus, and humerus from the fissure fills of the Cromhall Quarry, England, that has been hypothesized to be a theropod (Yates 2007) or sauropodomorph (Ezcurra 2010), but has more recently been hypothesized to belong to the Silesauridae (Fraser et al. 2002, Baron et al. 2017b), which would make it the youngest non-dinosaur dinosauromorph outside of the United States (Langer et al. 2013, Marsh 2018a).

*Asia*—Triassic dinosauromorphs are known from two countries in eastern Asia (Fig. 20). Indian occurrences are found at three stratigraphic levels in the Triassic strata of the Pranhita-Godavari Valley in east-central India. The dinosaur *Alwalkeria maleriensis* Chatterjee and Creisler (1994) was found in the Lower Maleri Formation (Chatterjee 1987) and the holotype specimen was later determined to be a chimera, so it is only known from the partial end of a femur and astragalus (Remes and Rauhut 2005). *Alwalkeria maleriensis* was first thought to

be a coelophysid ('podokesaurid') theropod (Chatterjee 1987) but is now thought to be an indeterminate saurischian dinosaur (Remes and Rauhut 2005, Langer et al. 2010, Novas et al. 2011). The Lower Maleri Formation is considered to be equivalent in age to the *Hyperodapedon* Assemblage Zone of the Ischigualasto-Villa Unión Basin of Argentina (Langer 2005) and late Carnian based on the presence of the phytosaur *Parasuchus hislopi* Lydekker (1885) (Datta et al. 2019). A purported indeterminate theropod from the age-equivalent Tiki Formation (Madhya Pradesh State, India) requires further investigation and identification (Chatterjee and Majumdar 1987).

The Upper Maleri Formation of the Pranhita-Godavari Valley includes fragmentary remains of two indeterminate dinosauriforms, the sauropodomorph dinosaurs *Nambalia roychowdhurii* Novas et al. (2011) and *Jaklapallisaurus asymmetrica* Novas et al. (2011), and a *Guaibasaurus*-like dinosaur (Novas et al. 2011). The overlying Dharmaram Formation includes *J. asymmetrica* and another indeterminate sauropodomorph as well as the proximal end of a femur referred to the Neotheropoda (Novas et al. 2011). The Upper Maleri Formation (Fig. 20) is considered later Norian in age owing to the lack of 'Ischigualastian' vertebrate taxa (Langer 2005, Novas et al. 2011) and the Lower Dharmaram Formation is considered latest Norian to Rhaetian (Bandyopadhyay and Sengupta 2006, Kutty et al. 2007; Datta et al. 2019).

The sauropodomorph dinosaur *Isanosaurus atavipachi* Buffetaut et al. (2000) is from the Nam Phong Formation at Phu Nok Khian hill (Chaiyaphum Province), Thailand. This formation is constrained in age by vertebrate and palynomorph fossils to the Late Norian or Rhaetian (Racey et al. 1996, Buffetaut et al. 2000).

### Trends in Late Triassic dinosauromorph biostratigraphy and biogeography

There are obvious hypotheses to be made from reviewing the global Triassic dinosauromorph record (Fig. 21), and many have already been reviewed by Langer et al. (2013). Even given the ambiguous nature of the taxonomy of *Nyasasaurus parringtoni* (Nesbitt et al. 2013), it is clear that the earliest known dinosauromorphs include silesaurid dinosauriforms from the Middle Triassic (Anisian) of Tanzania and Zambia (Peacock et al. 2013, Barrett et al. 2015) and lagerpetid dinosauromorphs and silesaurid dinosauriformes from the earliest Late Triassic (Carnian) of northwestern Argentina (Ezcurra et al. 2017, 2019). Similarly, the oldest true dinosaurs are from the early Late Triassic (Carnian) of Argentina (Martínez et al. 2012), Brazil (Langer et al. 2018), and





Zimbabwe (Griffin et al. 2018). All of these data support the hypotheses surrounding a Gondwanan origin for early dinosauro-morph groups (Irmis 2011, Baron 2020, Müller and Garcia 2020), but this could be the result of preservation and sampling bias. Here, we focus on unambiguous dinosauro-morph body fossils, although Middle Triassic footprints from Poland have been referred to a dinosauro-morph trackmaker (Brusatte et al. 2010, Niedźwiedzki et al. 2013). However, this referral has been disputed (e.g., Padian 2013), as inferring trackmakers is notoriously difficult (Gatesy and Falkingham 2020). Taken at face value, this would place non-dinosaurian dinosauro-morphs in Laurasia ~10 Ma earlier than any Gondwanan occurrence (Brusatte et al. 2010). Confirmation will probably require body fossils, but it demonstrates that a Gondwanan origin for Dinosauro-morpha should not be taken for granted (Baron 2020). Indeed, the Carnian occurrence of *Silesaurus opolensis* from Europe is not much younger than the South American occurrences (Fig. 21).

Unfortunately, fossiliferous Carnian terrestrial sedimentary rocks are seemingly absent in North America, perhaps with the exception of part of the the Popo Agie Formation (Chugwater Group) of Wyoming (Lucas et al. 2002, Gauthier et al. 2011, Fitch et al. 2018, 2020), which yielded the purported dinosaur *Poposaurus gracilis*, now understood to be a bipedal non-loricatan pseudosuchian (Gauthier et al. 2011, Nesbitt 2011). A significant issue with the fossil record of the Chinle Formation in the American Southwest is that, in addition to the entire formation being Norian in age, its lower part (the lower part of the Blue Mesa Member and the Shinarump Member/Mesa Redondo Member) is depauperate of fossils. This is especially true at PEFO where no fossils are currently known from the lower part of the Blue Mesa Member (Parker and Martz, 2011). The Blue Mesa Member preserves neotheropods as well as non-dinosaurian dinosauro-morphs and dinosauriforms, demonstrating that these groups co-existed through all of Chinle Formation time (Adamanian–Apachean). However, a preservation bias appears to affect our understanding of the first appearances of these groups in western North America. This is further complicated by the presence of a sizeable unconformity between the base of the Chinle Formation and the underlying Early–Middle Triassic Moenkopi Formation (Pipiringos and O’Sullivan 1978, Rasmussen et al. 2020). Because the Blue Mesa Member is Norian in age

(Ramezani et al. 2011, 2014), it appears the entire Carnian record is missing in Arizona, which is unfortunate because Carnian rocks elsewhere preserve the earliest records of dinosaurs (see previous section). The potentially oldest vertebrate faunal assemblage in the Chinle Formation in Arizona is that from Davis Ranch near St. Johns collected by Ned Colbert in 1946 (Camp et al. 1947, E. H. Colbert 1946 unpublished field notes, AMNH). Based on surviving color slides (AMNH and PEFO archives) the sites appear to be in the lower part of the Chinle Formation, the Bluewater Creek Member and below the upper part of the Blue Mesa Member. Colbert’s notes only mention metoposaurs and phytosaurs from these sites, but the AMNH collection needs to be reexamined and possibly even prepared. Furthermore, the sites need to be relocated and placed stratigraphically, but this is complicated by the land ownership. The Bluewater Creek Member assemblage at Six Mile Canyon in New Mexico (Heckert and Lucas 2002, Heckert et al. 2012, Irmis et al. 2011) could also be older than the upper part of the Blue Mesa Member at PEFO, but this also needs to be further investigated as the upper parts of the Blue Mesa Member and the Bluewater Creek Member may be at least partially equivalent (Marsh et al. 2019b). Unfortunately, all of these older North American sites have been assigned ages based solely on biostratigraphy and more work is needed to determine if they truly are Carnian in age.

Vertebrate paleontology work is also continuing in the Early–Middle Triassic Moenkopi Formation of southwestern United States (e.g., Nesbitt 2005, Formoso et al. 2019) and presently no dinosauro-morph material has been recovered. *Rotodactylus* isp. tracks (e.g., GRCA 33186 and WUPA P3-002) do occur in the Holbrook Member of the Moenkopi Formation (e.g., Henderik et al. 2017, Marsh et al. 2020), with a maximum depositional age of ~241 Ma (Rasmussen et al. 2020), but again the dinosauro-morph origin of these tracks is disputed (Padian 2013). Nonetheless, the Moenkopi Formation remains the best target for discovering the earliest dinosauro-morphs in North America. Also needed are precise radioisotopic dates from Otischalkian sites in Texas, New Mexico, and Wyoming, as well as more vertebrate sites from the Newark Supergroup. Vertebrate fossils are known from Carnian strata in the Newark Supergroup, such as the Vinita Formation (Richmond basin, Sues and Hopson 2010) and Falling Creek Formation (Taylorsville basin, Dilkes and Sues 2009), but these records presently do not

**Figure 21. A. (pg. 41).** Hypothesized biostratigraphic ranges of Triassic dinosauro-morphs. B. Simplified phylogenetic hypotheses of dinosauro-morph relationships with colors corresponding to clades in A. Silhouettes used from [phylopic.org]; see acknowledgements for full links. Timescale modified from Lucas (2010) and Kent et al. (2017).



include dinosauromorphs and more sampling is needed.

### The importance of new specimens and apomorphy-based identifications

The similar bauplans and degree of homoplasy present in the skeletal anatomy of divergent Late Triassic archosauromorphs groups make identifications of fragmentary fossils difficult. In some cases, the presence of dinosauromorphs in Triassic assemblages hinges on such fragmentary fossils that often end up being determined to be other kinds of reptiles. For example, certain purported dinosaur specimens from the Middle-Upper Triassic of Poland represent tanystropheid archosauromorphs (Skawiński et al. 2016) and the purported dinosaur from the Upper Triassic Popo Agie Formation of Wyoming *Poposaurus gracilis* is actually a non-loricatan pseudosuchian (Gauthier et al. 2011, Nesbitt 2011). Using discrete apomorphies to identify fragmentary specimens like those from PEFO reported here allows for unambiguous determinations of the presence of certain clades in their stratigraphic context. This has been shown to be especially important in determining the identity and stratigraphic ranges of early dinosaur specimens (Nesbitt et al. 2007, Irmis et al. 2007a, Nesbitt et al. 2013). Further, apomorphy-based identifications allow for a more direct comparison of dinosauromorph assemblages around the world. Many of the taxa known only from fragmentary specimens highlighted in the discussion (e.g., *Velocipes guerichi*, *Alwalkeria maleriensis*, *Smok wawelski*) may potentially be more useful for vertebrate biostratigraphy if identified with published apomorphies. Also important is the increasing use of high-resolution geochronologic techniques to better understand the depositional ages of dinosauromorph-bearing formations (Martínez et al. 2011, Ramezani et al. 2011, 2014, Kent et al. 2014, 2017, Mariscano et al. 2015, Langer et al. 2018, Bordy et al. 2020, Desojo et al. 2020). In some cases, these new age determinations have clarified that purported Late Triassic dinosaur fossils are actually Early Jurassic in age. Examples of this include *Anchisaurus polyzelus* Marsh, 1885 and *Podokesaurus holyokensis* Talbot, 1911 from the Newark Supergroup of eastern North America (Olsen et al. 2002, 2011), and *Eocursor parvus* from the Upper Elliot Formation of South Africa (Olsen et al. 2011, McPhee et al. 2017).

These new and revised techniques have revised existing hypotheses regarding the distribution of early dinosauromorphs and allowed new hypotheses regarding such phenomena as the noticeable lack of Triassic ornithischian dinosaurs (Ferigolo and Langer 2007,

Padian 2013, Müller and Garcia 2020), the late dispersal of sauropodomorphs into North America (Rowe et al. 2010, Olsen et al. 2011, Marsh and Rowe 2018), and the temporal and spatial co-occurrence of derived dinosaurs and their ancestors (e.g., Irmis et al. 2007b). Likewise, they have also allowed for the recognition of non-dinosaurian clades in new areas such as the presence of tanystropheids and azendohsaurids (previously restricted to Europe and Africa) in the Chinle Formation of western North America (e.g., Pritchard et al. 2015; Marsh et al. 2017) based on fossils originally thought to be dinosaurian.

### CONCLUSIONS

This study resulted from a dramatic increase in dinosauromorph fossils collected from PEFO in the 13 years since the last review of these taxa at the park (Irmis et al. 2007a, Nesbitt et al. 2007). Spurred by the discovery of silesaurid dinosauriforms (Parker et al. 2006, Nesbitt et al. 2007, Irmis et al. 2007a), a significant number of dinosauromorph fossils have been recovered from the Chinle Formation, mainly at PEFO and Ghost Ranch, NM (Fig. 1) (Irmis et al. 2007b, Nesbitt et al. 2009a). This marked increase is the results of further sampling of the Chinle Formation, along with new finds in South America and Africa (e.g., Nesbitt et al. 2010, Langer et al. 2018, Martínez and Apaldetti 2017, Griffin et al. 2018), demonstrating the continued importance of identifying key outcrops in specific time intervals to improve our understanding of the evolution of the dinosaurian lineage. Just as important has been the reinvestigation of existing collections given this new understanding (e.g., Kammerer et al. 2012, 2020, Nesbitt et al. 2017). Once thought to be fairly well understood and straightforward, these new finds and insights are showing that ornithodiran evolution was quite complex and that diversification was very rapid following the end-Permian extinction. As with previous studies (e.g., Nesbitt et al. 2007), we find that despite significant increased sampling, only theropod dinosaurs were present in North America (excluding Greenland) during the Late Triassic, differing from time equivalent areas in South America, Europe, and Africa. Much of this has been made possible by the use of apomorphy-based identifications, new 'Rosetta stone' specimens of non-dinosaurian dinosauromorph taxa, and improved geochronological resolution of Late Triassic strata. Future studies need to target younger stratigraphic units in western North America including the base of the Chinle Formation and Dockum Groups, the Popo Agie Formation in Wyoming, and the Moenkopi

Formation in Utah, Arizona, and New Mexico to test ideas about dinosaur origins. Likewise, younger stratigraphic units, e.g. the Owl Rock Member of the Chinle Formation and the Redonda Formation of the Dockum Group also require improved sampling to further investigate the first appearances of sauropodomorphs and ornithischians in western North America, both of which occur in overlying Jurassic rocks (Marsh 2018b).

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