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The first pectoral and forelimb material assigned to the lagerpetid *Lagerpeton chanarensis* (Archosauria: Dinosauromorpha) from the upper portion of the Chañares Formation, Late Triassic

MASON B. MCCABE & STERLING J. NESBITT

Abstract

The posture of the earliest dinosaurs is thought to be bipedal whereas their pseudosuchian relatives and stem archosaurs are thought to be typically quadrupedal. Therefore, the transition from quadrupedality to bipedality lies somewhere between the origin of Avemetatarsalia (bird-line archosaurs) and Dinosauria. However, studying this transition is hampered by the lack of forelimb fossils from many of the close relatives of dinosaurs and it is not clear if the morphology of the few dinosauromorphs that have forelimb material is unique or represents the plesiomorphic condition. New forelimb fossils of dinosaur relatives and careful assessments of their osteology are sorely needed to help address this knowledge gap. Here we present the first pectoral (left scapulocoracoid) and forelimb (right humerus) bones of an avemetatarsalian from the upper portion of the Chañares Formation of Argentina. We hypothesize that the bones pertain to the important early ornithodiran *Lagerpeton chanarensis*, but the scapulocoracoid and humerus does not precisely match any non-dinosaurian avemetatarsalian. The bones were prepared from a concretion that only consisted of *Lagerpeton chanarensis* and the cynodont *Massetognathus pascuali*. We identify the bones as belonging to *Lagerpeton chanarensis* because the distal end of the femur possesses an inflated crista tibiofibularis – a lagerpetid character state – and the newly recognized pectoral and forelimb bones are generally similar to those of the lagerpetid *Dromomeron romeri* and *Ixalerpeton polesinensis*, with tall and constricted anteroposteriorly narrow scapular blades and a humerus with a highly asymmetrical proximal end. The length of humerus and the proportions of the proximal and distal end in *Lagerpeton chanarensis* are also more similar to that of *Dromomeron romeri*. Overall, the scapulocoracoids and humeri of lagerpetids are similar in proportion across taxa, but comparing the length of the forelimbs to the hindlimbs is hampered by the lack of articulated or unambiguously associated individuals of any member of the group. Currently, it is still not clear if the anatomy of the pectoral girdle and forelimb of lagerpetids, and thus posture, is unique for lagerpetids or represents the ancestral condition for ornithodirans.

Key words: Archosauria, Dinosauromorpha, Upper Triassic, Argentina, osteology, anatomy.

1. Introduction

In the past 20 years, our understanding of the early evolution of Avemetatarsalia has been broadened to include the diverse subclades Aphanosauria, Lagerpetidae, and Silesauridae that lie outside Dinosauria (IRMIS et al. 2007; NESBITT et al. 2010, 2017; EZCURRA et al. 2020). The addition of anatomical information from these groups helps in our reconstruction of the relationships and diversity of early Avemetatarsalia, but also in how the dinosaurian body plan evolved over millions of years (SERENO & ARCUCCI 1994a, b; NESBITT et al. 2010, 2014, 2018; CABREIRA et al. 2016; MÜLLER et al. 2018; EZCURRA et al. 2016, 2019). However, the anatomy of species from early avemetatarsalian subgroups is incomplete. The most commonly preserved elements for early avemetatarsalian are elements of the hindlimbs and pelvic girdle (SERENO & ARCUCCI 1994a, b; CABREIRA et al. 2016; MÜLLER et al. 2018; SMITH et al. 2018) and these parts of the anatomy are responsible for much of our knowledge of the biomechanical transformations from quadrupedal stem archosaurs to fleet-footed and bipedal dinosaurs (or close relatives). However, with

the introduction of quadrupedal silesaurids as one of the closest relatives of dinosaurs (DZIK 2003; NESBITT et al. 2020), the simple story of single transformation of quadrupedality to bipedality appears to be more complicated than previously considered. Moreover, it is not currently clear if some of the anatomical character states in the hindlimbs and pelvis of early avemetatarsalians are unique to subclades (e.g., lagerpetids) or represent plesiomorphies along the branches outside Dinosauria.

Understanding the biomechanical transitions within Avemetatarsalia has been a challenge largely because of the lack of forelimb and pectoral girdle material in most early avemetatarsalians. Many of the characteristic states that are diagnostic for early dinosaurs are in the forelimbs (SERENO 1994; SERENO & ARCUCCI 1994b; DELCOURT & DE AZEVEDO 2013), but there are few outgroups to optimize these character transformations. This is a critical gap in avemetatarsalians that is slowly being filled (Aphanosauria: NESBITT et al. 2017; Lagerpetidae: CABREIRA et al. 2016, and Silesauridae: DZIK & SULEJ 2007; EZCURRA et al. 2019, 2020; NESBITT et al. 2020), but key taxa still lack any information from the pectoral girdle and forelimb.

One of these key taxa, *Lagerpeton chanarensis* (ROMER 1971; SERENO & ARCUCCI 1994b), was monumental in understanding the origin of the dinosaurian body plan, but is still only represented by parts of the vertebral column, pelvic girdle, and hindlimb. Here, we identify the first putative forelimb and pectoral girdle of *Lagerpeton chanarensis*. This material, collected from the holotype locality of *Lagerpeton chanarensis*, includes a left scapulocoracoid and humerus associated with a diagnostic distal end of the left femur. These new assignments add to our growing understanding of forelimb evolution in early archosaurs and avemetatarsalians.

Abbreviations: GR, Ruth Hall Museum of Paleontology, Ghost Ranch, Abiquiú, New Mexico, U.S.A.; MCZ, Museum of Comparative Zoology, Harvard University, Boston, U.S.A.; PVL, Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, Paleontología de Vertebrados, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; NHMUK, Natural History Museum, London, U.K.; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; ULBRA, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Brazil.

2. Material and methods

The newly identified elements (Table 1) were collected by ALFRED ROMER and crew during the initial discovery of the Chañares Formation assemblage in 1964–1965 from expeditions conducted in the Ischigualasto-Villa Unión Basin of Argentina and were deposited in the MCZ collections. This Chañares Formation archosaur assemblage has been instrumental in sorting out the relationships between archosaurs and is one of the most important collections of Late Triassic archosaurs in southern Pangea (ROMER 1971; BONAPARTE 1975; SERENO & ARCUCCI 1994a, b; NESBITT et al. 2009, 2010; BRUSATTE et al. 2010; LANGER

et al. 2010, 2013; BITTENCOURT et al. 2015; CABREIRA et al. 2016, EZCURRA & MARTÍNEZ 2016, MÜLLER et al. 2018; EZCURRA et al. 2019).

The material was prepared (likely from ARNOLD LEWIS from the MCZ) from a concretion containing at least one cynodont identified as *Massetognathus pascuali* (MCZ VPRA-3801). The cynodont material was prepared completely out of the rock, left with some stabilizing matrix, or was left in small associations within larger chunks of matrix. One of us (SJN) found the material among the nearly completely prepared specimens, so the exact association of the avemetatarsalian specimens was not recorded. The specimens were further prepared by SJN using a carbide needle under a stereomicroscope and much of the original epoxy was removed and replaced with a thin coating of Paraoid B-72 in acetone. Photography of the specimens was done by STERLING NESBITT. Surface scanning was conducted using an Artec Space Spider and processed in Artec software. Models are available as 3D mesh files in online supplementary information.

3. Systematic paleontology

Archosauria COPE, 1870, SENSU GAUTHIER, 1986

Avemetatarsalia BENTON, 1999

Lagerpetidae ARCUCCI, 1986, *sensu* NESBITT et al., 2009

Taxonomic assignment: The morphology of the femur, scapulocoracoid, and humerus, in combination, does not possess the exact combination of character states in taxa previously collected from the upper portion of the Chañares Formation. Based on the character states of the femur, we refer this material to *Lagerpeton chanarensis* based on a series of observations. The distal end of the femur (MCZ 101540) shares unique character states to that of *Lagerpeton chanarensis* (PVL 4619,

Table 1. Measurements of the elements referred to the dinosauiromorph *Lagerpeton chanarensis*.

Element	Dimension	mm
left scapulocoracoid	Max. length	45.1
	Max. width at midshaft	4.9
	Max. width at distal end	10.5
	Max. width at proximal end	8.5
left humerus	Max. length	48.5
	Max. width at midshaft	3.5
	Max. width at distal end	8.5
	Max. width at proximal end	9
distal end of left femur	Max. length	34.5
	Max. width at midshaft	3.5
	Max. width at distal end	10.5
	Max. width at proximal end	na

Table 2. Comparison of scapula length to humerus length and humerus length to proximal humerus width ratios of various Triassic species.

Species	Specimen Number	Scapula Length (mm)	Humerus Length (mm)	Proximal Humerus Width (mm)	Scapula Length/Humerus Length	Proximal Humerus Width/Humerus Length
<i>Lagerpeton chanarensis</i>	MCZ 101540	40.2	48.5	10.5	0.829	0.216
<i>Ixalerpeton polesinensis</i>	ULBRA-PVT059	38.5	51.5	14.5	0.748	0.282
<i>Marasuchus lilloensis</i>	PVL 3871	25	38.6	9.8	0.648	0.254
<i>Scleromochlus taylori</i>	NHUK R3146A, NHUK R3556	11	19.5	n/a	0.564	n/a
<i>Raeticodactylus filisurensis</i>	BNM 14524	n/a	82	22.0	n/a	0.268
<i>Asilisaurus kongwe</i>	NMT RB159	93.2	90.6	25.9	1.029	0.286
<i>Tawa hallae</i>	GR 242	84	87	20	0.966	0.230
<i>Saturnalia tupiniquim</i>	MCP 3845-PV	92	97	33.5	0.948	0.345
<i>Euparkeria capensis</i>	SAM 5867	37.4	37.8	n/a	0.989	n/a
<i>Azendohsaurus madagaskarensis</i>	FMNH PR 2755	n/a	191	100	n/a	0.524
<i>Polesinesuchus aurelioi</i>	ULBRA-PVT003	49.6	60	19	0.827	0.317
<i>Poposaurus gracilis</i>	YPM VP 057100	205	175	61	1.171	0.349
<i>Tropidosuchus romeri</i>	PVL 4601	87.5	67.5	30.1	1.296	0.446

PVL 4625, MCZ 4121) and bears the following lagerpetid synapomorphy – an inflated crista tibiofibularis on the distal end of the femur (SERENO & ARCUCCI 1994b; MÜLLER et al. 2018). Within Lagerpetidae, the high angle (~135°) of the anteromedial corner in distal view and the lack of a broad groove on the posterolateral side of the crista tibiofibularis (in distal view) are shared with *Lagerpeton chanarensis* and *Ixalerpeton polesinensis*. The proportions of the scapula and the humerus of *Ixalerpeton polesinensis* clearly differ from those in MCZ 101540 (see below). We have not found any unique characters of the forelimb and pectoral girdle (see description below), but these elements are generally consistent with the morphology of those of other lagerpetids and early avemetatarsalians. These elements fall into the current size range of other known lagerpetid fossils and has the characteristics that are associated with the clade (Table 2) (LANGER et al. 2007; NESBITT et al. 2018, 2020).

The discovery conditions and association also help with our identification (see above also). The elements were found in the same concretion as the cynodont *Massetognathus pascuali* (MCZ VPRA-3801), a common taxon in the Chafñares Formation found in direct association with fossils of *Lagerpeton chanarensis* (ROMER 1971; EZCURRA et al. 2017).

Description: The left scapulocoracoid of MCZ 101542 (Fig. 1) is mostly complete but has an eroded anterior edge and a partial eroded posterior edge of the coracoid and the antero-distal corner of scapular blade is broken. A piece of bone (possibly a fragment of dislocated rib) is adhered to the medial side of the scapular blade. In lateral view, the scapular blade bears near parallel anterior and posterior edges whereas the most distal end expands both anteriorly and posteriorly. Within Lagerpetidae, the scapula of *Ixalerpeton polesinensis* (ULBRA-PVT059) has a more anteriorly and posteriorly expanded scapular blade

in lateral view than MCZ 101542 (Fig. 2), so MCZ 101542 appears not to match that morphology. The proximal end of the scapula is also anteroposteriorly longer proportionally than in MCZ 101542. *Dromomeron romeri* (GR 1071) has a more strap-like scapular blade with more paralleled anterior and posterior sides distally than MCZ 101542, but the long scapular blades of *Dromomeron romeri* of MCZ 101542 are more similar to each other than either is to *Ixalerpeton polesinensis*. Compared to *Lagosuchus talampayensis* (PVL 3871), the scapular blade of MCZ 101542 is much more strap-like (near parallel anterior and posterior side) and the distal end expands more in *Lagosuchus talampayensis*. The scapulae of non-dinosaurian dinosauriforms (*Asilisaurus kongwe*, NMT RB159; *Silesaurus opolensis*, DZIK 2003) and early dinosaurs (*Saturnalia tupiniquim*, MCP 3845-PV) have generally similar shapes, but the anterior and posterior edges diverge for much of the length of the scapular blade, creating a biconcave shape in lateral view compared to MCZ 101542. The scapular blades slightly diverge just distal to the proximal end to create a gradually widening blade in the early diverging avemetatarsalian *Teleocrater rhadinus* (NHUK PV R6795) and members just outside Archosauria (the proterochampsid *Tropidosuchus romeri*, PVL 4604; *Euparkeria capensis*, SAM-PK-5867).

Proximally, the scapula of MCZ 101542 expands anteriorly and posteriorly relative to the constricted portion of the scapular blade just distal to the proximal end. The posterior expansion forms half of the glenoid whereas the anterior expansion forms a finger-like acromion process that is raised laterally to the rest of the scapular surface. A raised acromion process has been suggested to be a synapomorphy of Archosauria (NESBITT 2011) but also found in the close archosaur relative proterochampsids (EZCURRA 2016), thus giving support that MCZ 101542 belongs

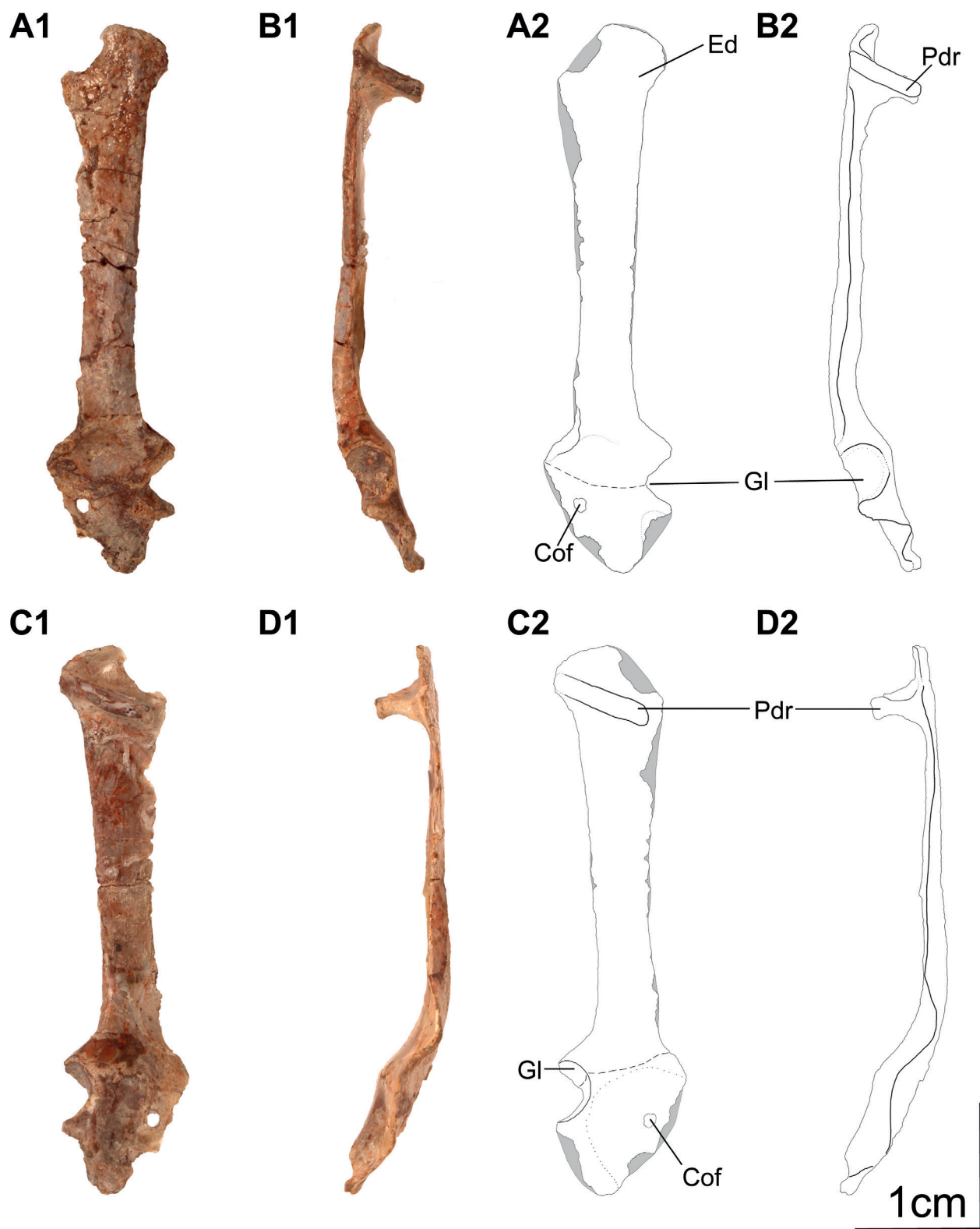


Fig. 1. Left scapulocoracoid (MCZ 101542) referred to the dinosauiromorph *Lagerpeton chanarensis*: **A1**: lateral; **B1**: posterior; **C1**: medial; **D1**: anterior. Line Drawing **A2**: lateral; **B2**: posterior; **C2**: medial; **D2**: anterior. – Scale: 1 cm. Abbreviations: **Cof**: coracoid foramen; **Gl**: glenoid; **Pdr**: possible dislocated rib; **Ed**: expanded distal end.

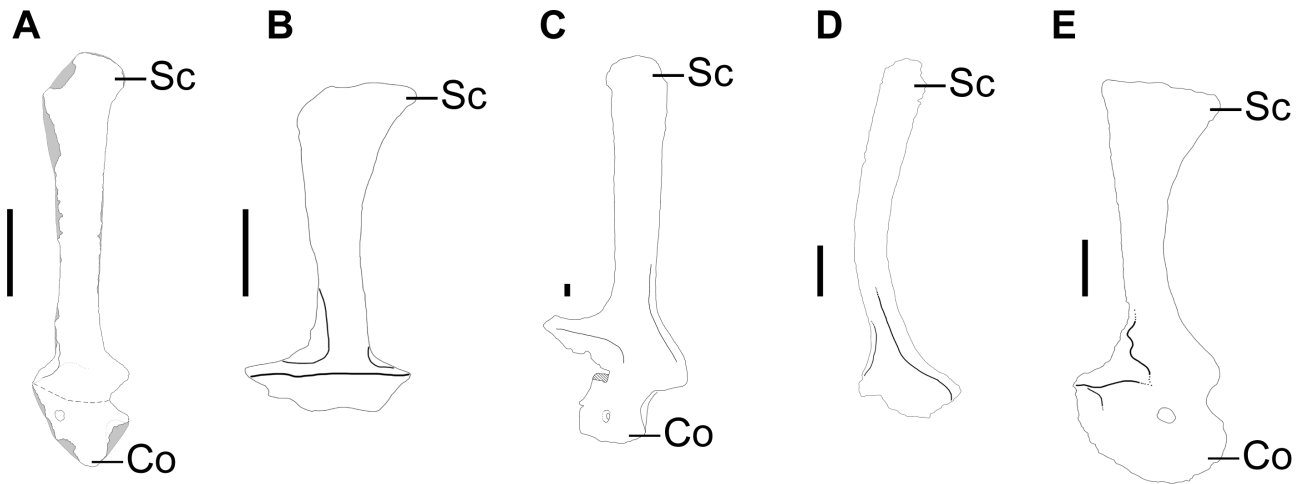


Fig. 2. Line drawings of scapulocoracoids from various Triassic archosauriforms in lateral view: **A:** Left scapulocoracoid of *Lagerpeton chanarensis* (MCZ 101542); **B:** Left scapula of *Ixalerpeton polesinensis* (ULBRA-PVT059); **C:** Right scapulocoracoid of *Herrerasaurus ischigualastensis* (PVSJ 53 reversed); **D:** Left scapula of *Dromomeron romeri* (GR 238); **E:** Right scapulocoracoid of *Tropidosuchus romeri* (PVL 4604 reversed). – Scale bars: 1 cm. Abbreviations: **Sc:** scapula; **Co:** coracoid.

to a crown archosaur or one of the closest relatives. The glenoid of MCZ 101542 is directed posteroventrally like that of other avemetatarsalians (e.g., lagerpetids, *Lagosuchus talampayensis*, silesaurids, dinosaurs). The coracoid and scapula of MCZ 101542 meet at a poorly defined suture given that they are partially coossified. The circular coracoid foramen is located close to the contact with the scapula on the anterior half of the element, which suggests that much of the anterior portion of the coracoid is missing. The glenoid contribution of the coracoid is about half of the entire glenoid and is directed posteriorly. The defining rim of the glenoid is pronounced and extends posteriorly beyond the rest of the coracoid as in *Lagosuchus talampayensis* (PVL 3871). The ventral edge of the coracoid is broken but it appears that the posteroventral portion of the coracoid does not expand into a postglenoid process as there are in dinosaurs (e.g., *Saturnalia tupiniquim*, MCP 3845-PV; *Herrerasaurus ischigualastensis*, PVSJ 53). Moreover, the posterior portion of the coracoid is rounded like that of non-archosaurian archosauriforms (e.g., *Tropidosuchus romeri*, PVL 4604; *Euparkeria capensis*, SAM 5867).

As preserved, the left humerus of MCZ 101541 has a partially eroded deltopectoral crest and the bone surface of the distal condyles are eroded (Fig. 3). The element is gracile with a total length of 48.5 mm and a midshaft width of 3.5 mm (Table 1), with a much larger proximal expansion than distal expansion. Overall, the gracile proportions of MCZ 101541 are unlike early archosaurs and their close relatives. Within Lagerpetidae, the humerus of *Ixalerpeton polesinensis* (ULBRA-PVT059) is more robust than MCZ 101541 (Fig. 4), with proportionally much larger proximal and distal expansions. The proportions of the humerus of *Lagosuchus talampayensis* (PVL 3871) matches that of MCZ 101541, with overall weakly expanded articular ends. The weakly expanded proximal end of silesaurid humeri (e.g., *Asilisaurus kongwe*, NMT RB159; *Silesaurus opolensis*, DZIK 2003) still have proportionally larger midshafts, whereas

dinosaurs (e.g., *Saturnalia tupiniquim*, MCP 3845-PV) and aphanosaurs (e.g., *Teleocrater rhadinus*, NMT RB 477) have proportionally much larger proximal and distal expansions. Similarly, the close relatives of archosaurs (e.g., *Tropidosuchus romeri*, PVL 4604; *Euparkeria capensis*, SAM 5867) also have greater proximal and distal expansions.

In lateral view, the shape of MCZ 101541 is sigmoidal with the lateral distal condyle curving from the midshaft posteriorly. The partially eroded deltopectoral crest is thin, and the peak of the crest lies well distal of the proximal surface. The position of the peak of the crest of MCZ 101541 is similar to *Ixalerpeton polesinensis* (ULBRA-PVT059), though the crest in *Ixalerpeton polesinensis* is much better defined and to the small deltopectoral crest in *Lagosuchus talampayensis* (PVL 3871). The deltopectoral crest of MCZ 101541 is much more gracile than in most other avemetatarsalians (e.g., *Teleocrater rhadinus*, NMT RB 477; *Asilisaurus kongwe*, NMT RB159; *Saturnalia tupiniquim*, MCP 3845-PV) and proximate outgroups of Archosauria (e.g., *Euparkeria capensis*, SAM-PK-5867). The head of the humerus of MCZ 101541 is well-defined and rounded proximally. The medial edge of the head appears to lack a well-defined medial tuberosity similar to that of *Ixalerpeton polesinensis* (ULBRA-PVT059), *Teleocrater rhadinus* (NMT RB 477) and *Euparkeria capensis* (EWER 1965), and this is in contrast to the well-defined feature in most dinosauriforms (*Asilisaurus kongwe*, NMT RB159; *Herrerasaurus ischigualastensis*, PVSJ 373).

The long axis of the proximal portion and long axis of the distal portion are twisted about 90° from each other in MCZ 101541; it appears this high degree of twisting is from crushing and was not present in life. Distally, the condyles only slightly expand from the shaft. The lateral and medial condyles are separated by gaps that expand proximally on both sides. The medial condyle expands anteriorly further than the lateral condyle and the medial condyle is slightly larger overall. Proportionally, the small condyles of MCZ 101541 are similar in *Ixalerpeton*

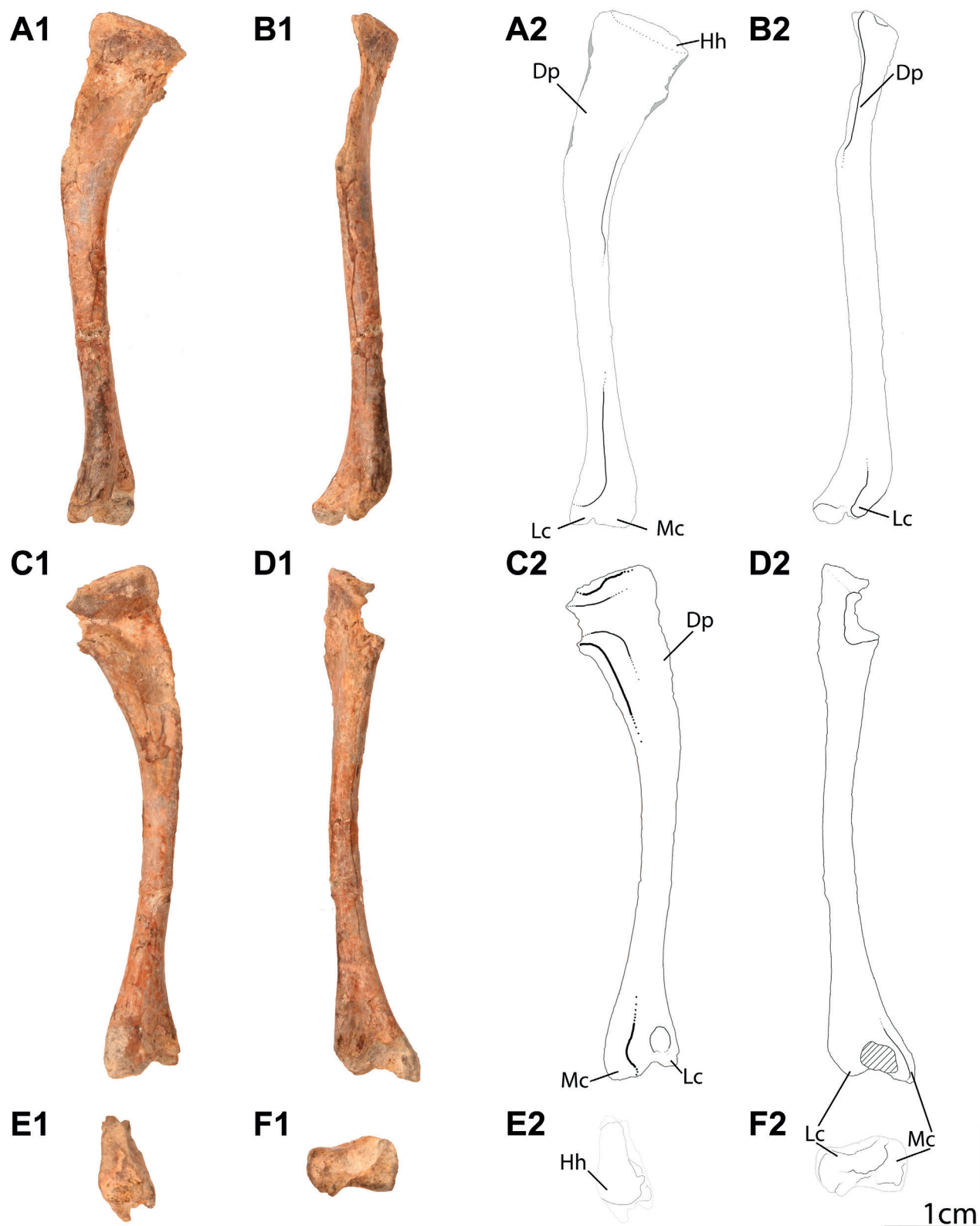


Fig. 3. Left humerus (MCZ 101542) referred to the dinosauiromorph *Lagerpeton chanarensis*: **A1**: posterior; **B1**: lateral; **C1**: anterior; **D1**: medial; **E1**: proximal; **F1**: distal. Line Drawing **A2**: posterior; **B2**: lateral; **C2**: anterior; **D2**: medial; **E2**: proximal; **F2**: distal. – Scale: 1 cm. Abbreviations: **Dp**: deltopectoral crest; **Hh**: humeral head; **Lc**: lateral condyle; **Mc**: medial condyle.

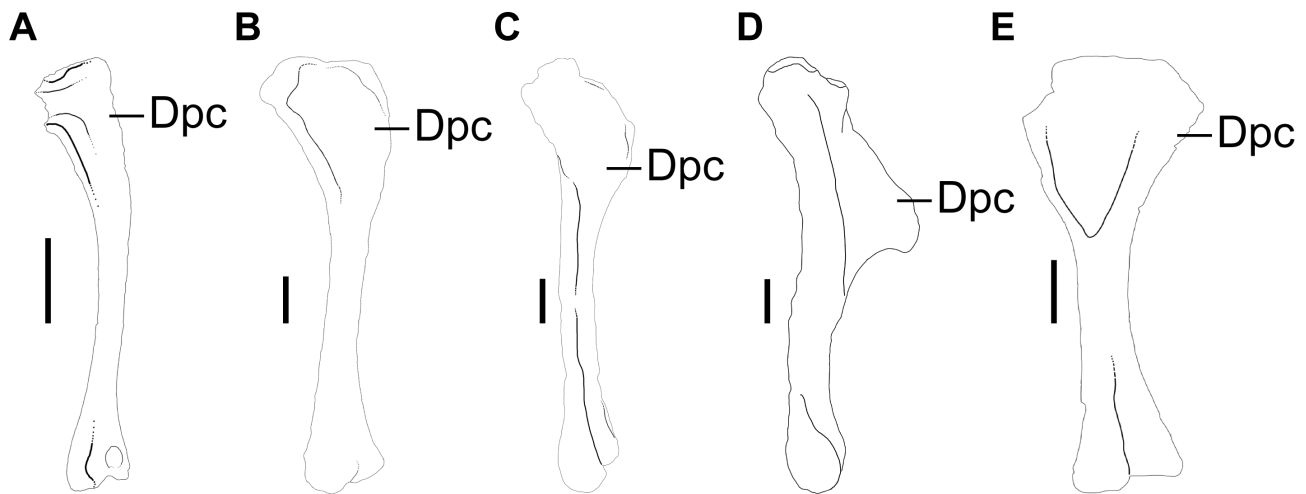


Fig. 4. Line drawings of humeri in medial view of various Triassic archosauriforms for comparison: **A:** Left humerus of *Lagerpeton chanarensis* (MCZ 101542); **B:** Left humerus of *Ixalerpeton polesinensis* (ULBRA-PVT059); **C:** Left humerus of *Asilisaurus kongwe* (NMT RB159); **D:** Right humerus of *Saturnalia tupiniquim* (MCP 3845-PV reversed); **E:** Right humerus of *Tropidosuchus romeri* (PVL 4604 reversed). – Scale bars: 1 cm. Abbreviations: **Dpc**: deltopectoral crest.

polesinensis (ULBRA-PVT059) and *Asilisaurus kongwe* (NMT RB159), but larger in dinosaurs, pseudosuchians, and non-archosaurian archosauriforms.

The left femur of MCZ 101540 is missing the proximal half, but the distal end is well preserved (Fig. 5). The preserved portion of the femur shares the most features with that of *Lagerpeton chanarensis* (MCZ 4121, PVL 4619). The part of the preserved shaft is largely curved suggesting that the entire shaft would have been sigmoidal like *Lagerpeton chanarensis* (ROMER 1971). The distal end of MCZ 101540 preserves clear medial and lateral condyles and an inflated crista tibiofibularis. In lateral view, the lateral condyle expands farther distally than the crista tibiofibularis and the medial condyle. In distal view, the medial condyle expands posteromedially and the anteromedial corner has an angle of $\sim 135^\circ$ like that of *Lagerpeton chanarensis* and *Ixalerpeton polesinensis* (ULBRA-PVT059) and unlike the more squared off anteromedial condyle of *Dromomeron* (NESBITT et al. 2009; MÜLLER et al. 2018). In contrast, the anteromedial corner of the femur of *Lagosuchus talampayensis* (PVL 3870) has a much greater angle than that of any lagerpetid. The crista tibiofibularis of MCZ 101540, located between the condyles, is larger than either condyle, and a groove demarcates the crista tibiofibularis from the lateral condyle like in other lagerpetids (NESBITT et al. 2009). The expanded crista tibiofibularis is present in all other lagerpetids (IRMIS et al. 2007; NESBITT et al. 2009; MARTÍNEZ et al. 2012; MÜLLER et al. 2018; GARCIA et al. 2019) but also expanded in the contemporary taxon *Lagosuchus talampayensis* (PVL 3871) although this expansion is less than that of lagerpetids. In MCZ 101540, the posterolateral edge of the crista tibiofibularis is rounded like *Lagerpeton chanarensis* and *Ixalerpeton polesinensis* (ULBRA-PVT059) and does not have a wide groove in distal view like that of *Dromomeron* (MÜLLER et al. 2018). The lateral condyle of MCZ 101540 projects laterally and is the anteroposterior length of the condyle is less than that of the anteroposterior length of the medial condyle, like that in *Lagerpeton chanarensis* (MCZ 4121) and *Ixalerpeton polesinen-*

sis (ULBRA-PVT059), and *Dromomeron* (NESBITT et al. 2009). This is in contrast to the lateral condyle of *Lagosuchus talampayensis* (PVL 3870) where the condyle is proportionally larger than the medial condyle.

5. Discussion

The osteology of Lagerpetidae is still largely unknown and regions such as the skull, pectoral girdle, forelimb, and neck have only recently been described (CABREIRA et al. 2016; KAMMERER et al. 2020). *Ixalerpeton polesinensis* contains skeletal material from much of these regions, but because there are few comparisons that can be made to other lagerpetids, the categorization of derived versus plesiomorphic morphology within the clade is difficult. Overall, the scapula and the humerus of *Ixalerpeton polesinensis* and *Lagerpeton chanarensis* do not share any unique character states that we can identify among avemetatarsalians and the variation between the two species seems to span the gamut of morphologies present throughout the base of Archosauria through early dinosaurs. The scapulocoracoid and humerus of *Lagerpeton chanarensis* is more gracile (high length to low midshaft width) than most other early avemetatarsalians (with the exception of *Scleromochlus taylori*).

The proportions of the scapulae and humeri of Triassic archosaurs and other archosauriforms (Table 2) shows that the proportions between the two elements in *Lagerpeton chanarensis* is high relative to closely related taxa. A longer humerus than scapula appears to be plesio-

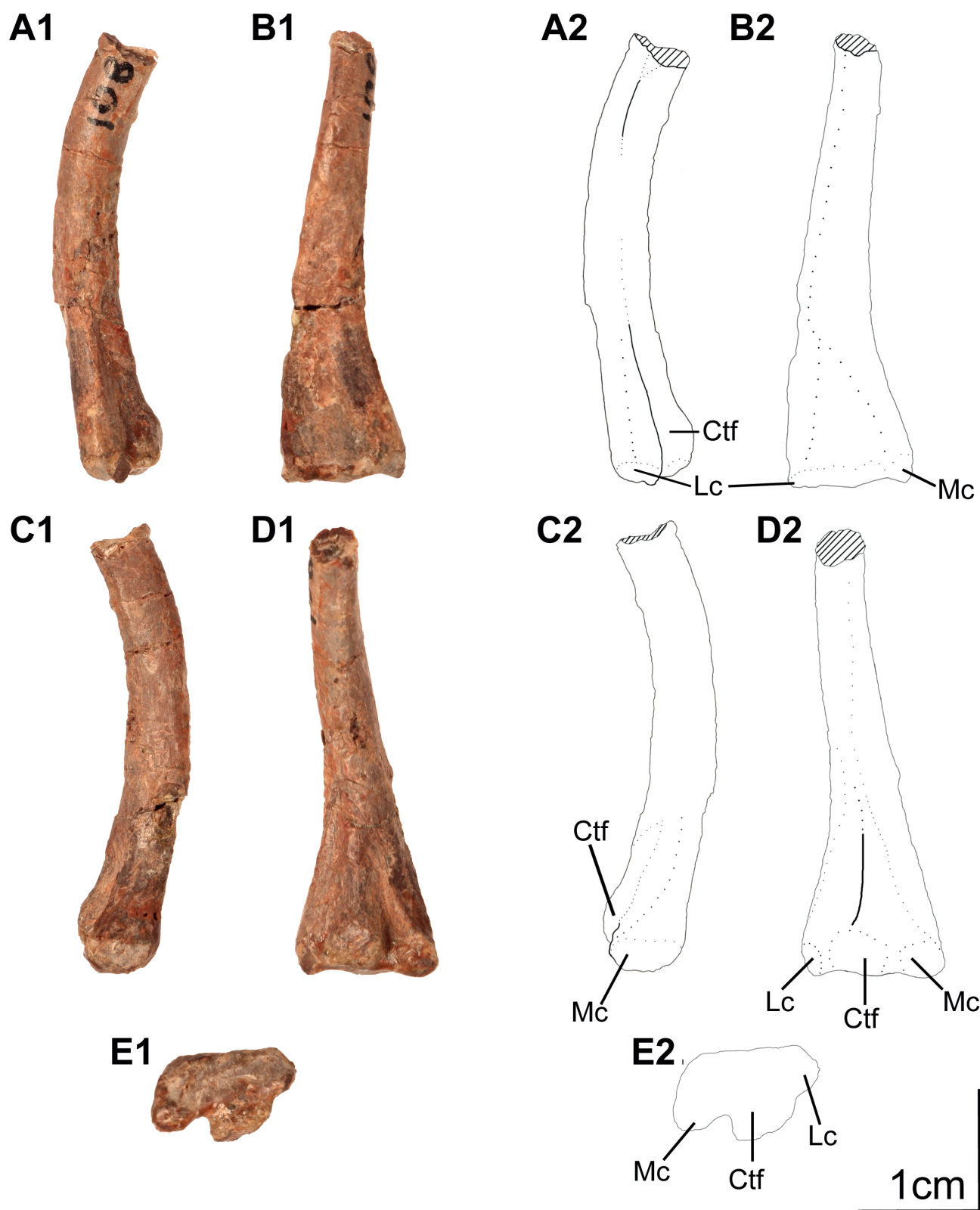


Fig. 5. Distal end of left femur (MCZ 101542) referred to the dinosauiromorph *Lagerpeton chanarensis*: **A1**: lateral; **B1**: anterior; **C1**: medial; **D1**: posterior; **E1**: distal. Line Drawing **A2**: lateral; **B2**: anterior; **C2**: medial; **D2**: posterior; **E2**: distal. – Scale: 1 cm. Abbreviations: **Ctf**: crista tibiofibularis; **Lc**: lateral condyle; **Mc**: medial condyle.

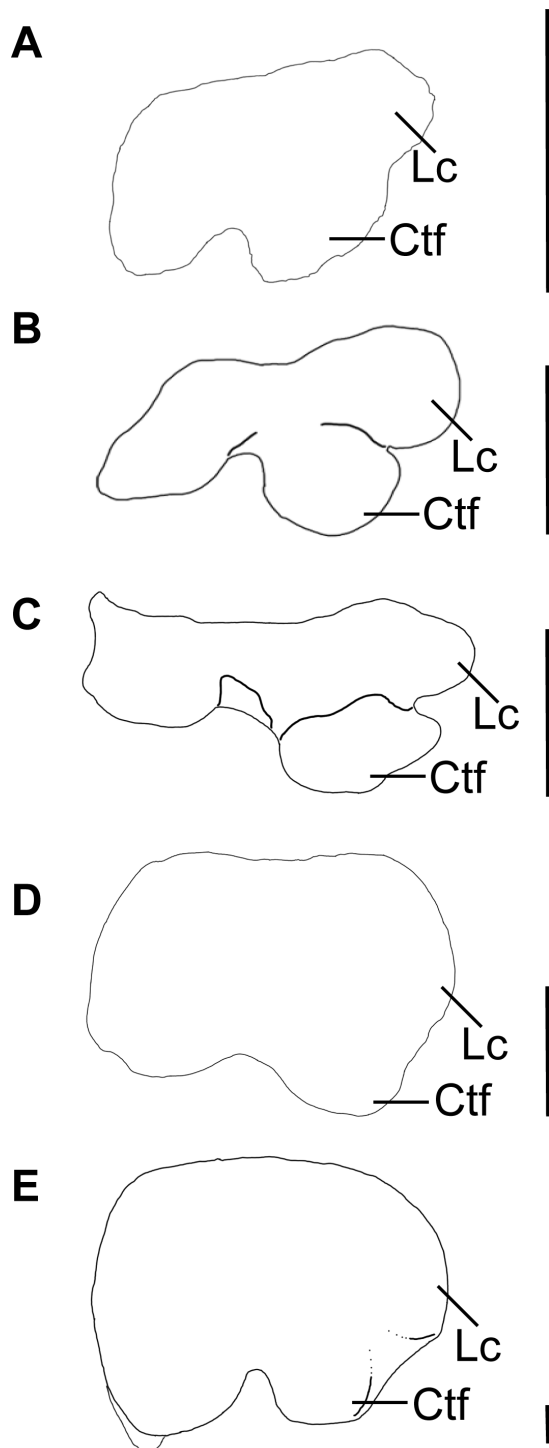


Fig. 6. Line drawings of femora in distal view of various Triassic archosauriforms for comparison: **A:** Left femur of *Lagerpeton chanarensis* (MCZ 101542); **B:** Left femur of *Ixalerpeton polesinensis* (ULBRA-PVT059); **C:** Left femur of *Dromomeron romeri* (GR 238); **D:** Left femur of *Asilisaurus kongwe* (NMT RB169); **E:** Right femur of *Herrerasaurus ischigualastensis* (PVSJ 373 reversed). – Scale bars: 1 cm. Abbreviations: Ctf: crista tibiofibularis; Lc: lateral condyle.

morphic in avemetatarsalians and there appears to be a general trend toward the scapula lengthening relative to the humerus to where the two elements are about the same length in early dinosaurs (Table 2). The ratio in *Euparkeria capensis* is nearly one-to-one for the elements, but the ratio in *Tropidosuchus romeri* is divergent from all other closely related archosauriforms and just within Archosauria. The ornithodiran *Scleromochlus taylori* has a humerus (NHMUK PV R3556) that is almost double the length of the scapula (NHMUK PV R3146A) and the proximal and distal end only marginally expand relative to the midshaft. Descriptions of *Scleromochlus taylori* have interpreted the animal to be superficially similar to members of the group Lagerpetidae, with both being speculated of being saltatorial (WOODWARD 1907; SERENO & ARCUCCI 1994b; BENTON 1999). Lagerpetidae has been shown in various phylogenetic analyses (BARON 2020; EZCURRA et al. 2020) to be closely related to Pterosauria. Different analyses place Pterosauria within Lagerpetidae, within Dinosauromorphia as sister taxon, and other combinations within Ornithodira. These results can be supported by the similar morphology found in both groups. Lagerpetids and early pterosaurs have scapulae that are shorter than their humeri and wide well-developed deltopectoral crest.

Lagerpeton chanarensis is aberrant among early archosaurs with its long scapula and gracile humerus combined with an elongated hindlimb with two functional toes. Unfortunately, there are no other lagerpetids that can be directly compared because even the most complete lagerpetid, *Ixalerpeton polesinensis*, lacks the pes. Moreover, it is not known if the aberrant morphology of *Lagerpeton chanarensis* is plesiomorphic for other lagerpetids (e.g., *Dromomeron gregorii*) or that *Lagerpeton chanarensis* was an outlier even among the slender-bodied clade. With *Lagerpeton chanarensis* currently considered to be one of the earliest diverging members of Lagerpetidae (NESBITT et al. 2009; MÜLLER et al. 2018; GARCIA et al. 2019) and the pectoral and forelimb material referred to this species, these new data may have a bearing on whether the plesiomorphic condition of Dinosauromorphia is quadrupedal or bipedal. However, the length of the scapula and humerus compared to that of the forelimb as a whole, the forelimb/hindlimb ratio and their relationship to quadrupedality or bipedality is not currently known and may be a fruitful avenue of future research. What is clear is that *Lagerpeton chanarensis* demonstrates that early avemetatarsalians had a variety of forms and that some of these forms had unique evolutionary history during the early radiation of archosaurs.

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