Journal of Vertebrate Paleontology e2170805 (6 pages)
© by the Society of Vertebrate Paleontology
DOI: 10.1080/02724634.2023.2170805

SHORT COMMUNICATION

ENIGMATIC HUMERUS FROM THE MID-PERMIAN OF SOUTH AFRICA BRIDGES THE ANATOMICAL GAP BETWEEN "PELYCOSAURS" AND THERAPSIDS

P. J. BISHOP, *[1,2] L. A. NORTON, [3] S. JIRAH, [3] M. O. DAY, [3,4] B. S. RUBIDGE, [3] and S. E. PIERCE [1]; [1]Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, U.S.A., pbishop@fas.harvard.edu, spierce@oeb.harvard.edu; [2]Geosciences Program, Queensland Museum, Brisbane, Queensland 4011, Australia; [3]Evolutionary Studies Institute, School of Geosciences, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa, luke.norton@wits.ac.za, sifelani.jirah@wits.ac.za, bruce.rubidge@wits.ac.za; [4]Natural History Museum, London SW7 5BD, United Kingdom, michael.day@nhm.ac.uk

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

Citation for this article: Bishop, P. J., L. A. Norton, S. Jirah, M. O. Day, B. S. Rubidge, and S. E. Pierce. (2023) Enigmatic humerus from the mid-Permian of South Africa bridges the anatomical gap between "pelycosaurs" and therapsids. *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2023.2170805

Submitted: October 5, 2022
Revisions received: December 13, 2022
Accepted: December 23, 2022
First published online: March 3, 2023

The origin and radiation of therapsids from non-therapsid synapsid ancestors ("pelycosaurs" for brevity) was a key event in the evolution of the mammalian lineage. Distinct from the problem of the biogeographic and temporal circumstances surrounding this event is the question of how the therapsid body plan was assembled. The incompleteness of the fossil record shrouds both questions in uncertainty (Angielczyk & Kammerer, 2018; Brocklehurst et al., 2017, 2022a; Kemp, 2006, 2009). Notably, the earliest-known therapsids are already highly distinct from their sister group, the sphenacodontid "pelycosaurs," diagnosed by dozens of cranial and postcranial synapomorphies (Kemp, 2006; Sidor & Hopson, 1998). Given the exceptionally long ghost lineage separating the oldest known, well-supported members of Sphenacodontidae and Therapsida (>30 Ma; Duhamel et al., 2021; Fröbisch et al., 2011; Sidor & Hopson, 1998), this level of morphological disparity is not unexpected. However, the dearth of more intermediate forms obfuscates attempts to understand the pattern of anatomical transformation from "pelycosaurs" to therapsids.

The pronounced morphological gap between known "pelycosaurs" and therapsids necessarily results in paleobiological interpretations of therapsid origins that tend toward a 'quantum leap' narrative. This is particularly acute for functional morphology related to the postcranial skeleton, such as breathing and locomotion, because postcranial anatomy is poorly known for the basalmost members of many therapsid lineages (e.g., Kammerer, 2011; Liu et al., 2009, 2010). One exception to this is the therapsid clade Biarmosuchia, where the basal members *Biarmosuchus* and *Hipposaurus* are represented by substantial postcranial material (Boonstra, 1965; Sigogneau & Tchudinov, 1972; Tchudinov, 1983), and have frequently served as a partial proxy for the hypothetical ancestral therapsid (e.g., Kemp, 2006, 2009; Rubidge & Sidor, 2001). These taxa already possess a suite of 'typical therapsid' postcranial traits, including a simplified shoulder and knee joint anatomy, less ossified humeral head and modified femoral muscle insertions; however, they also exhibit remarkable autapomorphies, including long, gracile limbs and a tuber-bearing calcaneum (see aforementioned references). Their utility for inferring the basal therapsid condition is therefore questionable. Postcranial material is also known for some basal anomodonts, but as with biarmosuchians, they too are already typically therapsid in structure, with simplified and less well ossified joints (Brinkman, 1981; Cisneros et al., 2015) or are ostensibly autapomorphic (Fröbisch & Reisz, 2011). Given this, the wide anatomical gap between "pelycosaurs" and therapsids persists.

This paper describes a peculiar partial humerus from the mid-Permian (Capitanian) of the Main Karoo Basin, South Africa, that helps close the void between "pelycosaurs" and therapsids. Although demonstrably of synapsid affinity, it cannot be assigned to any currently known clade, blurring the distinction between "pelycosaur" and therapsid, and raising the question of where the boundary is drawn between the two groups. Irrespective of whether it belongs to a derived "pelycosaur" or primitive therapsid, this specimen can provide important insight into the origin of the therapsid body plan.

Institutional Abbreviations—**BP**, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; **MCZ VPRA**, Vertebrate Paleontology (Reptiles and Amphibians) collection, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; **UMZC**, University Museum of Zoology, Cambridge, U.K.

MATERIAL AND METHODS

Specimen BP/1/7395 was collected in 2013 on the farm Wolwehoek, part of Hendriks Kraal 298, in the Beaufort West district (32°19.017′S, 22°6.559′E). It was found ex situ on a small exposed area of greenish-gray siltstone, and the locality's geomorphology constrains the specimen to deriving from the lower Karelskraal Member of the Abrahamskraal Formation. This places it in the upper *Diictodon–Styracocephalus* Subzone of the *Tapinocephalus* Assemblage Zone, dated to between 262–260 Ma (Day

---

*Corresponding author.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

et al., 2022). Most matrix had already weathered off the bone surface naturally prior to discovery. To document the three-dimensional geometry, the specimen was digitized by photogrammetry using RealityCapture (v1.2, Epic Games, Slovakia). Due to logistical constraints, this was undertaken prior to the remaining small amount of matrix being mechanically prepared away from the ventral surface (Movie S1). For purposes of comparison and illustration, this study also created digital models of the humerus of MCZ VPRA-3357 *Dimetrodon limbatus* (Bishop et al., 2023) and UMZC T.883, an indeterminate Tanzanian gorgonopsian (Kemp, 1982). The latter was generated using a GoSCAN 20 laser surface scanner (Creaform, U.S.A.).

RESULTS

Description of anatomical features assumes the humerus is oriented lateral to the body, parallel to the horizontal, thus presenting dorsal, ventral, anterior, and posterior aspects. As preserved, BP/1/7395 comprises the proximal end of a left humerus (Fig. 1), estimated to represent approximately one-third of the entire bone. Measured along the inferred proximodistal axis it is 75 mm long, suggesting that the length of the complete bone was between 150–200 mm. Structurally the bone is largely well preserved, with only minor fragmentation of part of the humeral head and deltopectoral crest (DPC). Although the anterodistal part of the DPC is missing, it remains intact proximally, indicating the full breadth of the bone; maximum anteroposterior width is 94 mm. Surface preservation of the bone is generally excellent. All bone surface is covered with finished (periosteal) bone, including the articular surface and margin of the DPC. At least three regions exhibit a surface texture indicative of muscle scarring.

The most distinctive feature is the articular surface of the caput. It is remarkably well ossified and has a characteristic strap shape that spirals across the terminal head, running diagonally from anterodorsal to posteroventral ends of the bone. Although convex across most of its extent, the surface is gently concave (in the anteroposterior direction) at its anteriormost limit (Fig. 1I). The articular surface is prominent relative to the surrounding bone, such that the boundary of the surface is well delimited, constraining the area that in life would have supported articular cartilage. This is particularly apparent anteroventrally, where a sharp crest is formed separating articular surface from the base of the DPC. Discrete parts of the articular surface extend out onto the dorsal and ventral aspects of the bone, forming rounded lips, the dorsal more prominently everted than the ventral. The anteroposterior length of the articular surface, 46 mm, comprises ca. 48% of the full width of the bone.

The DPC is incomplete distally, and as such its full size or shape is unknown. Proximally it has a broadly rounded profile in dorsal (or ventral) view, with no indication of a greater tuberosity or otherwise discrete angle of bone. What is preserved of the leading margin is fully ossified, and bears a cross-hatched or striate surface texture, particularly on the ventral side, indicative of fibrous attachment of the pectoral and deltoid musculature. Notably, the DPC forms a broad, obtuse angle with the main body of the bone, around 140° when viewed proximally. As a consequence, the DPC gently grades into the main body, giving the bone an overall flattened appearance.

The dorsal surface of the bone is mostly smooth, but where the DPC adjoins the main body there is a longitudinally oriented patch of striate scarring texture (Fig. 1A, B, K). This scarring runs proximally almost up to the level of the articular surface. Its position, orientation, and extent are comparable to a scar or ridge that previous authors have observed and interpreted in theriodonts as demarcating the insertion of the homolog of the mammalian teres minor muscle (Lai et al., 2018; Sigogneau-Russell, 1989). The ventral surface of the bone presents a broad and shallow 'bicipital fossa' formed between the DPC anteriorly and the well-developed lesser tuberosity posteriorly (described below).

On the posteroproximal corner of the bone is an enlarged process bearing a striate surface texture on its posterior aspect; this is interpreted as the homolog of the mammalian lesser tuberosity (LT), where the subscapularis (and subcoracoideus, if it existed) muscle inserted. In addition to its large size, occupying the entire corner of the bone, it is notable in its proximal extent, projecting proximally beyond the surrounding bone. This forms a distinct, smooth-surfaced furrow between the LT and the posterior margin of the articular surface.

DISCUSSION

Identification as a Synapsid

Three groups of medium- to large-bodied tetrapods are recorded from the *Tapinocephalus* Assemblage Zone of the Main Karoo Basin (Day & Rubidge, 2020): rhinesuchids (Temnospondyli), pareiasaurs ("parareptiles"), and therapsids (Synapsida). A temnospondyl affinity for BP/1/7395 is rejected on the basis of its strong degree of ossification, well-defined and strongly convex articular surface, blade-like DPC, and terminally positioned LT (e.g., Pawley, 2007; Pawley & Warren, 2004). A pareiasaur affinity is rejected given the well-defined and strongly convex articular surface, and the lack of a sharp longitudinal ridge on the dorsal aspect where the DPC meets the main body of the bone (Van den Brandt et al., 2021). Deduction implies the owner of BP/1/7395 to have been a synapsid. Several anatomical features support assignment to Sphenacodontoidea (sensu Fröbisch et al., 2011), yet, as outlined below, the unique combination of these features is highly distinctive and incongruent with the conditions known to typify both (eu)pelycosaurs and therapsids.

The suite of traits in BP/1/7395 clearly indicates that it represents a hitherto unknown genus of synapsid. However, in both "pelycosaurs" and therapsids, humeral anatomy is seldom sufficiently diagnostic on its own to legitimately recognize a taxon. Many previous instances of taxa erected on the basis of a humerus have subsequently been deemed nomina dubia (e.g., '*Dimetrodon kempae*' [Reisz, 1986], '*Eccasaurus priscus*' [Kammerer, 2011], '*Cynodraco major*' [Sigogneau, 1970]). With additional future discoveries, it would be expected that multiple species, and possibly genera, may be found to share the same humeral anatomy as that observed in BP/1/7395. Consequently, this paper refrains from erecting a new taxon.

Comparison to "Pelycosaurs" and Therapsids

BP/1/7395 preserves two key traits that typify large (adult) eupelycosaurs and are not observed in any known therapsid humeri (Fig. 2, Movie S1):

1. The specimen is exceptionally well ossified, including both the articular surface and the surrounding bone (margins of DPC and LT). The boundary of the articular surface is consequently clearly delineated, which is generally not the case in non-mammalian therapsids.
2. The articular surface (Fig. 2, dotted) is unmistakably 'screw-like' in morphology, spiraling obliquely across the terminal end of the bone; it is markedly convex dorsoventrally and has a gently concave recess at the anteriormost limit (Fig. 2, gray). These features are essentially identical to the complex structure observed in "pelycosaurs" (Jenkins, 1971; Romer & Price, 1940) and stem amniotes (e.g., Holmes, 1977; Romer, 1922). In contrast, the articular surface of known therapsids is much simpler in construction, being broadly saddle-shaped or ovoid in construction, and being gently convex to gently concave dorsoventrally and anteroposteriorly.

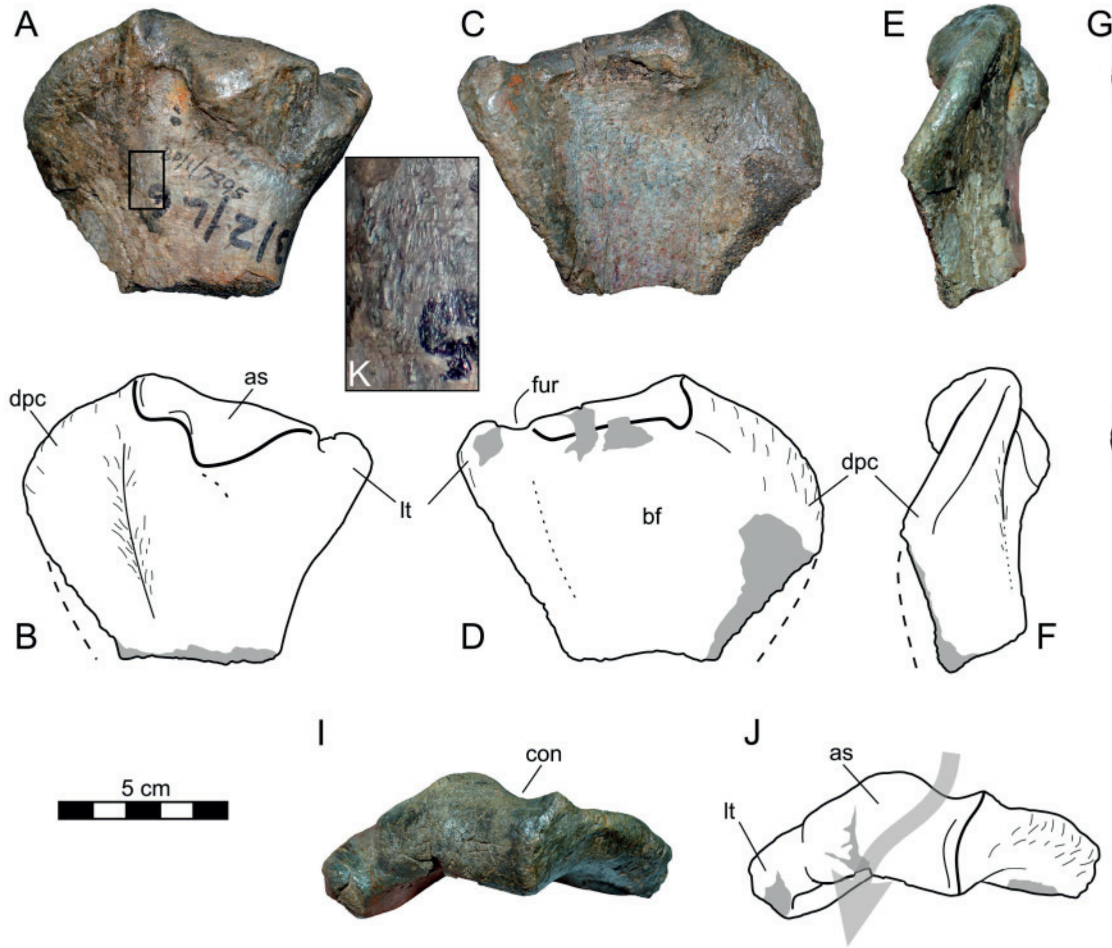

FIGURE 1. Photographs and interpretive drawings of an isolated sphenacodontoid humerus BP/1/7395, in **A**, **B**, dorsal, **C**, **D**, ventral, **E**, **F**, anterior, **G**, **H**, posterior, and **I**, **J**, proximal views. **K**, inset highlighting surface texture of a longitudinal patch of muscle scarring on the dorsal surface. Gray shading denotes broken bone or abraded surface. Arrow in **J** illustrates spiral path the articular surface takes in wrapping around the terminal end of the bone. **Abbreviations**: **as**, articular surface; **bf**, bicipital fossa; **con**, concavity; **dpc**, deltopectoral crest; **fur**, furrow; **lt**, lesser tuberosity.

There are also four features that are unknown in "pelycosaurs," and which bear greater resemblance to the condition observed in therapsids:

3. The LT (Fig. 2, vertical hatching) is proximally sited to form the posteroproximal corner of the bone. "Pelycosaurs" possess a well-defined tubercle in this region of the humerus (inferred as homologous to the LT; Romer, 1922), but it is always distal to the terminal end, since the articular surface extends to the posteroproximal corner instead. In contrast, the LT of therapsids occupies the posteroproximal corner of the humerus; sometimes not recognizable as a discrete process (due to generally lower ossification of the proximal end of the bone as a whole), its existence is nonetheless indicated by a local thickening of the bone and muscle scarring. Remarkably, the LT in BP/1/7395 projects proximally beyond the articular surface, a feature atypical of non-mammalian therapsids; indeed, it is only known in a select group of derived, fossorial dicynodonts (e.g., Cluver, 1978; Ray & Chinsamy, 2003).
4. The articular surface is anteroposteriorly constricted, forming <50% of the full width of the bone, due to its posterior part being displaced by the proximal migration of the LT. In "pelycosaurs," the articular surface occupies effectively the entire width of the terminal end of the bone.
5. The DPC (Fig. 2, diagonal hatching), although incomplete, clearly adjoins the main part of the bone at an obtuse angle, and gently grades into the main body, a trait typical of therapsids. By contrast, in "pelycosaurs" the DPC adjoins the shaft more abruptly, tending to form a distinct angle in many sphenacodontids.
6. A longitudinal patch of muscle scarring occurs on the dorsal surface, level with the DPC and extending proximally to approach the articular surface (Fig. 2, horizontal hatching). A scar with this disposition is widely observed in theriodonts and some dicynodonts and dinocephalians (e.g., Lai et al., 2018; Sigogneau-Russell, 1989). The humeri of large "pelycosaurs" also bear a longitudinal patch of scarring (inferred to be homologous), but it is consistently more distally located, at around the level of the distal base of the DPC (Romer & Price, 1940).

These observations collectively support the assignment of BP/1/7395 to Sphenacodontoidea, but also indicate that the specimen does not belong to any known "pelycosaur" or therapsid group. The mix of traits typical to both groups (as currently understood) suggests that it either represents (a) a highly derived sphenacodontian "pelycosaur," more crownward than Sphenacodontidae, or (b) a primitive therapsid, more stemward than Biarmosuchia.

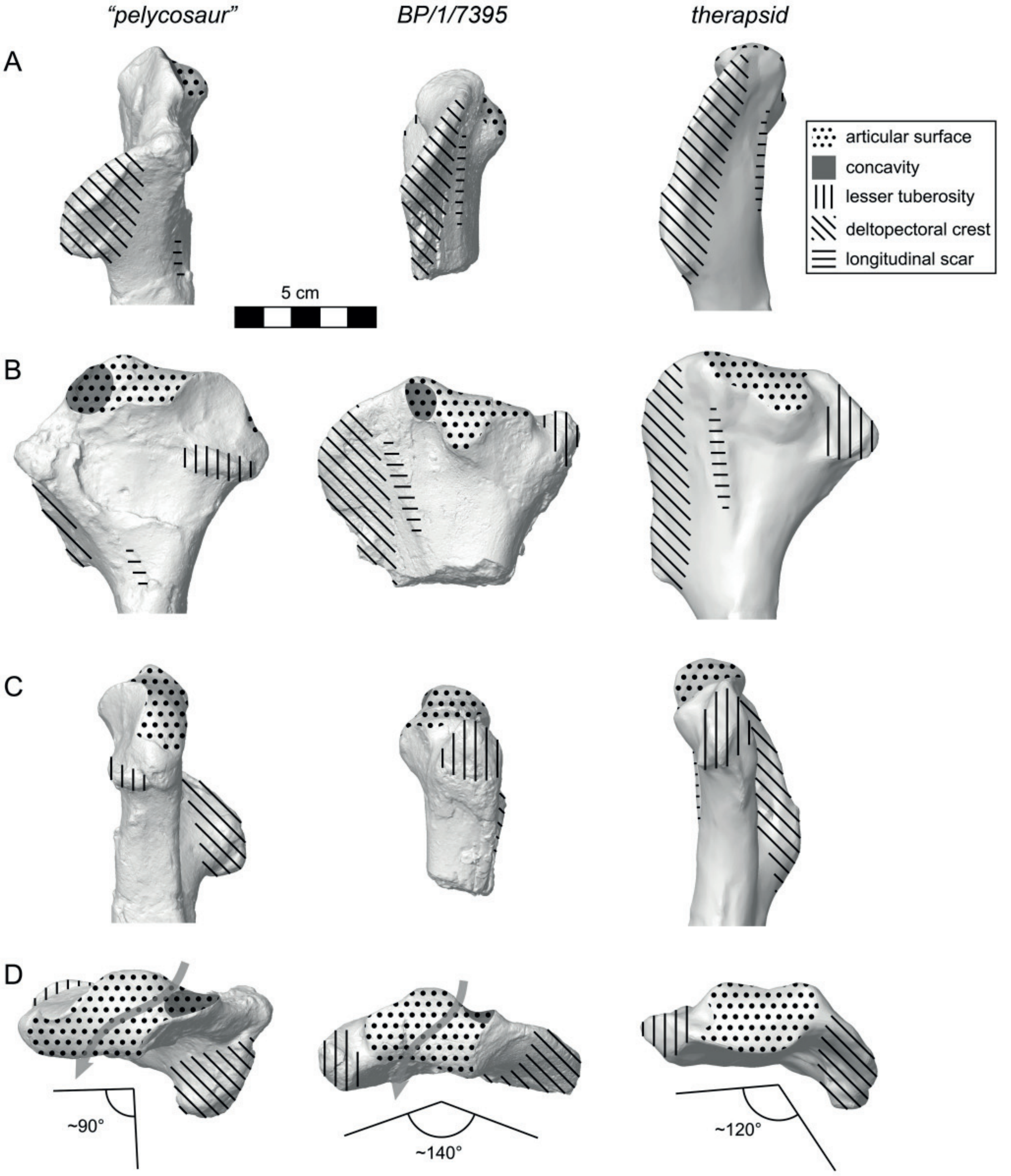

FIGURE 2. Comparison of key points of similarity and difference between BP/1/7395 and the proximal humeral morphology typically observed in "pelycosaurs" and non-cynodont therapsids. **A**, anterior view; **B**, dorsal view; **C**, posterior view; **D**, proximal view. Representing "pelycosaurs" is the sphenacodontid *Dimetrodon limbatus* (MCZ VPRA-3357), and representing therapsids is an indeterminate gorgonopsian (UMZC T.883).

Implications for Synapsid Evolution

Regardless of whether it represents an advanced "pelycosaur" or a primitive therapsid, BP/1/7395 helps bridge the pronounced morphological gap currently separating the two groups. Indeed, the intermediary nature of the specimen raises the question of where the phylogenetic line should be drawn between "pelycosaurs" and therapsids. It is therefore remarkable that the transitional anatomy observed in BP/1/7395 occurs in the uppermost stratigraphic member of the Abrahamskraal Formation, so late in the Guadalupian. Such a late occurrence could be explained by a more recent and rapid evolution of therapsids from a paraphyletic Sphenacodontidae in the early Permian (short ghost lineage; Kemp, 2006, 2009), as opposed to a gradual and protracted evolutionary history extending back into the Carboniferous (long ghost lineage; Fröbisch et al., 2011; Sidor & Hopson, 1998). Alternatively, BP/1/7395 may be a highly derived, late-surviving member of a monophyletic Sphenacodontidae which is partially convergent with therapsids. Irrespective of the length of the therapsid ghost lineage, high-precision geochronology constrains the Karelskraal Member to 260.8–260.23 Ma (Day et al., 2022), indicating that the form of primitive synapsid represented by BP/1/7395 persisted ~10 Ma after *Raranimus dashankouensis*, the oldest-known probable therapsid (Duhamel et al., 2021; Liu et al., 2009). *Raranimus* is thus far represented by a single partial snout, rendering it difficult to evaluate whether cranial characters evolved at similar or different rates to postcranial characters during the transition to therapsids.

Within the context of the forelimb, however, the combination of primitive and derived features observed in BP/1/7395 provides insight into the sequence of anatomical and functional transformation that took place between "pelycosaurs" and therapsids. The insertions of key shoulder muscles, namely the sub(coraco)scapularis and teres minor homolog, evidently shifted proximally prior to the re-organization of joint structure. This suggests that important changes to muscle leverage occurred first, whilst still relying on a fundamentally screw-like articular morphology to help guide and constrain joint motion (Bishop et al., 2022). It is predicted that, were the scapulocoracoid of this animal to be found, the glenoid would retain a decidedly screw-like structure, rather than the simple hemi-sellar morphology that typifies known therapsid groups (Brocklehurst et al., 2022b; Kemp, 1982). Intriguingly, an isolated scapulocoracoid of '*Brithopus priscus*,' from the mid-Permian of Russia, appears to possess a somewhat screw-like glenoid (Efremov, 1954:fig. 36); it was referred by Kammerer (2011) to Dinocephalia incertae sedis, but it may belong to a more primitive animal altogether. One aspect of BP/1/7395 that may not be relevant to understanding therapsid origins is the proximally projecting LT; this may instead be an autapomorphy related to digging or other forceful use of the forelimbs, since it is also observed in fossorial dicynodonts (e.g., Cluver, 1978; Ray & Chinsamy, 2003) and monotremes (Pridmore et al., 2005).

Stratigraphic Implications

The Abrahamskraal Formation, which comprises the lower *Eodicynodon* Assemblage Zone and the overlying *Tapinocephalus* Assemblage Zone, has produced a rich late Guadalupian fauna characterized by a diversity of primitive representatives of most therapsid clades (Day & Rubidge, 2020; Rubidge & Day, 2020). Many taxa compare closely with the most primitive therapsid faunas known from Russia, Brazil, and China. The Formation notably also records the youngest-known "pelycosaur," the varanopid *Heleosaurus scholtzi*. The primitive anatomy of BP/1/7395 adds another vestige of the early Permian to the Abrahamskraal fauna and provides further evidence that the taxic diversity of the *Tapinocephalus* Assemblage Zone was greater than that represented by named taxa. If BP/1/7395 represents a highly derived "pelycosaur," this would signify the presence of a considerably larger "pelycosaur" in the Main Karoo Basin than yet known. Currently, the only known "pelycosaurs" here are small varanopids of estimated snout–vent lengths <40 cm (Botha-Brink & Modesto, 2009). Yet, comparison to sphenacodontids (Romer & Price, 1940) and basal therapsids (e.g., Boonstra, 1965; Cisneros et al., 2015; Orlov, 1958) suggests that the owner of BP/1/7395 likely had a snout–vent length >1 m. BP/1/7395 demonstrates that the Abrahamskraal Formation may in time provide even further illumination of the transition between "pelycosaurs" and therapsids, and highlights the value of continued collecting efforts and of a better understanding of the postcranial anatomy of basal synapsids for biogeographic, stratigraphic, and morphological studies.

ACKNOWLEDGMENTS

B. Zipfel, M. Lowe, and C. Byrd are thanked for access to specimens; M. Van den Brandt, J. Benoit, K. Angielczyk, and M. Wright are thanked for helpful discussion; M. Van den Brandt provided specimen photographs and M. Wright provided the digital model of UMZC T.883. The constructive comments of J. Lungmus and B. Peecook on an earlier manuscript draft are gratefully acknowledged. This work was supported by the United States National Science Foundation (grants DEB-1754459 and EAR-2122115 to SEP), GENUS (DSI/NRF Centre of Excellence in Palaeosciences, UID 86073), NRF African Origins Platform, the Palaeontological Scientific Trust (PAST) and its Scatterlings projects.

DATA ACCESSIBILITY

Models of the specimens illustrated in Figure 2 are freely accessible from the respective housing museum collections.

ORCID

P. J. Bishop http://orcid.org/0000-0003-2702-0557
L. A. Norton http://orcid.org/0000-0002-9434-9267
S. Jirah http://orcid.org/0000-0002-6747-4388
M. O. Day http://orcid.org/0000-0002-7947-8204
B. S. Rubidge http://orcid.org/0000-0003-2477-1873
S. E. Pierce http://orcid.org/0000-0003-0717-1841

LITERATURE CITED

Angielczyk, K. D. & Kammerer, C. F. (2018). Non-Mammalian synapsids: the deep roots of the mammalian family tree. In F. E. Zachos & R. J. Asher (Eds.) *Mammalian Evolution, Diversity and Systematics* (pp. 117–198). De Gruyter.

Bishop, P. J., Brocklehurst, R. J., & Pierce, S. E. (2023). Intelligent sampling of high-dimensional joint mobility space for analysis of articular function. *Methods in Ecology and Evolution*, 14, 569–582.

Boonstra, L. D. (1965). The girdles and limbs of the gorgonopsia of the *Tapinocephalus* zone. *Annals of the South African Museum*, *48*, 237–249.

Botha-Brink, J., & Modesto, S. P. (2009). Anatomy and relationships of the Middle Permian varanopid *Heleosaurus scholtzi* based on a social aggregation from the Karoo Basin of South Africa. *Journal of Vertebrate Paleontology*, *29*, 389–400.

Brinkman, D. (1981). The structure and relationships of the dromasaurs (Reptilia: Therapsida). *Breviora*, *465*, 1–34.

Brocklehurst, N., Day, M. O., Rubidge, B. S., & Fröbisch, J. (2017). Olson's Extinction and the latitudinal biodiversity gradient of tetrapods in the Permian. *Proceedings of the Royal Society of London, Series B*, *284*, 20170231.

Brocklehurst, N., Ford, D. P., & Benson, R. B. J. (2022a). Early origins of divergent patterns of morphological evolution on the mammal and reptile stem-lineages. *Systematic Biology*, *71*, 1195–1209.

Brocklehurst, R. J., Fahn-Lai, P., Regnault, S., & Pierce, S. E. (2022b). Musculoskeletal modeling of sprawling and parasagittal forelimbs provides insight into synapsid postural transition. *iScience*, *25*, 103578.

Cisneros, J. C., Abdala, F., Jashashvili, T., Bueno, A. d. O., & Dentzien-Dias, P. (2015). *Tiarajudens eccentricus* and *Anomocephalus africanus*, two bizarre anomodonts (Synapsida, Therapsida) with dental occlusion from the Permian of Gondwana. *Royal Society Open Science*, *2*, 150090.

Cluver, M. A. (1978). The skeleton of the mammal-like reptile *Cistecephalus* with evidence for a fossorial model of life. *Annals of the South African Museum*, *76*, 213–246.

Day, M. O., Ramezani, J., Frazer, R. E., & Rubidge, B. S. (2022). U-Pb zircon age constraints on the vertebrate assemblages and palaeomagnetic record of the Guadalupian Abrahamskraal Formation, Karoo Basin, South Africa. *Journal of African Earth Sciences*, *186*, 104435.

Day, M. O., & Rubidge, B. S. (2020). Biostratigraphy of the *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology*, *123*, 149–164.

Duhamel, A., Benoit, J., Rubidge, B. S., & Liu, B. (2021). A re-assessment of the oldest therapsid *Raranimus* confirms its status as a basal member of the clade and fills Olson's gap. *Naturwissenschaften*, *108*, 26.

Efremov, I. A. (1954). The terrestrial vertebrate fauna from the Permian copper sandstones of the western Fore-Urals. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, *54*, 1–416.

Fröbisch, J., & Reisz, R. R. (2011). The postcranial anatomy of *Suminia getmanovi* (Synapsida: Anomodontia), the earliest known arboreal tetrapod. *Zoological Journal of the Linnean Society*, *162*, 661–698.

Fröbisch, J., Schoch, R. R., Müller, J., Schindler, T., & Scheweiss, D. (2011). A new basal sphenacodintid synapsid from the Late Carboniferous of the Saar-Nahe Basin, Germany. *Acta Palaeontologica Polonica*, *56*, 113-120.

Holmes, R. (1977). The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology*, *152*, 101–140.

Jenkins, F. A., Jr. (1971). The postcranial skeleton of African cynodonts. *Bulletin of the Peabody Museum of Natural History*, *36*, 1–216.

Kammerer, C. F. (2011). Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology*, *9*, 261–304.

Kemp, T. S. (1982). *Mammal-like Reptiles and the Origin of Mammals.* Academic Press.

Kemp, T. S. (2006). The origin and early radiation of the therapsid mammal-like reptiles: a palaeobiological hypothesis. *Journal of Evolutionary Biology*, *19*, 1231–1247.

Kemp, T. S. (2009). Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy. *Palaeontologia africana*, *44*, 1–12.

Lai, P. H., Biewener, A. A., & Pierce, S. E. (2018). Three-dimensional mobility and muscle attachments in the pectoral limb of the Triassic cynodont *Massetognathus pascuali* (Romer, 1967). *Journal of Anatomy*, *232*, 383–406.

Liu, J., Rubidge, B. S., & Li, J. (2009). New basal synapsid supports Laurasian origin for therapsids. *Acta Palaeontologica Polonica*, *54*, 393–400.

Liu, J., Rubidge, B. S., & Li, J. (2010). A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont. *Proceedings of the Royal Society of London, Series B*, *277*, 285–292.

Orlov, J. A. (1958). Predatory deinocephalians from the Isheevo Fauna (titanosuchians). *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, *72*, 1–114.

Pawley, K. (2007). The postcranial skeleton of *Trimerorhachis insignis* Cope, 1878 (Temnospondyli): a plesiomorphic temnospondyl from the Lower Permian of North America. *Journal of Paleontology*, *81*, 873–894.

Pawley, K., & Warren, A. A. (2004). Immaturity *vs* paedomorphism: a rhinesuchid stereospondyl postcranium from the Upper Permian of South Africa. *Palaeontologia africana*, *40*, 1–10.

Pridmore, P. A., Rich, T. H., Vickers-Rich, P., & Gambaryan, P. P. (2005). A Tachyglossid-Like Humerus from the Early Cretaceous of South-Eastern Australia. *Journal of Mammalian Evolution*, *12*, 359–378.

Ray, S., & Chinsamy, A. (2003). Functional aspects of the postcranial anatomy of the Permian Dicynodont *Diictodon* and their ecological implications. *Palaeontology*, *46*, 151–183.

Reisz, R. R. (1986). Pelycosauria. *Handbuch der Paläoherpetologie*, *17A*, 1-100.

Romer, A. S. (1922). The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History*, *46*, 517–606.

Romer, A. S., & Price, L. I. (1940). Review of the Pelycosauria. *Special Papers of the Geological Society of America*, *28*, 1–538.

Rubidge, B. S., & Day, M. O. (2020). Biostratigraphy of the *Eodicynodon* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology*, *123*, 141–148.

Rubidge, B. S., & Sidor, C. A. (2001). Evolutionary Patterns Among Permo-Triassic Therapsids. *Annual Review of Ecology and Systematics*, *32*, 449–480.

Sidor, C. A., & Hopson, J. A. (1998). Ghost lineages and "mammalness": assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology*, *24*, 254–273.

Sigogneau-Russell, D. (1989). Theriodontia I. *Handbuch der Paläoherpetologie*, *17B*, 1–123.

Sigogneau, D. (1970). *Révision systématique des Gorgonopsiens sud-africains.* Centre National de la Recherche Scientifique.

Sigogneau, D., & Tchudinov, P. K. (1972). Reflections on some Russian eotheriodonts (Reptilia, Synapsida, Therapsida). *Palaeovertebrata*, *5*, 79–109.

Tchudinov, P. K. (1983). Early therapsids. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, *202*, 1v229.

Van den Brandt, M. J., Benoit, J., Abdala, F., & Rubidge, B. S. (2021). Postcranial morphology of the South African middle Permian pareiasaurs from the Karoo Basin of South Africa. *Palaeontologia africana*, *55*, 1–91.

Handling Editor: Pia A. Viglietti.