Most Triassic terrestrial diapsids belong to two clades, Lepidosauromorpha or (the more diverse) Archosauromorpha. Nevertheless, the phylogenetic relationships of some Triassic diapsids have remained uncertain for decades because of the lack of preservation of phylogenetically relevant anatomical regions or because of unusual combinations of features. One of these enigmatic forms is the small-sized *Sphodrosaurus pennsylvanicus* from the Upper Triassic Hammer Creek Formation of the Newark Supergroup in Pennsylvania (USA). It was first identified as a procolophonid parareptile, later as a probable rhynchosaur archosauromorph, and more recently as an indeterminate neodiapsid. Here we revise the anatomy of *Sphodrosaurus pennsylvanicus* in order to include it for the first time in a quantitative phylogenetic analysis, which is focused on Permo–Triassic neodiapsids. *Sphodrosaurus pennsylvanicus* is recovered in this analysis as a doswelliid protochampsian within Archosauromorpha. As a result, this taxon is added to the list of doswelliids known from the Carnian–Norian of the eastern and south-western USA. Previous authors recognized that the most unusual feature of *Sphodrosaurus pennsylvanicus* is its proportionally very large skull. Phylogenetic generalized least squares regressions confirmed that *Sphodrosaurus pennsylvanicus* has a larger skull than the vast majority of Permo–Triassic diapsids. Optimization in the phylogeny of the skull width to presacral length ratio shows the most likely scenario is that the extremely broad skull of *Sphodrosaurus pennsylvanicus* is autapomorphic, but it is not unique among archosauromorphs, being paralleled by hyperodapedontine rhynchosaur and the protochampsian *Proterochampsia barrionuevoi*. Exploration of a morphospace of linear measurements shows that *Sphodrosaurus pennsylvanicus* shares strong similarities with the probably semi-aquatic *Proterochampsia barrionuevoi*, suggesting that the former species may have had a similar mode of life. A linear discriminant analysis of ungual functional categories found that the only preserved ungual of *Sphodrosaurus pennsylvanicus* was suitable for digging or some other way of substrate processing.

**Keywords**: Diapsida; Proterochampsia; Doswelliidae; Newark Supergroup; phylogeny; functional morphology

---

**Introduction**

Most Late Triassic continental tetrapod assemblages are numerically dominated by diapsid reptiles. The vast majority of species that represent this diapsid diversity belong to different lepidosauromorph and archosauromorph groups (e.g. rhynchocephalians, tanystropheids, rhynchosaur, allakotosaur, dinosaurs, phytosaurs, aetosaurs, ‘rauisuchians’) (Brusatte et al. 2010; Evans & Jones 2010; Langer et al. 2010; Nesbitt et al. 2013, 2022; Ezcurra & Butler 2018; Ezcurra et al. 2021a; Spiekmann et al. 2021). However, some taxa could not be clearly referred to any of these groups, resulting in uncertain phylogenetic relationships, or their phylogenetic positions have been controversial in recent decades (e.g.* Pachystropheus rhaeticus*: Huene 1935; *Elachistosuchus huenei*: Janensch 1949; *Sphodrosaurus pennsylvanicus*: Colbert 1960; *Colobops noviportensis*: Pritchard et al. 2018). These species are generally represented by specimens with limited anatomical information, which is the main reason for their uncertain phylogenetic position. Some of these Late Triassic enigmatic diapsids have been re-examined recently using modern technologies (e.g. computed tomography scanning) and/or updated comparisons with more recently described specimens (e.g. Sobral et al. 2015; Pritchard et al. 2018; Pritchard & Sues 2019; Scheyer et al. 2020). An improved understanding of the affinities of these species is important to account for the phylogenetic diversity of diapsids during their evolutionary radiation in the Late Triassic and to determine how the Triassic–Jurassic mass extinction impacted different clades.
Here we revise the phylogenetic relationships of one of these enigmatic Late Triassic diapsids, *Sphodrosaurus pennsylvanicus* from the Upper Triassic (Norian) Hammer Creek Formation in Lancaster County, Pennsylvania, USA (Fig. 1). The holotype of *Sphodrosaurus pennsylvanicus* consists of a partial skeleton originally preserved mostly as a natural mould in a block of hornfelsed mudstone (Fig. 2). This specimen was first reported by Price (1956) who, based on observations of colleagues, referred it to the procolophonoid parareptile *Hypsognathus fenneri*, but provided no anatomical justification for this identification. Subsequently, Colbert (1960) described and discussed the anatomy of the specimen in detail and – although he initially had identified it as a specimen of *Hypsognathus* – found enough differences with other procolophonids to propose a new genus and species, *Sphodrosaurus pennsylvanicus*. Colbert (1960) based the procolophonid affinities of *Sphodrosaurus pennsylvanicus* mainly on the presence of a large skull and a ‘frill’ in the posterior region of the cranium, composed of what he considered quadratejugal, squamosal and tabular, which resembled that of the most deeply nested procolophonids. Nevertheless, he noted that the great length and robustness of the hindlimb and the long, sharp pedal unguals clearly differ from the condition present in other known procolophonids. The placement of *Sphodrosaurus pennsylvanicus* as a procolophonid was followed by Kuhn (1969) and Ivakhnenko (1979) in their systematic overviews of the group.

Baird (1986) was the first to express doubts regarding the procolophonid affinities of *Sphodrosaurus pennsylvanicus* and instead considered this species a probable rhynchosaur. After this radical proposal, Paul Olsen (Lamont-Doherty Earth Observatory, Columbia University) removed the remaining fragments of bone in some regions of the natural mould. Subsequently, Peter Kroehler (National Museum of Natural History, Washington, DC) generated high-quality latex casts that presented exquisite and previously unavailable details of the anatomy of *Sphodrosaurus pennsylvanicus*. Sues et al. (1993) redescribed the skeletal structure and revised its phylogenetic affinities based on the information provided by these new casts. They concluded that the purported procolophonid-like ‘frill’ of the skull actually comprises the posterior regions of the hemimandibles and, thus, there was no evidence to support procolophonid affinities. They also could not find

---

**Figure 1.** Some of the rift basins of the Triassic–Jurassic Newark Supergroup (highlighted in black) in the eastern United States, with inset showing the site for the holotype of *Sphodrosaurus pennsylvanicus* (marked by a black star) in strata of the Newark Supergroup (highlighted in grey) in Lancaster County, Pennsylvania. **Abbreviations:** DE, Delaware; NJ, New Jersey.
Evidence in support of either rhynchosaurian or archosauriform affinities. However, Sues et al. (1993) considered that the species could be referable to Neodiapsida based on the presence of an atlanto-occipital joint apparently positioned well anterior to the craniodentibular articulation, a slender and sigmoid femoral shaft, and possibly a forelimb proportionally shorter than the hindlimb and ventral keels on the cervical and anterior dorsal centra. As a result, Sues et al. (1993) interpreted *Sphodrosaurus pennsylvanicus* as Neodiapsida incertae sedis, but clearly distinguishable from other known diapsids because of a unique combination of character states, namely the presence of a proportionally very large head, atlanto-occipital joint anterior to craniodentibular joint, external surface of mandibular bones distinctly ornamented, and cervical and anterior dorsal centra with strongly developed ventral keels. The phylogenetic relationships of *Sphodrosaurus pennsylvanicus* among neodiapsids have remained enigmatic ever since. Here we revise the phylogenetic relationships of *Sphodrosaurus pennsylvanicus* based on new observations of its anatomy, comparisons with the large amount of new data about Triassic diapsids that have become available in the last three decades, and its inclusion for the first time in a quantitative phylogenetic data set focused on Permian–Triassic neodiapsids.

**Material and methods**

**Phylogenetic analysis**
To test the phylogenetic relationships of *Sphodrosaurus pennsylvanicus*, we scored this species in the phylogenetic data matrix of the CoArTreeP (the Complete...
Archosauromorph Tree Project; see Ezcurra [2016] for the first iteration of this project). This is the most extensive phylogenetic dataset currently available for Permain and Triassic archosauromorphs, and it has been shown to be useful for determining the relationships of taxa either within Archosauromorpha and/or their inclusion among early Lepidosauromorpha or non-saurian neodiapsids (e.g. Scheyer et al. 2020; Ezcurra et al. 2022).

The character and taxonomic sample of this matrix has been expanded multiple times in recent years (e.g. Ezcurra et al. 2017, 2020a, b, 2021a, b, 2022; Nesbitt et al. 2017; Sengupta et al. 2017; Ezcurra & Butler 2018; Wynd et al. 2019; Scheyer et al. 2020; Sues et al. 2021). Some of these expansions were conducted independently, and there is no currently available data matrix that integrates all the information in a single data set. Thus, we merged all of these recent datasets in this paper. We deactivated the following 40 terminals before the tree searches because they were scored only for the purpose of morphological disparity analyses, are not diagnostic at the species level, or are combinations of operational taxonomic units: ISIR 1132, Protanystropheus antiquus, Trachelosaurus fischeri, Tanystropheus haasi, UFRGSPV- 492-T, Malerisaurus all NA, Arctosaurus osborni, CRILAR-Pv 461, CRILAR-Pv 462, CRILAR-Pv 497, Chañaes rhynchosaur, PVSJ 2728, Eorosaurus olsoni, Archosaurus complete, FC-DPV 2641, UFSM 11444, UFSM 11394, Vohuuenia fredericki, C. rossicus combined, C. magnus combined, Chasmatosuchus vjushkovi, Koilamasuchus gonzaleziazi, Kalisuchus rewanensis holotype, NMQR 3570, CRILAR-Pv 499, Shansisuchus kayeheensis, Uralsaurus combined, Osmolskina czakoviensis, Osmolskina complete, Triopticus primus, Otter Sandstone archosaur, Dagasuchus santacruzensis, Ctenosauromus koeneni, Hypselorhachis mirabilis, Waldhaus poposauroid, Vytshegosuchus zeshartensis, Bystrowisuchus flerovi, Bromsgroveia walkeri, Lutungutali siwensis and Nyasasaurus parringtoni. Characters 9 and 119 were also removed (following Ezcurra et al. 2017; Sengupta et al. 2019a).

We also modified 60 characters, added 40 characters, and added seven terminals that were not present in previous versions of this data matrix: the Palaeozoic diapsid Orovenator mayorum, the lepidosauromorphs Marmoretta oxoniensis and Huehuecuetzpalli mixtecus, the pseudosuchian archosaur Revuellosaurus callenderi, and the enigmatic diapsids Elachistosuchus huenei, Feralisaurus corami and Sphodrosaurus pennsylvanicus. The new data set is composed of 190 active terminals and 887 active characters. The following characters were considered additive because they represent nested sets of homologies: 1, 2, 7, 10, 17, 19–21, 28, 29, 34, 36, 40, 42, 46, 50, 54, 66, 71, 74–76, 100, 122, 127, 146, 153, 156, 157, 171, 176, 177, 187, 202, 221, 227, 263, 266, 278, 279, 283, 324, 327, 331, 337, 342, 345, 351, 352, 354, 361, 365, 368, 370, 377, 379, 386, 387, 398, 410, 414, 424, 425, 430, 435, 446, 448, 454, 455, 458, 460, 463, 464, 470, 472, 478, 482, 483, 485, 489, 490, 502, 504, 510, 516, 520, 521, 529, 537, 546, 552, 556, 557, 567, 569, 571, 574, 581, 582, 588, 636, 648, 652, 662, 701, 731, 735, 737, 738, 743, 749, 766, 784, 803, 810, 816, 850, 851, 872, 875, 885 and 888. Modifications to the data matrix and the revised matrix are available in Supplemental material 1 and the data matrices in Supplemental material 2.

The matrix of discrete morphological characters was analysed under equally weighted (eqWs) and implied weighted (IW; k = 3, 7, 10) maximum parsimony using TNT v. 1.5 (Goloboff et al. 2008; Goloboff & Catalano 2016). The search strategy initially used a combination of the tree-search algorithms sectorial searches, drifting (five iterations), and tree fusing (one round) for each replication, until 100 hits (using four initially unconstrained replications as starting point) of the same minimum tree length were achieved (not collapsing trees during search, multiplying trees by fusing after hitting best score, and saving no more than one tree per replication) – all these parameters are default settings. The shortest trees obtained and retained in memory were then subjected to a final round of tree bisection and re-connection branch swapping. Zero-length branches in any of the recovered most parsimonious trees (MPTs) were collapsed into polytomies. Branch support was quantified using decay index (Bremer support) values and a bootstrap resampling analysis, with 1000 pseudo-replicates and reporting both absolute and GC (Bremer support) values and a bootstrap resampling analysis, – i.e. the difference between the frequencies of recovery in pseudo-replicates of the clade in question and the most frequently recovered contradictory clade) frequencies (Goloboff et al. 2003). Finally, analyses forcing topological constraints were conducted to find the minimum number of steps necessary to force alternative sub-optimal positions for Sphodrosaurus pennsylvanicus. The monophyletic groups and specific positions in which Sphodrosaurus pennsylvanicus was forced are detailed in the Discussion section.

Skull size analyses

The proportionally large skull of the holotype of Sphodrosaurus pennsylvanicus is one of the most unusual features of this species. However, previous discussions about the relative size of the skull were based...
on qualitative comparisons and lacked an explicit phylogenetic context (Colbert 1960; Sues et al. 1993). Unfortunately, the skull of *Sphodrosaurus pennsylvanicus* is represented only by the posterior region of the palate and both hemimandibles. Thus, it is not straightforward to determine how large the skull is in comparison to those of other Triassic diapsids and how allometry may have influenced its proportional size in comparison to the postcranium.

The preserved posterior region of the skull of *Sphodrosaurus pennsylvanicus* only allows the measurement of widths to use as proxies for skull size. The maximum cranial width is more commonly recorded for Triassic diapsids than the maximum mandible width because the hemimandibles are commonly disarticulated and displaced from each other. We lack direct information regarding the cranial width of *Sphodrosaurus pennsylvanicus* because the bones of the lower temporal region are not preserved. However, the right hemimandible seems to be in natural position with respect to the palate, because the external edge of the lateral ramus of the pterygoid is overlapped by the hemimandible and the quadrate ramus of the pterygoid is directed towards the glenoid region of the hemimandible. In particular, the latter indicates that the hemimandible is not displaced posteriorly or skewed anteromedially to posterolaterally with respect to the palate, because the quadrate ramus of the pterygoid and the pterygoid ramus of the quadrate would form a relatively straight line between the main body of the pterygoid and the mandibular glenoid fossa. Since the maximum width of the mandible is slightly narrower than the cranium in articulated diapsid skulls, we calculated the maximum skull width of *Sphodrosaurus pennsylvanicus* as twice the maximum width between the lateral-most margin of this hemimandible and the mid-width of the palate. This should be considered an estimate of maximum skull width, possibly slightly lower than the actual value, because slight displacement of the hemimandible with respect to the palate cannot be completely ruled out. We choose the
total length of the presacral vertebral series as a proxy for postcranial size because it is completely preserved in *Sphodrosaurus pennsylvanicus*. Previous studies of archosauromorph body size have used the femoral length as a proxy (e.g., Sookias et al. 2012; Turner & Nesbitt 2013; Pradelli et al. 2022), but the proximal end of the femur of *Sphodrosaurus pennsylvanicus* is damaged (Fig. 3). Nevertheless, we also conducted the following analyses using femoral length as the independent variable to test whether the results were congruent with those recovered using the presacral vertebral length.

We used phylogenetic generalized least squares (pGLS) regressions between these variables to explore whether *Sphodrosaurus pennsylvanicus* is an outlier, accounting for the phylogenetic non-independence of species, in a broad taxonomic sample of Permo-Triassic diapsid taxa scored in our phylogenetic analysis. The regressions were conducted for the complete sample of MPTs found under eqWs and IWs (k = 10) (5600 and 75 MPTs, respectively; see Results). The regressions were conducted with the function ‘gls’ of the R package nlme (Pinheiro et al. 2021) with an expected covariance under a Brownian model and a variance function with fixed variances from the diagonal of the variance-covariance matrix of the time-calibrated phylogenetic tree. Each of these trees was time-calibrated using the minimum branch length (mbl) method with three different minimum branch lengths: 0.1, 0.5 and 1 million years – higher mbl values resulted in a calibration of the origin of Archosauromorpha older than that estimated by previous studies (i.e. >260 Mya; Ezcurra et al. 2014). The time calibrations were conducted with the function ‘timePaleoPhy’ of the R package paleoPhy (Bapst 2012). Species without either of the two measurements used for these regressions were pruned only after the time calibration of the trees to retain the temporal information provided by all taxa. To reduce computational times, the topology and branch lengths of the pruned trees were compared to each other with the function ‘unique.multiPhylo’ of the R package ape (Paradis & Schliep 2019), and repeated trees were deleted. The pGLS regressions were conducted on these trees. We selected manually two of the MPTs recovered under eqWs and one of the trees found under IWs (k = 10), because they include the topological differences in the interrelationships among the species more closely related to *Sphodrosaurus pennsylvanicus*, each calibrated with mbl values of 1 My and 0.1 My, to graph the pGLS residuals more clearly.

The ratio between skull width and presacral vertebral length was optimized on one of the two topologies found under equal weights and the topology recovered under implied weights (to reduce computational times), each calibrated with mbl values of 1 My and 0.1 My, using the ‘contMap’ function of the R package phytools, which uses maximum likelihood as the optimality criterion (Revell 2012). Finally, the phylogenetic signal, local indicator of phylogenetic association (local Moran’s I), and phylogenetic correlogram of the skull width-presacral length ratio were calculated for the two above-mentioned phylogenies calibrated with mbl of 1 My and 0.1 My using the ‘phyloSignal’, ‘lipaMoran’ and ‘phyloCorrelogram’ functions, respectively, of the R package phylosignal (Keck et al. 2016). All these analyses and graphics were conducted in R 4.1.1 (R Development Core Team 2021), and the files and codes are available in Supplemental material 3.

**Morphospace exploration**

We used the femoral and tibial length in addition to the skull width and presacral length to build a three-dimensional morphospace of linear measurements and expand the quantitative comparisons with other taxa beyond the skull width-to-postcranium relationship. The partially preserved skeleton of *Sphodrosaurus pennsylvanicus* limits the number of informative measurements that could be taken from the specimen. Thus, we decided to use the ratio of femoral length to tibial length and the ratio of femoral + tibial length to presacral length to generate a biplot showing the relationship between the posterior stylopodium and zeugopodium and the postcranial presacral length. A heatmap depicting the ratio of skull width to presacral length was superimposed on the biplot to generate a three-dimensional morphospace to show the interrelationships among the skull, presacral vertebral, and hindlimb variables. The heatmap was built with the function ‘filled.contour’ of the R package akima (Akima & Gebhardt 2021), and the graphic was built in R 4.1.1 (R Core Team 2021) after the log10 transformation of the variables. Files and codes are available in Supplemental material 4.

**Pedal ungual functional morphology analysis**

The possible function of the only available pedal ungual of *Sphodrosaurus pennsylvanicus* was studied quantitatively using the database and analyses described by Thomson & Motani (2021). This analysis was originally based on a data set of keratinous claw sheaths of extant amniote specimens, but there is a strong correlation between the shape of the bony ungual and the keratinous sheath. Mann et al. (2021) recently used this analysis to assess the functional morphology of the ungual of a late Carboniferous eureptile, and this procedure is followed here (see Mann et al. [2021] for a discussion of the caveats associated with the use of bony unguals.
Due to preservational limitations (see Mann et al. 2021), we used nine linear measurements and one angular variable to sample the shape of the unguals. These variables were quantified for 76 extant amniote species and *Sphodrosaurus pennsylvanicus* following the methods described by Thomson & Motani (2021). The two outlier taxa (*Gopherus* and *Cyclopes*) were removed from the data set prior to the analyses to avoid biasing the results (Mann et al. 2021). The data set was log_{10} transformed and subjected to a pGLS regression, with the dorsal curve length of the ungual as the independent variable, using the ‘procD.pgl’ function of R package geomorph v. 3.3.1 (Adams et al. 2021). The phylogeny used for the pGLS was taken from Thomson & Motani (2021) with the addition of *Sphodrosaurus pennsylvanicus* after the results of our phylogenetic analyses. Subsequently, the pGLS residuals were subjected to a linear discriminant analysis (LDA) using the ‘lda’ function of the R package MASS v. 7.3.51.6 (Venables & Ripley 2002) to determine the major axes of between-group variation in the extant taxa and whether the ungual of *Sphodrosaurus pennsylvanicus* could be assigned to any of the eight functional groups proposed by Thomson & Motani (2021): amplexorial (grasping), cursorial (running or hopping), generalist (multipurpose), gryporial (hook-and-pull digging), scalporial (scratch digging), suspensorial (hanging) and tenasorial (grappling). The misidentification rate of the LDA was calculated using a confusion matrix. The pGLS residuals for *Sphodrosaurus pennsylvanicus* were projected into a plot showing the first two linear discriminant axes using the function ‘predict’ of R employing all equal priors (prob = 0.125). All these analyses and graphics were

---

**Figure 4.** Lower jaw on the latex cast of the holotype of *Sphodrosaurus pennsylvanicus*. A, posterior region of the left hemimandible in lateral view; B, posterior region of the right hemimandible in lateral view; C, close-up of the lateroventral edge of the angular of the left hemimandible in ventral view; D, posterior region of the right dentary and splenial in lateroventral view; E, posterior region of the right hemimandible in medial view; and F, drawing of (E). The arrows point towards the anterior direction. **Abbreviations:** an, angular; an.tub, angular tuberosities; co, coronoid; dt, dentary; dt.tub, dentary tuberosities; FIC, foramen intermandibularis caudalis; gr, groove; pra, prearticular; rap, retroarticular process; ri, ridge; spl, splenial. Scale bars: A, B = 5 mm; C–F = 2 mm.
conducted in R 4.1.1 (R Core Team 2021) using the codes of Thomson & Motani (2021). Files and codes are available in Supplemental material 4.

Figure 5. Postcranial axial skeleton on the latex cast of the holotype of *Sphodrosaurus pennsylvanicus*. A, cervical series in ventral view; B, atlas-axis in ventral and slightly posterior views; C, presacral vertebrae and ribs 10–12 in ventral view; D, presacral vertebra 13 in posteroverentral view; and E, presacral vertebra 19 in anteroventral view. The arrows point towards the anterior direction. **Abbreviations**: ?, indeterminate bone; aas, anterior articular surface; amax, anterior margin of axial centrum; atl, atlas; atlint, atlantal intercentrum; atlna?, possible atlantal neural arch; ax, axis; axce, axial centrum; axint, axial intercentrum; ca, capitulum; Cv5, cervical vertebra 5; di, diapophysis; lribA–E, left cervical rib A–E; pa, parapophysis; pas, posterior articular surface; per, proximal end of rib; PS7, presacral vertebra 7; rribA–C, right cervical rib A–C; tu, tuberculum; vk, ventral keel. Scale bars: A = 5 mm; B–E = 2 mm.

**Institutional abbreviations**
BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University
of the Witwatersrand, Johannesburg, South Africa; ISI, Indian Statistical Institute, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; NHMUK PV, Natural History Museum, Palaeontology Vertebrates, London, UK; NMQR, National Museum, Bloemfontein, South Africa; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; RC, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; SAM-PK, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayern – Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany; TMM, Texas Memorial Museum, Austin, USA; UMZC, University Museum of Zoology, Cambridge, UK.

Systematic palaeontology
Diapsida Osborn, 1903 (Gauthier & de Queiroz [2020])
Archosauroomorpha Huene, 1946 (Gauthier [2020a])
Archosauromorphaes Gauthier, Kluge & Rowe, 1988 (Gauthier [2020b])
Proterochampsa Bonaparte, 1971 sensu Kischlat (2000)
Doswelliidae Weems, 1980 sensu Sues, Desojo & Ezcurra (2013)
*Sphodrosaurus pennsylvanicus* Colbert, 1960
(Figs 2–6, 7A, B, D, 8)

Holotype. Franklin and Marshall College, North Museum, no. 2321, natural mould of a partial skull and postcranial skeleton exposed in ventral view (Figs 2, 3).

Type horizon and locality. Hammer Creek Formation (Triassic: late early or early middle Norian), Newark Supergroup. Abandoned quarry about 3.2 km (2 miles) east of Bowmanville, Lancaster County, Pennsylvania, USA (Colbert 1960; Sues et al. 1993; Fig. 1). The Hammer Creek Formation is laterally correlated to the Passaic Formation (formerly ‘Brunswick Formation’) in New Jersey, and the latter has now been precisely dated as late early or early middle Norian using palaeomagnetic data (Olsen et al. 2010). See Sues et al. (1993) for additional information about the type locality and the geological setting of the Hammer Creek Formation.

Emended diagnosis. *Sphodrosaurus pennsylvanicus* is a small-sized reptile (presacral vertebral column length c. 136 mm and femoral length c. 57 mm) that differs from other known neodiapsids in the following combination of character states (autapomorphies among non-archosaurian archosauriforms indicated with an asterisk): skull proportionately very large, with a skull width-presacral vertebral series length ratio of c. 0.44 (similar ratio present in hyperodapedontine rhynchosaurids and a larger ratio present in *Proterochampsia barriomuevoi*); absence of external mandibular fenestra (shared by *Doswellia kaltenbachii*); external surface of posterior mandibular bones distinctively sculptured by longitudinal ridges and grooves (also present in *Proterochampsia barriomuevoi*); angular with laterally projecting ridge that separates lateral and ventral sides on the ventrolateral surface of the bone (also present in *Tropidosuchus romeri* and rhadinosuchines); ridge on the ventrolateral surface of the angular and posterior end of dentary with rounded, low tuberosities*; angular and posterior end of the dentary with a well-defined longitudinal groove that has a smooth surface*; angular and prearticular with sub-equal dorsoventral contribution to the medial wall of the postdental region of the hemimandible* (also present in phytosaurs); retroarticular process restricted to the ventral half of the hemimandible* (also present in phytosaurs) and ventrolaterally oriented in lateral view*; presacral vertebral 3–12 with large parapophysis occupying half or more of the anteroposterior length of the centrum/base of neural arch*; cervical rib shafts plate-like, strongly compressed*; dorsal vertebrae with a well-developed ventral keel restricted to the anterior two-thirds of the series*; proportionally short posterior dorsal vertebrae, with a centrum length-height ratio of ~1.33 (measured on the 19th presacral vertebra; also present in *Chanareusuchus bonapartei* and several other archosauriforms); dorsal vertebrae with ventral margin of synapophysis positioned partially on lateral surface of centrum*; scapula with distal half of the blade with a convex anterior margin*; plate-like pubis without anterior apron (also present in *Doswellia kaltenbachii*); and metatarsal II with a deeply grooved anteromedial surface for reception of metatarsal I (also present in *Tropidosuchus romeri*).

Results

Anatomical revision
The holotype of *Sphodrosaurus pennsylvanicus* has previously been described in detail by Colbert (1960) and Sues et al. (1993). The latter authors corrected some previous misinterpretations and added a substantial
Figure 6. Shoulder girdle and ulna and radius on the latex cast of the holotype of *Sphodrosaurus pennsylvanicus*. A, right shoulder girdle; B, drawing of (A); C, possible left shoulder girdle; D, right coracoid in probable lateral view; E, distal ends of left ulna and radius and proximal end of indeterminate left metacarpal; and F, distal end of the ulna and radius in distal view. The arrow points towards the anterior direction. **Abbreviations**: ?, indeterminate bone; ac?, possible acromion process; cf, coracoid foramen; cl, clavicle; co, coracoid; dr, dorsal rib; ga, gastralia; gf?, possible glenoid fossa; leco?, possible left coracoid; lsco?, possible left scapula; mtc, metacarpal; pa, parapophysis; ra, radius; sc, scapula; scb, scapular blade; ul, ulna. Scale bars: A–C, E = 5 mm; D, F = 2 mm.
number of new anatomical details based on the reprep-ration of the specimen and new latex casts. Thus, we consider that it is not necessary to provide another complete redescription of *Sphodrosaurus pennsylvanicus*. Here we will focus on anatomical regions that required a more detailed description or where we provide a different interpretation from that by previous authors. These descriptions are complemented with comparisons with other Triassic terrestrial diapsids, mainly those published during the last 30 years. These re-descriptions and comparisons are intended to provide new information to discuss the phylogenetic relationships of *Sphodrosaurus pennsylvanicus*.

**General state of preservation.** The holotype of *Sphodrosaurus pennsylvanicus* is preserved as a natural mould of a partial skeleton in ventral view (Figs 2, 3). As a result, the dorsal surface of the palate, the dorsal margins of the hemimandibles, the neural arches of the vertebras, and the lateral surfaces of the femur and tibia are not exposed. Some of the bones are partially preserved or embedded in matrix, as is the case for part of the shoulder girdle, left anterior zeugopodium, right posterior autopodium and some ribs. No osteoderms could be identified in the specimen.

**Palate.** The right pterygoid of *Sphodrosaurus pennsylvanicus* preserves the lateral ramus and the proximal half of the posterolateral (or quadrat) ramus (Figs 2, 3; Table 1). The posterior margin of the lateral ramus extends directly laterally based on the orientation of the vertebral series and the relationship with the right hemimandible and the preserved region of the left pterygoid. A laterally oriented lateral ramus of the pterygoid occurs in most archosauromorphs (Ezcurra 2016). However, the lateral ramus of the pterygoid is posterolaterally oriented in protorosuchids (e.g. Protorosuchus fargusi: SNSB-BSPG 1934 VIII 514, RC 59; Protorosuchus alexanderi: NMQR 1484), Sarmatosuchus otschevi (Gower & Sennikov 1997), most erythrosuchids (e.g. Guchengosuchus shiguaiensis: Peng 1991; Garjainia prima: Ezcurra et al. 2019; Butler et al. 2019b; Erythrosuchus africanus: Gower 2003), Pseudochampsa ischigualastensis (Trotteyn & Ezcurra 2014), some specimens of Chaoncaresuchus bonapartei (PVL 4586, MCZ 4037) and various pseudosuchians (e.g. Nicrosaurus kapffi: NHMUK PV R42743; Riojasuchus teniusceps: Baczko & Desojo 2016; Revueltosaurus callenderi: Parker et al. 2021; Batrachotomus kupferzellensis: Gower 1999). There is no evidence of palatal teeth on the lateral ramus of the pterygoid of *Sphodrosaurus pennsylvanicus*, and palatal teeth are absent in this region in lepidosauromorphs, some tanystropheids, Malerisaurus langstonti, rhynchosaurus, Teyujagua paradoxa, erythrosuchids and eucrocopod archosauromorphs (Ezcurra 2016; Schoch & Sues 2018; Simões et al. 2018; Pinheiro et al. 2020; Nesbitt et al. 2022).

**Lower jaw.** The lateral surface of the hemimandibles bears a series of prominent ridges that have an antero-posterior main axis and generally form an anastomizing pattern (Fig. 4A, B; Table 1). This kind of ornamentation closely resembles that present in the protorochampsian Proterochampsia barriomeuvoi (PVSJ 77). Coarse ornamentation is also present on the lateral surface of the postdentary bones of the doswelliids Doswellia kaltenbachi and Rugarhynchos sixmilensis (Dilkes & Sues 2009; Wynd et al. 2019). However, the mainly antero-posteriorly oriented ridges of Rugarhynchos sixmilensis are restricted to the posterior region of the surangular (Wynd et al. 2019) and the sculpture of Doswellia kaltenbachi is extensive but it has a reticular pattern (Dilkes & Sues 2009). The postdentary bones of rhadinosuchine protorochampsids have a mostly smooth external surface, with the exception of a ridge that extends along the suture between the surangular and angular and another ridge that extends along the ventrolateral surface of the angular (Dilkes & Arcucci 2012). The position of the suture between the surangular and angular, and thus the presence of the former ridge, cannot be determined in *Sphodrosaurus pennsylvanicus*. However, a ridge in the same position as the ventrolateral ridge on the angular of rhadinosuchines occurs in *Sphodrosaurus pennsylvanicus* (Fig. 4A, B: ri), but this structure also extends onto the dentary in the latter species (see below). The posterior end of this ridge has a flat, smooth surface in *Sphodrosaurus pennsylvanicus*, but, more anteriorly, it bears a series of rounded, very low and laterally oriented tuberosities (Fig. 4C: an.tub).

A longitudinal groove with a smooth surface is present immediately dorsal to the ventrolateral ridge on both hemimandibles of *Sphodrosaurus pennsylvanicus* (Fig. 4A, B: gr) and, as far as we are aware, this feature seems to be unique for this species. The posterior end of this groove narrows dorsoventrally and bows dorsally, matching the slightly dorsally concave ventral margin of this region of the hemimandible. Sues et al. (1993) reported that the retroarticular process was not distinct in *Sphodrosaurus pennsylvanicus*. We confirm that the retroarticular process is very short, and it is also dorsoventrally very low, being restricted to the ventral third of the hemimandible (Fig. 4A, B: rap). A similar, ventrally restricted retroarticular process is present in phytosaurs (e.g. Stocker et al. 2017), but the process is slightly ventrolaterally oriented in *Sphodrosaurus pennsylvanicus*. No suture between bones can be identified on the lateral surface of the hemimandibles of
**Sphodrosaurus pennsylvanicus**, which is probably due to the coarse ornamentation on the bones.

The right hemimandible preserves a more anterior region than the left one, and it is inferred that it should include the posterior portion of the dentary (Fig. 4B; see below). The ventrolateral groove of the angular does not extend onto this region of the mandible and the external surface of the dentary is sculptured by very shallow but well-defined, sub-circular to sub-oval depressions of variable size and distributed without a distinct pattern. The dorsal margin of the dentary bears four rounded tuberosities, which have an anteroposterior main axis (Fig. 4B: dt.tub). The three anterior tuberosities are arranged close to each other and separated by a transverse groove. There is no evidence to suggest that these tuberosities are the bases of broken teeth, and thus they are identified here as bony sculpturing.

The medial surface of the hemimandibles was not described in previous accounts of the anatomy of *Sphodrosaurus pennsylvanicus*, but it is well preserved and informative (Fig. 4E, F). The dorsal regions of both hemimandibles are obscured due to a lack of preservation or the bone entering into the matrix. In contrast to the heavily sculptured external surface, the inner surface of the lower jaw is smooth. The posterior region of the hemimandible is sub-equally divided dorsoventrally by a mostly longitudinal and slightly sigmoidal suture between the prearticular and the angular. A similarly extensive contribution of the angular to the medial surface of the hemimandible, ventral to the adductor fossa,
is also present in phytosaurs (Bona et al. 2022). The suture between the prearticular and angular cannot be identified on the posterior tip of the hemimandible and terminates anteriorly on the posterior margin of an anteromedially facing foramen intermandibularis caudalis (Fig. 4E, F: FIC). This foramen occurs in disparate diapsid clades, being present in the non-saurians Orovenator mayorum (Ford & Benson 2019), Claudiozaurus germaini (Carroll 1981) and Youngina capensis (SAM-PK-K7578), the choristoderan Simoedosaurus lemoinei (Sigogneau-Russell & Russell 1978), the lepidosaur Gephyrosaurus bridensis (= angular foramen; Evans 1980), the allokotosaurian Trilophosaurus buettneri (TMM 31025-5), hyperodapodontine rynchosaurous (e.g. Isalorhynchus genovefae: Whatley 2005; Hyperodapedon sanjuanensis: Gentil & Ezcurra 2022; Teyumbaita sulcognathus: Montefeltro et al. 2010), phytosaurs (e.g. Parasuchus hislop: Chatterjee 1978; Nicosaurus kapffi: NHMUK PV R42744), Ornithosuchus woodwardi (Bona et al. 2022) and ornithischian dinosaurs (= internal or inferior mandibular fenestra; e.g. Heterodontosaurus tucki: Norman et al. 2011; Lesothosaurus diagnosticus: Porro et al. 2015; Scelidosaurus harrisonii: Norman 2020). Both prearticular and angular contribute to the posterior margin of the FIC, resembling the condition in Gephyrosaurus bridensis, Trilophosaurus buettneri and phytosaurs. As in Trilophosaurus buettneri and early archosaurs, the anterior margin of the FIC of Sphodrosaurus pennsylvanicus is delimited by the splenial. By contrast, the FIC is completely enclosed by the prearticular in non-saurian diapsids and at least the vast majority of hyperodapodontine rynchosaurous.

Both the prearticular and angular have a sub-triangular, anteriorly tapering anterior end in medial view. The anterior end of the prearticular fits between the coronoid bone and the posterior end of the splenial and the angular fits between the splenial and the dentary. The presence of an unexpanded and straight anterior end of the prearticular resembles the condition in Proterochampsia barriouneuvi (PVSJ 77) and phytosaurs (e.g. Nicosaurus kapffi: NHMUK PV R42744). The presence of a coronoid bone in Sphodrosaurus pennsylvanicus is established here because of distinct sutures separating it from the splenial and prearticular as well as the presence of a distinctly convex surface that is absent in surrounding bones. The presence of a coronoid bone as an independent post-embryonic mandibular ossification occurs in non-saurian Palaeozoic neodiapsids, choristoderans, early-diverging lepidosauromorphs and Triassic archosauromorphs with the exception of aetosaurs and pterosaurs (Bona et al. 2022), whereas the coronoid bone has not been identified to date in the archosauromorph genus Tanystropheus (Spiekman et al. 2020).

The more anterior regions of both hemimandibles of Sphodrosaurus pennsylvanicus have a distinct longitudinal suture that separates the broadly exposed splenial from another, ventrally restricted bone in medial view. This suture is anterior to the level of the coronoid bone, and then reaches the anterior end of the preserved portion of the hemimandible. As a consequence, this is strong evidence for the preservation of the dentaries in Sphodrosaurus pennsylvanicus. One of the most interesting implications of the preservation of the posterior region of the dentary is that there is no external mandibular fenestra. Such a mandibular opening is present in Teyujagua paradoxa (Pinheiro et al. 2016), and it is a synapomorphy of Archosauriformes (Gauthier et al. 1988). The loss of an external mandibular fenestra is uncommon among known Triassic archosauriforms, occurring only in Doswellia kaltenbachi (Weems 1980; Dilkes & Sues 2009) and pterosaurs (with the exception of Austriadraco dallavecchiai; Wellnhofer 2003). The suture between the dentary and splenial curves gradually ventrally towards the anterior end of the lower jaw, and, at the anterior end of the preserved region of the right hemimandible, it is already positioned on the ventral margin (Fig. 4D).

**Position of the atlanto-occipital joint.** Colbert (1960) described the posterior region of the skull – both hemimandibles – of Sphodrosaurus pennsylvanicus as extending as far back as about the fourth or fifth cervical vertebra. This condition, and the recognition of both pterygoids as very likely in natural position with respect to each other and the hemimandibles, led Sues et al. (1993) to suggest that, although the basicranial region was not preserved, the atlanto-occipital joint would have been placed well forward of the craniofacial joint. However, we doubt that this condition can actually be determined in Sphodrosaurus pennsylvanicus. The basal articulation between the pterygoid and basipterygoid process of the basisphenoid or parabasiphenoid is positioned level with the base of the post-erolateral (or quadrate) ramus of the pterygoid in diapsids. In Sphodrosaurus pennsylvanicus, the atlas is positioned only a few millimetres posterior to the level

---

**Table 1.** Measurements (in mm) of cranial bones on the latex cast of the holotype of Sphodrosaurus pennsylvanicus. Asterisks indicate incomplete measurements, where the value given is the maximum measurable. The maximum deviation of the digital calliper is 0.02 mm, but measurements were rounded to the nearest 0.1 mm.

| Measure                                | Value |
|----------------------------------------|-------|
| Right pterygoid width at level of lateral ramus | 16.9  |
| Left hemimandible length               | 26.9* |
| Left hemimandible length               | 37.3* |
| Left half of cranial width             | c. 29.9 |

---

Re-assessment of the Triassic reptile Sphodrosaurus 1655
where the basal articulation should be located (Figs 2, 3). This does not leave room for the basioccipital bones and, thus, we interpret that the vertebral series is preserved forward from its natural position. The parasphe-noid/basisphenoid and basioccipital have different proportional lengths in diapsids and, as a result, we think that the position of the atlanto-occipital joint with respect to the craniomandibular articulation cannot be determined with confidence.

**Presacral vertebrae.** We confirm the count of 23 presacral vertebrae of Sues et al. (1993; contra Colbert 1960), and the first sacral vertebra is articulated with the presacral series (Colbert 1960) (Figs 2, 3, 5; Table 2). The length of the cervical series is 29.8 mm, that of the dorsal series is 106.2 mm, and that of the complete presacral series is 136.0 mm (lengths measured as the sum of each of the centrum lengths). The identification of the position of the cervico-dorsal transition is difficult because of the limited exposed surface of each vertebra and the dorsoventral compression of the specimen, which has affected the orientation of the ribs. It is possible that *Sphodrosaurus pennsylvanicus* has seven cervical vertebrae based on the location of the shoulder girdle with respect to the vertebral series and the position of the first rib with an orientation mainly orthogonald to the vertebral series (Figs 2, 3). However, this count should be considered speculative.

The atlantal intercentrum is displaced a few millimetres anterior to the axial intercentrum and centrum (Fig. 5A, B). It (Fig. 5B; atlna) has a transversely concave posteroventral surface for the reception of the axial intercentrum. A poorly preserved bone to the left of the atlantal intercentrum may represent an atlantal neural arch, but it cannot be confidently identified (Fig. 5B: atlna?). A transversely elongated bone, with a ventral median apex, is preserved on the right half of the anteroventral margin of the axial centrum. This bone is interpreted as the axial intercentrum (Fig. 5B: axint), and its displacement relative to the midline indicates that it was not fused to the axial centrum. The right lateral surface of the axial centrum has an anteriorly positioned, sub-triangular parapophysis with a posterior apex. The pronounced median longitudinal keel of the axis (Sues et al. 1993) extends ventrally slightly beyond the ventral rims of the centrum, as also on the fourth and sixth to ninth presacral vertebrae (the condition on the fifth cervical vertebra cannot be determined due to damage; Fig. 5A: vk). Such well-developed longitudinal ventral keels are also present on the cervical vertebrae of some erythrosuchids (e.g. *Garjainia prima*: Maidment et al. 2020; *Erythrosuchus africanus*: SAM-PK-3028), proterochampsids (e.g. *Proterochampsa barrionuevoi*: PVSJ 606; *Tropidosuchus romeri*: PVL 4601; *Chanaresuchus bonapartei*: PVL 4575), the doswelliid *Rugarhynchos sixmilensis* (Wynd et al. 2019), and a few Triassic archosaurs (e.g. *Riojasuchus tenuisceps*: Baczko et al. 2019; *Aetosauroidea scagliai*: PVL 2059; *Batrachotomus kuperzellensis*: Gower & Schoch 2009; *Asilisaurus kongwe*: Nesbitt et al. 2020; *Herrerasaurus ischigualastensis*: PVSJ 407). The ventral keel is present on the first 16 presacral vertebrae of *Sphodrosaurus pennsylvanicus* and clearly absent on the 19th presacral vertebra (the ventral surface of the centrum is damaged on the 17th and 18th presacral vertebrae; Figs 2, 3, 5). Ventral keels on most of the dorsal vertebrae also occur in *Petrolacosaurus kansensis* (Reisz 1981), *Tanytropheus* spp. (SMNS 54628, 55341), *Shringasaurus indicus* (ISIR specimens), *Trilophosaurus buettneri* (Spielmann et al. 2008), erythrosuchids (e.g. *Garjainia prima*: Maidment et al. 2020; *Bharitalesuchus tapani*: Ezcurra et al. 2021b), *Proterochampsa barri(oneuoi* (PVSJ 606), and a few Triassic archosaurs (e.g. *Arizonasaurus babbitti*: Nesbitt 2005; *Batrachotomus kuperzellensis*: Gower & Schoch 2009).

The anterior or posterior articular surface of the centrum is sufficiently exposed on presacral vertebrae 13, 14 and 17–19 to determine that they are amphicoelous and not notochordal (Fig. 5D, E). By contrast, notochordal centra occur in Palaeozoic non-saurian diapsids, rhychocephalian lepidosauromorphs and the Permian archosauromorph *Aenigmastropheus parringtoni* (Ezcurra et al. 2014). We confirm the absence of postaxial intercentra in *Sphodrosaurus pennsylvanicus*, which is an apomorphy of Archosauromorpha present in most Permo–Triassic species (Pritchard et al. 2015; Ezcurra 2016).

The cervical vertebrae are proportionally short antero-posteriorly (Figs 2, 3; Table 2), contrasting with the elongated cervical vertebrae of *Proterosaurus speneri* (Gottmann-Quesada & Sander 2009), tanytropheids and dinocephalosaurids (Spiekman et al. 2021), some allokotosaurs (Sen 2003; Nesbitt et al. 2022), *Prolacerta broomi* (Gow 1975), *Litorosuchus somnii* (Li et al. 2016), the doswelliid *Jaxtasuchus salomonii*, *Doswellia kaltenbachii* and *Rugarhynchos sixmilensis* (Weems 1980; Dilkes & Sues 2009; Schoch & Sues 2014; Wynd et al. 2019) and most archosaurs. The parapophysis quickly migrates dorsally in the cervical series and is placed on the anterodorsal corner of the centrum by the sixth vertebra (Fig. 5A: pa). It is anteroposteriorly long, occupying the anterior half or more than half of the anteroposterior length of the centrum from the third to the twelfth presacral vertebrae (Fig. 5A, C: pa). This condition differs from that in other known diapsids. The diapophysis is well exposed on the left side of the fifth and sixth cervical vertebrae (Fig. 5A: di). It is
the left ribs has a slightly expanded proximal end, sides of and parallel to the cervical vertebrae (Colbert 1960). As a result, four or more cervical rib shafts extend parallel to each other and overlap the ventromedial surface of the preceding element in ventral view. The ribs are very long, in which the longest rib is four times the length of the anterior-middle postatlantal cervical vertebrae (Colbert 1960). A posterior cervical and dorsal rib shafts are gradually bowed throughout their length, contrasting with the sharp, right-angle bent present in the anterior and middle dorsal ribs of the doswelliids Doswellia kaltenbachi and Jaxtasuchus salomoni (Dilkes & Sues 2009; Schoch & Sues 2014). The posterior surface of the middle dorsal rib shafts of Sphodrosaurus pennsylvanicus has a well-defined longitudinal groove. The proximal ends of the dorsal ribs are sufficiently exposed to determine that they are diachephalous back to at least the 17th presacral position, where a very short capitulum and a longer tuberculum are present. Dichocephalous anterior and middle dorsal ribs are also present in erythrosuchids and eucrocodileops (Hughes 1963; Ezcurra 2016). By contrast, non-saurian diapsids and lepidosauromorphs (Gauthier 1986; Nesbitt 2011; Pritchard et al. 2015; Ezcurra 2016). The cervical rib shafts of Sphodrosaurus pennsylvanicus are strongly dorsoventrally compressed, contrasting with the rod-like shafts of early diapsids and saurians.

The posterior cervical and dorsal rib shafts are gradually bowed throughout their length, contrasting with the sharp, right-angle bent present in the anterior and middle dorsal ribs of the doswelliids Doswellia kaltenbachi and Jaxtasuchus salomoni (Dilkes & Sues 2009; Schoch & Sues 2014). The posterior surface of the middle dorsal rib shafts of Sphodrosaurus pennsylvanicus has a well-defined longitudinal groove. The proximal ends of the dorsal ribs are sufficiently exposed to determine that they are diachephalous back to at least the 17th presacral position, where a very short capitulum and a longer tuberculum are present. Dichocephalous anterior and middle dorsal ribs are also present in erythrosuchids and eucrocodileops (Hughes 1963; Ezcurra 2016). By contrast, non-saurian diapsids and lepidosauromorphs all have holoccephalous dorsal ribs, and most non-archosauromorph archosauromorphs have diachephalous ribs restricted to the anterior third of the trunk series.

**Gastralia and sacrum.** There is no new anatomical information or comparison to provide here about these anatomical regions.

**Shoulder girdle.** Colbert (1960) and Sues et al. (1993) identified a partially exposed and crushed right shoulder girdle (Figs 2, 3, 6A, B, D; Table 3). We agree with this interpretation. The anterior end of the proximal end of the scapula is not exposed, and only the posterior

| Table 2. Measurements (in mm) of the postcranial axial skeleton on the latex cast of the holotype of Sphodrosaurus pennsylvanicus. Asterisks indicate incomplete measurements, where the value given is the maximum measurable. Abbreviations: PS, presacral; S, sacral. The maximum deviation of the digital calliper is 0.02 mm, but measurements were rounded to the nearest 0.1 mm. |
|-----------------|-----------------|-----------------|-----------------|
|                  | Centrum length  | Centrum posterior width | Centrum length |
| Axial intercentrum width | 5.5              | 6.9               | 6.8             |
| PS3 centrum length    | 5.7              | 5.9               | 6.3             |
| PS4 centrum length    | 5.5              | 5.9               | 6.2             |
| PS5 centrum length    | 5.0              | 6.1               | 6.2             |
| PS6 centrum length    | 4.9              | 6.7               | 6.6             |
| PS7 centrum length    | 5.0              | 5.7               | 6.6             |
| PS8 centrum length    | 4.6              | 5.6               | 6.6             |
| PS9 centrum length    | 5.3              | 5.5               | 6.5             |
| PS10 centrum length   | 5.8              | 6.0               | 6.8             |
| PS11 centrum length   | 5.8              | 6.0               | 6.8             |
| PS12 centrum length   | 5.9              | 6.1               | 6.9             |
| PS13 centrum length   | 6.5              | 6.7               | 7.0             |
| PS14 centrum length   | 5.1*             | 6.7               | 7.0             |
| PS15 centrum length   | 6.4              | 6.7               | 7.0             |
| PS16 centrum length   | 6.0              | 5.7               | 5.9             |
| PS17 centrum length   | 6.4              | 5.9               | 5.9             |
| PS18 centrum length   | 6.9              | 5.9               | 5.9             |
| PS19 centrum length   | 6.8              | 5.9               | 5.9             |
| PS20 centrum length   | 6.8              | 5.9               | 5.9             |
| PS21 centrum length   | 7.0              | 6.7               | 6.7             |
| PS22 centrum length   | 6.5              | 6.7               | 6.7             |
| PS23 centrum length   | 6.3              | 6.7               | 6.7             |
| PS9 centrum posterior width | 6.7             | 6.1               | 6.1             |
| PS12 centrum posterior width | 6.1             | 6.1               | 6.1             |
| PS13 centrum posterior width | 6.2             | 6.2               | 6.2             |
| S1 centrum length     | 6.6              | 6.6               | 6.6             |
| Longest cervical rib length (PS8) | 22.1* | 22.1* | 22.1* |
| Longest dorsal rib length (PS7/8) | 55.3 | 55.3 | 55.3 |
margin of the base and the anterior and anterodistal margins of the distal end of the scapular blade are exposed (Fig. 6B). This shows that the scapular blade is very long (Colbert 1960), the anterior margin of its distal half is convex, and it does not expand anteriorly at its distal end. However, we cannot determine the complete anteroposterior width of the blade at its base or whether the distal end of the blade expands posteriorly, because these regions are covered with matrix. The absence of an anterior expansion of the distal end of the scapular blade resembles the condition in non-saurian diapsids (e.g. Youngina capensis: Gow 1975; Cladiosaurus germani: Carroll 1981), some tanystrophoids (e.g. Amotosaurus rotfeldensis: Fraser & Riepe 2006; Tanystropheus longobardicus: Spiekman et al. 2021), proterosuchids (e.g. Proterosuchus alexandri: NMQR 1484), Sarmatosuchus otschevi (Gower & Sennikov 1997), pterosaurs (e.g. Austriadraco dallavaccia: Wellnhofer 2003; Dimorphodon macronyx: NHMUK PV R41212-13) and some early dinosaurs (e.g. Herrerasaurus ischigualastensis: Sereno 1994; Tawa hallae: Nesbitt et al. 2009). By contrast, rhycho-saurs, allokotosaurs, non-archosaurian eucrocopods, Triassic pseudosuchians and most early avemetatarsali-ans have an anterodistal expansion that gives the anterior margin of the blade a concave profile in side view (Nesbitt 2011; Nesbitt et al. 2015; Ezcurra 2016). The proximal end of the right scapula of Sphodrosaurus pennsylvanicus is strongly overlapped by poorly preserved partial bones. One of those was interpreted as a forelimb bone by Colbert (1960), but we cannot determine its identity. The posterior end of the proximal surface of the scapula is deeply depressed and likely represents part of the glenoid surface. A rod-like, partially exposed bone is preserved immediately next to the proximal surface of the scapula. Because of its position it could be part of a clavicle, but it could also be part of a rib shaft (Fig. 6B: dr/cl).

A blocky bone is preserved immediately next to and partially in contact with the probable glenoid region of the scapula (Fig. 6A, B, D: co). Its size and position suggest that it could be a coracoid. In agreement with this interpretation, there is a foramen on the most extensively exposed surface of the bone, whose size, position and orientation are congruent with the coracoid foramen of other diapsids (Fig. 6D: cf). The closest edge to this foramen should be the proximal margin of the coracoid, and it is partially well exposed, showing that the scapula and coracoid are not fused to each other. Following this interpretation, the coracoid lacks a posterior expansion, resembling the condition in most hyperodapedontine rnychosaurians (Chatterjee 1974; Benton 1983), Garjainia madiba (Gower et al. 2014), Halazhaisuchus qiaoensis (Sookias et al. 2014a), Tropidosuchus romeri (PVL 4604) and some archosaurs (e.g. Yarasuchus decanensis: ISIR 334/49; Erpetosuchus grantii: Benton & Walker 2002; Parasauchus histopi: Chatterjee 1978; Heterodontosaurus tucki: Santa Luca 1980). The dorsoventral height of the coracoid of Sphodrosaurus pennsylvanicus is 0.23 times the maximum proximodistal length of the scapula. A proportionally small coracoid is present in the vast majority of Permo–Triassic diapsids, with the exception of Hovasaurus boulei (Currie 1981), tanystrophoids (e.g. Amotosaurus rotfeldensis: Fraser & Riepe 2006; Macrocnemus bassanii: Jaquier et al. 2017; Tanystropheus longobardicus: Spiekman et al. 2021), Litorosuchus somnii (Li et al. 2016) and some early ptero-saurs (e.g. Peteinosaurus zambelli: Dalla Vecchia 2014; Eudimorphodon ranzii: Wild 1979), in which the height of the coracoid is two-thirds or more the length of the scapula. An unidentified plate-like bone is exposed between the coracoid and the vertebral series (Fig. 6B: ?).

In a very similar position to that of the shoulder girdle but on the left side of the skeleton, there are bones that have been interpreted as a humerus and an indeterminate element (Colbert 1960; Sues et al. 1993). The putative humerus lacks clear features providing strong support for this interpretation and, alternatively, this bone could be the left scapula (Figs 2, 3, lsq?, 6C; Table 3). Its putative proximal end and shaft are not dissimilar to the proximal end and base of the scapular blade of the right scapula. A low, blade-like ridge next to one of the margins of the expanded area of the bone may represent an acromion ridge (Fig. 6C: ac?) similar to that present in protero-champsids (e.g. Proterochampsia barriomuisei: PVSJ 606; Gualosuchus reigi: PULR 05). If the identification as the left scapula is correct, it shows that the scapular blade lacks the strong bend of the posterior margin present in non-saurian diapsids, non-crocopodan archosauromorphs, some allokotosaurs, Mesosuchus browni, Prolacerta broomi, proterosuchids and Sarmatosuchus otschevi (Pritchard et al. 2015; Ezcurra 2016). The indeterminate
bone preserved next to this possible scapula could be a poorly exposed left coracoid (Fig. 6C: lco?).

**Ulna and radius.** The distal regions of the left ulna and radius are exposed (Colbert 1960; Sues et al. 1993; Fig. 6E, F; Table 3). The distal end of the ulna is not much expanded, with a slightly convex articular surface (Sues et al. 1993), several times transversely broader than anteroposteriorly deep (Fig. 6F). A slightly convex distal articular surface of the ulna is widely distributed among diapsids, but the distal end is squared off, with a flat articular surface, in euryapsids and several suchian pseudosuchians (Nesbitt 2011; Ezcurra 2016). The distal end of the radius is narrower than that of the ulna and its articular surface is also slightly convex but sub-circular in distal view (Fig. 6F). The end of a bone preserved next to the distal ends of the radius and ulna possibly represents a metacarpal (Fig. 6E: mtc).

**Ilium.** Most of the acetabular region of the right ilium is exposed and the base of the postacetabular process is preserved (Fig. 7A, B; Table 4). The postacetabular wall is ventrally developed and, thus, the acetabulum was presumably completely (or nearly completely) closed. The acetabulum is deeply concave, with a smooth surface. There is no raised antitrochanter on the posterior region of the acetabulum, contrasting with its presence in several ornithodiran archosaurs (Nesbitt 2011; Ezcurra 2016; Ezcurra et al. 2020a). The ischial peduncle lacks a posterior expansion or heel (Fig. 7B: isp). The base of the postacetabular process suggests that it was distinctively posterodorsally oriented (Fig. 7B: poap), but this observation is tentative because part of the acetabulum is not exposed and thus the orientation for the ilium cannot be definitively determined.

**Pubis.** The pubis is plate-like without an anterior apron (Fig. 7A; Table 4), as in choristoderans, lepidosauromorphs, most tanystropheids, dinoccephalosaurs, Jesaioaurus lehmani, Trilophosaurus buettneri and Doswellia kaltenbachi (e.g. Sigogneau-Russell 1981; Fraser 1988; Jalil 1997; Dilkes & Sues 2009; Spielmann et al. 2008; Ezcurra 2016; Spiekman et al. 2021). The pubis is a proportionally short bone in *Sphodrosaurus pennsylvanicus*, with a pubis-femur length ratio of 0.32–0.34. Similarly short pubes are also present in non-suchian diapsids (e.g. *Claudiosaurus germani*: Carroll 1981; *Youngina capensis*: Gow 1975), several non-archosauromorph archosauriforms (e.g. *Macrocnemus fuyanensis*: Jiang et al. 2011; *Pamelaria dolichotrachela*: ISIR 316; *Trilophosaurus buettneri*: Spielmann et al. 2008; *Eifelosaurus triadicus*: Sues et al. 2021; *Prolacerta broomi*: BP/1/2676), proterochampsids (e.g. *Tropidosuchus romeri*: PVL 4604; *Chanaresuchus bonaparte*: PVL 4575), some non-suchian pseudosuchians (e.g. *Nundasuchus songaeensis*: Nesbitt et al. 2014; *Parasuchus hislopii*: Chatterjee 1978) and lagerpetid avemetatarsalians (Ezcurra et al. 2020a). The proximal surface for articulation with the ilium is concave.

**Ischium.** The single preserved ischium of *Sphodrosaurus pennsylvanicus* is severely damaged, but it can be determined that it is a plate-like bone, as reported by previous authors (Colbert 1960, p. 16) reported that

| Table 4. Measurements (in mm) of the right pelvic girdle and hindlimb on the lateral cast of the holotype of Sphodrosaurus pennsylvanicus. Asterisks indicate incomplete measurements, where the value given is the maximum measurable. The maximum deviation of the digital calliper is 0.02 mm, but measurements were rounded to the nearest 0.1 mm. |
|-----------------|-----------------|-----------------|-----------------|
| Ilium length    | 24.5*           | Pubis length    | 18.1            |
| Femur length    | 54.8*           | Tibia length    | 39.6            |
| Tibia proximal depth | 11.5          | Metatarsal I length | 8.9            |
| Metatarsal II length | 14.6          | Metatarsal II proximal width | 6.0            |
| Metatarsal III length | 12.0*         | Phalanx I-1 length | 4.9            |
| Phalanx II-1 length | 6.9            | Phalanx II-2 length | 4.4            |
| Phalanx II-3 length | 10.3           | Phalanx III-1 length | 7.8            |
| Metatarsal III proximal width | 6.0            | Phalanx II-1 length | 4.9            |
| Metatarsal III proximal width | 6.0            | Phalanx II-2 length | 4.4            |
| Metatarsal III proximal width | 6.0            | Phalanx II-3 length | 10.3           |
| Metatarsal III proximal width | 6.0            | Phalanx III-1 length | 7.8            |

- Table 4. Measurements (in mm) of the right pelvic girdle and hindlimb on the lateral cast of the holotype of *Sphodrosaurus pennsylvanicus*. Asterisks indicate incomplete measurements, where the value given is the maximum measurable. The maximum deviation of the digital calliper is 0.02 mm, but measurements were rounded to the nearest 0.1 mm.

- Pubis. The pubis is plate-like without an anterior apron (Fig. 7A; Table 4), as in choristoderans, lepidosauromorphs, most tanystropheids, dinoccephalosaurs, *Jesaioaurus lehmani*, *Trilophosaurus buettneri* and *Doswellia kaltenbachi* (e.g. Sigogneau-Russell 1981; Fraser 1988; Jalil 1997; Dilkes & Sues 2009; Spielmann et al. 2008; Ezcurra 2016; Spiekman et al. 2021). The pubis is a proportionally short bone in *Sphodrosaurus pennsylvanicus*, with a pubis-femur length ratio of 0.32–0.34. Similarly short pubes are also present in non-suchian diapsids (e.g. *Claudiosaurus germani*: Carroll 1981; *Youngina capensis*: Gow 1975), several non-archosauromorph archosauriforms (e.g. *Macrocnemus fuyanensis*: Jiang et al. 2011; *Pamelaria dolichotrachela*: ISIR 316; *Trilophosaurus buettneri*: Spielmann et al. 2008; *Eifelosaurus triadicus*: Sues et al. 2021; *Prolacerta broomi*: BP/1/2676), proterochampsids (e.g. *Tropidosuchus romeri*: PVL 4604; *Chanaresuchus bonaparte*: PVL 4575), some non-suchian pseudosuchians (e.g. *Nundasuchus songaeensis*: Nesbitt et al. 2014; *Parasuchus hislopii*: Chatterjee 1978) and lagerpetid avemetatarsalians (Ezcurra et al. 2020a). The proximal surface for articulation with the ilium is concave.

- Ischium. The single preserved ischium of *Sphodrosaurus pennsylvanicus* is severely damaged, but it can be determined that it is a plate-like bone, as reported by previous authors (Colbert 1960, p. 16) reported that
position of this fourth trochanter closely resemble those of several Triassic eucrocopods (Fig. 7C; e.g. *Dorosuchus neoetus*, *Euparkeria capensis*; Sookias et al. 2014b). Most of the distal end of the femur is covered by matrix, but it can be clearly determined that the medial distal condyle does not project markedly medi ally beyond the shaft, as occurs in lepidosauromorphs, *Cuyosuchus huenei*, *Shansisuchus shansisuchus* and eucrocopods (Nesbitt 2011; Ezcurra 2016). The length of the tibia is approximately 0.69–0.74 times the length of the femur (Fig. 7D; Table 4), a ratio similar to that of several Permo-Triassic diapsids. The proximal end of the tibia is distinctly anteroposteriorly expanded with respect to the shaft, resembling the condition in some eucrocopodan archosauriforms (e.g. *Chanaresuchus bonapartei*: PVL 4575; *Lewisuchus admixtus*: Ezcurra et al. 2020c; *Herrerasaurus ischigualastensis*: PVJ 373). It cannot be determined whether a cnemial crest was present, because most of the proximal surface of the bone is not exposed. The anteromedial surface of the distal region of the tibia is mostly flat, whereas the posteromedial surface is anteroposteriorly convex. The distal end of the tibia is slightly anteroposteriorly expanded, but considerably less than the proximal end, and the distal articular surface is mostly straight and slants slightly anteriorly in medial view, as in *Chanaresuchus bonapartei* (PVL 4575). The medial margin of the tibia is continuously convex in distal view, without any notch or facet for reception of an astragalar process. The rest of the distal surface of the tibia is not exposed.

**Metatarsus.** Metatarsals I, II and III are partially exposed, mainly in ventromedial view (Fig. 8; Table 4). Metatarsal I is a robust element with a strongly asymmetrical distal end, in which the medial condyle is considerably narrower transversely and less distally extended than the lateral one (Fig. 8A: ldc, mdc). This asymmetry should have resulted in a distinctly medially oriented first pedal digit (Sues et al. 1993), and a similar condition is also present in several Triassic archosauriforms (e.g. *Antarctanax shackletoni*: Peecook et al. 2018; *Proterosuchus fergusi*: SAM-PK-K140; *Euparkeria capensis*: UMZC T692; *Chanaresuchus bonapartei*: PVL 4575; *Parasuchus hislopi*: ISIR 42;
Lagerpeton chanarensis: PVL 4619. Metatarsal II is approximately as broad as metatarsal I at their midshafts, contrasting with the presence of a proportionally more robust metatarsal II in proterochampsids (Romer 1972; Arcucci 1990). The anteromedial surface of metatarsal II has a deeply concave surface that extends longitudinally from the proximal margin up to approximately the mid-length of the bone. As a result of this concavity, a flange-like portion of bone extends along the posteromedial margin of the metatarsal II and forms a nearly right-angled inflexion with the rest of the medial margin of the bone in proximal view (Fig. 8B: minf), as in Tropidosuchus romeri (PVL 4601). By contrast, the medial margin of metatarsal II of Chanaresuchus bonapartei (MCZ 4035, PVL 4575) and Gualosuchus reigi (PULR 05) is shallowly concave in proximal view. The distal end of metatarsal II and most of metatarsal III are not exposed.

Figure 9. Strict consensus tree of 5600 most parsimonious trees of 6279 steps found under equal weights.
Pedal phalanges. The first phalanx of digit I, the complete digit II and the first two phalanges of digit III are exposed (Fig. 8A, C; Table 4). Phalanx I-1 has well-developed dorsal and ventral proximal lips, which should have allowed a broad range of flexion and extension of the digit. Phalanx II-2 closely resembles phalanx I-1 in structure, including the presence of a well-developed proximal ventral lip (the dorsal lip is not exposed). The ungual of digit II is longer than the other phalanges of the same digit, as in Azendohsaurus madagaskarensis (Nesbitt et al. 2015), rhynchosaurids (e.g. Mesosuchus browni: SAM-PK-7416; Stenaulorhynchos stockleyi: Huene 1938), proterosuchids (Proterosuchus fergusi: SAM-PK-K140; ‘Chasmatosaurus’ yuani: IVPP V4067) and most proterochampsids (e.g. Proterochampsa barrionuevoi: PVSJ 606; Tropidosuchus romeri: PVL 4601; Chanaresuchus bonapartei: PVL 4575). The only preserved pedal ungual of Sphodrosaurus pennsylvanicus is very slightly recurved and proportionally long, without a distinct flexor tubercle. Immediately distal to the proximal end, the ventral margin of the ungual, below the lateral groove for the claw sheath, expands slightly laterally. As a result, the ventral surface of this area is transversely broader than that of the proximal end. The morphology of this ungual resembles that of proterochampsids (e.g. Proterochampsa barrionuevoi: PVSJ 606), but it seems to be less cylindrical in cross-section.

Phylogenetic analyses
The analysis of the phylogenetic data matrix under equal weights (eqWs) found 5600 MPTs of 6279 steps with a consistency index (CI) of 0.18697 and a retention index (RI) of 0.64183. The strict consensus tree (SCT) generated from these trees is generally well resolved, with only a few polytomies (Fig. 9). The high-level relationships depicted in this SCT are completely congruent with those of previous iterations of this dataset, although there are a few differences regarding the interrelationships of some low-level taxa or species (see Discussion). The species added here to this dataset are well resolved in the SCT: Orovenator mayorum is nested as the sister taxon to all other species with the exception of the species used to root the trees (Petrolacosaurus kansensis). Marmorotta oxoniensis, Feralisaurus corami and Elachistosaurus huenei are found as non-lepidosaurian lepidosauromorphs, Huchuecuetspalli mixtecus is resolved as the sister taxon to Salvador rufescens within Squamata, and Revueltasaurus callenderi is found as the sister taxon to Aetosauria. Regarding Sphodrosaurus pennsylvanicus, this species is recovered as deeply nested within Archosauromorpha and Archosauriformes and as a member of Proterochampsia. Within the latter clade, Sphodrosaurus pennsylvanicus is positioned as the earliest-branching member of Doswelliidae (Fig. 10A). The Bremer support values for Proterochampsia, Proterochampsidae and Doswelliidae are 2 and for the Doswelliidae + Proterochampsidae clade it is 3. The bootstrap frequencies for Proterochampsia, Doswelliidae and the clade Doswelliidae + Proterochampsidae all are less than 30%, but the absolute and GC bootstrap frequencies for Proterochampsidae are slightly higher, being 57% and 44%, respectively.

The analyses under implied weights (IWs) with k = 3 (90 MPTs: fit = 515.34859, CI = 0.18468 and RI = 0.63636), k = 7 (225 MPTs: fit = 351.67111, CI = 0.18641 and RI = 0.64050), and k = 10 (75 MPTs: fit = 287.18019, CI = 0.18644 and RI = 0.64057) show an overall topology of the SCTs very similar to the SCT generated under eqWs. In all these trees, Sphodrosaurus pennsylvanicus is recovered within Proterochampsia and Doswelliidae (Fig. 10B), as was the case in the eqWs analysis. However, a constant difference between the SCTs generated under IWs and that under eqWs is the position of Proterochampsa barrionuevoi as the sister taxon to Doswelliidae (Fig. 10B). Other major differences between the results of these analyses are: (1) the position of Prolacertoides jimusarensis in a polytomy with Allokotosauria and crownward archosauromorphs (IW k = 3) instead of as one of the earliest-branching crocodylomorphs (eqWs, IW k = 7, 10); (2) the position of Asperosaurus myama as an erythrosuchid (IW k = 3) instead of being one of the earliest-branching eucrocodylomorphs (eqWs, IW k = 7, 10); (3) the position of the clade Litopternaturia + Vancleavea campi as the sister taxon to Proterochampsia + crownward archosauriforms (IW k = 3) instead of being early-branching proterochampsians (eqWs, IW k = 7, 10); (4) the position of Polyphodon adorfi + Dorosuchus neoeus as the sister taxa to Euparkeria capensis and crownward archosauriforms (IW k = 3) instead of being an early proterochampsan and an early eucrocodyl, respectively (eqWs, IW k = 7, 10); (5) the position of Phytosauria as the sister taxon to Archosauria (IW k = 3) instead of being the earliest-branching pseudosuchians (eqWs, IW k = 7, 10); (6) the position of Ornithosuchidae as the sister taxon to Gracilisuchidae + Paracrocodylomorpha (IW k = 3) instead of forming a clade with Erpetosuchidae and Aetosauriformes (eqWs, IW k = 7, 10); (7) the position of Ticinosuchus ferox and Youngosuchus sinensis as early-branching poposauroids (IW k = 3 in the case of both taxa and IW k = 7, 10 only for the case of Youngosuchus sinensis) instead of being one of the sister taxa to Paracrocodylomorpha and the earliest-branching Loricata, respectively (eqWs); and (8) the position of...
Figure 10. Time-calibrated subtrees of strict consensus trees showing the interrelationships within Proterochampsia and the phylogenetic position of *Sphodrosaurus pennsylvanicus*. A, subtree found under equal weights; and B, subtree found under implied weights ($k = 10$). Values below each branch are absolute (left) and GC (Group present/Contradicted) (right) bootstrap frequencies, and values above some branches are Bremer supports higher than 1.
the clade *Austriadactylus cristatus* + *Preondactylus bufferinii* as the earliest-branching pterosaurs (IWs $k = 3$) instead of being more deeply nested in the clade (eqWs, IWs $k = 7, 10$).

**Skull width analyses**

The estimated maximum skull width of *Sphodrosaurus pennsylvanicus* accounts for 0.44 times the total length of the presacral series. This value is twice as high as the median for the taxa sampled here for this ratio (mean = 0.2182, standard deviation = 0.1279). The pGLS regressions show that *Sphodrosaurus pennsylvanicus* distinctly departs from the regression lines ($p < 0.0001$ for the 616 regressions using the pruned time-calibrated trees [mbl = 1, 0.5 and 0.1 My] derived from those found under equal weights and the 65 regressions using the pruned time-calibrated trees [mbl = 1, 0.5 and 0.1 My] derived from those found under implied weights; Fig. 11A), with a skull width (59.8 mm) approximately twice the presacral length predicted for the species (28.3–30.6 mm). The high pGLS residual values of *Sphodrosaurus pennsylvanicus* cluster it with species of the hyperodapedontine genus *Hyperodapedon*, which have skull width-presacral length ratios ranging from 0.37–0.42; the proterochampsian *Proterochampsa barrionuevoi* is the only species with a pGLS residual value higher than those of the aforementioned taxa (ratio = 0.61; Fig. 11D). The pGLS regressions between skull width and femur length show fairly congruent results with those reported using presacral length, in which hyperodapedontine rhynchosaurs, *Proterochampsa barrionuevoi*, *Machaeroprosopus pristinus*, rhynchocephalian lepidosauriforms, ‘Chasmatosaurus’ *yuani* and *Sphodrosaurus pennsylvanicus* show the highest values of positive residuals.

The optimization of the skull width-presacral length ratio on the phylogeny found under equal weights (with a traditional monophyletic Proterochampsidae – i.e. *Proterochampsa* + rhadinosaurs) shows a slight increase of the ancestral ratio of Proterochampsia with respect to that of its most recent ancestral node (i.e. Proterochampsia + Archosauria: 0.21–0.25 for the calibration with mbl = 1 My, and 0.19–0.21 for the calibration with mbl = 0.1 My). The high values for *Sphodrosaurus pennsylvanicus* (0.44) and *Proterochampsa barrionuevoi* (0.61) are optimized as independent acquisitions of large skulls from the ancestral conditions of Doswelliidae and Proterochampsidae, respectively, using maximum parsimony (state 1 → states 3 and 4) and maximum likelihood optimality criteria (0.21 [mbl = 0.1 My]0.25 [mbl = 1 My]–0.44 and 0.22 [mbl = 0.1 My]0.27 [mbl = 1 My]–0.61) (Fig. 11C). In the phylogeny found under implied weights (k = 10; in which *Proterochampsa* is recovered as the sister taxon to Doswelliidae) with a maximum likelihood optimization, the ancestral ratio of Proterochampsia increases substantially from the value of its most recent ancestral node (0.21–0.27 [mbl = 1 My], 0.19–0.26 [mbl = 0.1 My]). However, the ancestral ratio of the *Proterochampsa* + Doswelliidae clade shows a very minor increase or does not change with respect to the ancestral condition of Proterochampsia (0.27–0.28 [mbl = 1 My], 0.26–0.26 [mbl = 0.1 My]). Nevertheless, in this scenario, the values of *Sphodrosaurus pennsylvanicus* (0.44) and *Proterochampsa barrionuevoi* (0.61) are also optimized as independent ratio increases from their ancestral conditions (0.26 [mbl = 0.1 My]/0.27 [mbl = 0.1 My]/0.44 and 0.26 [mbl = 0.1 My]/0.28 [mbl = 1 My]/0.61). By contrast, the optimization of the ratio as a discrete character in the phylogeny found under implied weights shows an ambiguous result, in which the condition of *Sphodrosaurus pennsylvanicus* (state 3) could be a retention of the ancestral condition of Doswelliidae or an apomorphy derived from a lower ratio (ambiguous optimization as states 1, 2 and/or 3).

The phylogenetic signal of the skull width-presacral length ratio is significant ($p < 0.05$ for all the alternative methods used to compute phylogenetic signal) for all the analysed trees and both mbl calibration methods (1 My and 0.1 My). A more detailed exploration through each species of the trees found that the phylogenetic signal is significantly strong in tanystropheids and some early dinosaurs (reduced skull widths) and hyperodapedontine rhynchosaurs (increased skulls widths) (Fig. 11B). By contrast, the phylogenetic signal of *Sphodrosaurus pennsylvanicus* (phySig = 0.733–0.954) and *Proterochampsa barrionuevoi* (phySig = 0.991–0.998) is non-significant in all trees. Finally, the phylogenetic correlograms show that the phylogenetic signal of skull width change is lost no more than 10 My after its acquisition during the evolution of the species sampled here.

**Morphospace plot**

The plot of the hindlimb and presacral length variables shows that *Sphodrosaurus pennsylvanicus*, *Proterochampsa barrionuevoi* and *Chanaresuchus bonapartei* are positioned close to each other (Fig. 12A). In particular, the similarity between the former two species is highlighted when considering the skull width to presacral length ratio. Hyperodapedontine rhynchosaurs, which also have very broad skulls, are separated from *Sphodrosaurus pennsylvanicus* and *Proterochampsa barrionuevoi* by a ‘valley’ of lower skull width vs presacral length values (cooler colours in Fig. 12A). Species such as the early archosauromorphs *Chanaresuchus bonapartei*
Re-assessment of the Triassic reptile \textit{Sphodrosaurus}

A

\begin{itemize}
  \item pGLS eqW all trees 1my (slopes: 0.8567-0.8909; p=0.0001)
  \item pGLS IW all trees 1my (slopes: 0.8734-0.8877; p=0.0001)
  \item pGLS eqW all trees 0.5my (slopes: 0.8187-0.8530; p=0.0001)
  \item pGLS IW all trees 0.5my (slopes: 0.8276-0.8377; p=0.0001)
  \item pGLS eqW all trees 0.1my (slopes: 0.6622-0.7556; p=0.0001)
  \item pGLS IW all trees 0.1my (slopes: 0.6566-0.6765; p=0.0001)
\end{itemize}

B

\begin{itemize}
  \item Sphodrosaurus pennsylvanicus
  \item Proterochampsia
  \item Hyperodapedon sanjuanensis
  \item Hyperodapedon hungtify
  \item Hyperodapedon gordonii
  \item Macaeropus pristinus
  \item “Chasmatosaurus” yamii
  \item Parasuchus hislopai
  \item Decuriasuchus quadracolonia
  \item Clausodaurus germani
  \item Youninga capensis
\end{itemize}

C

\begin{itemize}
  \item Sphodrosaurus pennsylvanicus
  \item Proterochampsia
  \item Hyperodapedon sanjuanensis
  \item Hyperodapedon hungtify
  \item Hyperodapedon gordonii
  \item Macaeropus pristinus
  \item “Chasmatosaurus” yamii
  \item Parasuchus hislopai
  \item Decuriasuchus quadracolonia
  \item Clausodaurus germani
\end{itemize}

D

\begin{itemize}
  \item Proterochampsia
  \item Hyperodapedon sanjuanensis
  \item Hyperodapedon hungtify
  \item Hyperodapedon gordonii
  \item Macaeropus pristinus
  \item “Chasmatosaurus” yamii
  \item Parasuchus hislopai
  \item Decuriasuchus quadracolonia
  \item Clausodaurus germani
\end{itemize}
and *Euparkeria capensis* are positioned in this valley. All the other species included in this plot show more dissimilar body proportions with respect to those of *Sphodrosaurus pennsylvanicus*.

**Ungual functional category analysis**

The LDA found that the shape of the preserved pedal ungual of *Sphodrosaurus pennsylvanicus* can be predicted as gryporial with a 99% probability. The second most probable category, scalporial, is considerably less likely (prob = 0.7%). This result is consistent with the graphical exploration of the plots showing the distribution of the linear discriminant axes 1–3 (91.75% of accumulated variance), in which *Sphodrosaurus pennsylvanicus* is positioned close to the convex hulls of the gryporial and scalporial categories (Fig. 12B, C). The confusion matrix shows an overall misidentification of 27.0%, in which only one of the gryporial species was misidentified as scalporial and two of the scalporial species were misidentified as generalist. No species was misidentified as gryporial when it was not. As a result, the identification of the ungual of *Sphodrosaurus pennsylvanicus* as gryporial seems to be a robust result.

**Discussion**

**The phylogenetic relationships of *Sphodrosaurus pennsylvanicus* and other results of the cladistic analyses**

The phylogenetic relationships of *Sphodrosaurus pennsylvanicus* have changed substantially since its initial description as a procolophonid parareptile (Price 1956; Colbert 1960), being subsequently interpreted as a probable rhynchosaur (Baird 1986) and more recently as an indeterminate neodiapsid (Sues et al. 1993). Our results indicate for the first time that *Sphodrosaurus pennsylvanicus* is an archosauromorph and that it belongs to Doswelliidae (Figs 9, 10), a clade that has been previously identified in other Upper Triassic formations of the eastern and south-western United States (Weems 1980; Heckert et al. 2012; Lucas et al. 2013). Thus, the phylogenetic position of *Sphodrosaurus pennsylvanicus* as a doswelliid removes this species as a potentially unusual component of the Triassic vertebrate assemblages of North America. In the eqWs analysis, the position of *Sphodrosaurus pennsylvanicus* within the clade Doswelliidae + Proterochampsidae is supported by the presence of cervical vertebrae with a median longitudinal keel that extends ventral to the centrum rims on at least one anterior cervical vertebra (character 327: 1→2) and pedal unguals of digits II–IV longer than all non-ungual phalanges of the same digit (889: 0→1). *Sphodrosaurus pennsylvanicus* shares with other doswelliids the following synapomorphies: external mandibular fenestra absent (262: 1→0); posterior cervical and anterior dorsal ribs with short tuberculum (347: 1→0); pubis plate-like, with approximately constant transverse width anteroposteriorly (476: 1→0); and pubis without anterior apron (477: 1→0). By contrast, the absence of the following two synapomorphies excludes *Sphodrosaurus pennsylvanicus* from the clade composed of more deeply nested doswelliids: anterior-middle dorsal ribs with sharp flexure close to an angle of 90° between the proximal end and the rib shaft in anterior or posterior view (367: 0→1) and at least some anterior-middle dorsal ribs with lateral surface of the proximal half bearing a rugose ridge or flange (878: 0→1).

Under topological constraints with eqWs, the following numbers of additional steps are necessary to force placement of *Sphodrosaurus pennsylvanicus* into alternative phylogenetic positions: two steps to place it (i) as a proterochampsid (sister taxon to the genus *Proterochampsia*) or (ii) as a non-doswelliid, non-proterochampsid proterochampsian; four steps to place it (iii) within Pseudosuchia (as an early phytosaur) or (iv) as a non-archosauromorph archosauromorph (as the earliest-branching archosauromorph); five steps to place it (v) as the earliest-branching proterochampsian or (vi) within Avemetatarsalia (as the earliest-branching avemetatarsalian or an early pterosauromorph); and seven steps to place it (vii) as a non-proterochampsian, non-archosaurian archosauromorph (as the sister taxon to Proterochampsia + Archosaurus), (viii) as a lepidosauromorph (as a non-lepidosaurian lepidosauromorph), or (ix) as a non-saurian neodiapsid (as the sister taxon to Sauria). As a result, the phylogenetic position of *Sphodrosaurus pennsylvanicus* as a proterochampsian is
Figure 12. Morphospace plot and results of the linear discriminant (LD) analysis of ungual functional categories. A, morphospace built from a bivariate plot of log10(femoral length/tibial length) vs log10(femoral length + tibial length/presacral length) and adding a heatmap showing the log10(skull width/presacral length); B, bivariate plot of LD2 vs LD1; and C, bivariate plot of LD3 vs LD1.

Re-assessment of the Triassic reptile *Sphodrosaurus*
relatively well supported by our dataset and non-archosauromorph affinities are distinctly sub-optimal.

Contrasting with the eqWs results, the analyses under IWs found the genus Proterochampsia as the sister taxon to Doswelliidae (Fig. 10B), matching some recent results under a Bayesian framework (Wynd et al. 2019; see below) based on the presence of the following synapomorphies: strongly dorsoventrally compressed skull with mainly dorsally facing antorbital fenestrae and orbits (3: 0→1); foramina for the entrance of the cerebral branches of the internal carotids on the ventral surface of the bone close to the suture between basioccipital and parabasiphenoid (241: 0→1); axis with dorsoventrally very low neural spine (328: 0→1); jugal with height below the most ventral level of the orbit equal to or greater than half of the maximum height of the orbit in lateral view (625: 0→1); surangular-angular with distinct coarse ornamentation on the lateral surface (861: 0→1; present in Sphodrosaurus pennsylvanicus); and prearticular with ventral margin posterior to its contact with the splenial straight or ventrally curved on the anterior half of the bone in medial/lateral view (868: 1→0, present in Sphodrosaurus pennsylvanicus). By contrast, Proterochampsia is excluded from Doswelliidae (i.e. the clade composed of Sphodrosaurus pennsylvanicus and more deeply nested doswelliids) by the absence of the following synapomorphies: external mandibular fenestra absent (262: 1→0), posterior cervical and anterior dorsal ribs with short tuberculum (347: 1→0), and pubis without anterior apron (477: 1→0). The absolute bootstrap frequencies of the clade Proterochampsia + Doswelliidae are similar (21–24%) under the three different concavity constants tested here, but the GC bootstrap frequencies get sequentially more negative values (2% to −8% to −16%) when the k values are increased. This indicates that a higher penalization of homoplasy results in lower conflictive evidence for the clade. The branch supports for the clade Proterochampsia + Doswelliidae are always very low and those of a monophyletic Proterochampsidae under eqWs are considerably higher.

The vast majority of the differences between eqWs and IWs occur only when using a very low concavity constant (k = 3) and, thus, a strong downweighting of homoplasy. As a consequence, these results should be taken as extreme cases, but an exception is the position of the genus Proterochampsia as the sister taxon to Doswelliidae because it occurs with the three different k values tested here.

Beyond the interrelationships within Proterochampsia, the expansion and modifications in the phylogenetic matrix produced some different results in comparison to those reported in previous versions of this data set (Fig. 9). The main differences are the following (present in all trees under eqWs and IWs unless otherwise stated): (1) the non-saurian neodiapsids Hovasaurus boulei and Acratospondylus piveaeui are sister taxa to each other (which would represent a monophyletic Tangasauridae, although Tangasaurus mennelli is not included in the data set to test this hypothesis) instead of in a polytomy with Youngina capensis (contra Ezcurra et al. 2022); (2) Paliguana whitei is recovered as the sister taxon to a clade comprising Marmoretta oxoniensis + Fraxinisaura rozynekae + more crownward lepidosauromorphs instead of being the sister taxon to Fraxinisaura rozynekae (contra Ezcurra et al. 2022); (3) the Permian archosauromorphs Aenigmastreps parringtoni and Proterosaurus speneri are found as sister taxa to each other instead of these species being successive sister taxa to more deeply nested archosauromorphs (contra Ezcurra 2016); (4) Prolacertoides jimarsarensis is recovered as one of the earliest-branching crocopods (but under IWs k = 3 it is found as an early allokotosaurian or sister taxon to Allokotosauria + crownward archosauromorphs) and not as a member of the clade Jesairosaurus + Dinocephalosaurus + Tianystropheidae or an early allokotosaurian (contra Ezcurra 2016); (5) Boreoprica funerea is found as the earliest-diverging prolacertid and not as the sister taxon to Prolacertidae + more crownward archosauromorphs (contra Ezcurra 2016, but this position is recovered under IWs k = 3); and (6) Youngosuchus sinensis is positioned as the earliest-branching loricatan instead of being the sister taxon to all other poposauroids (contra Ezcurra et al. 2017; but the poposauroid affinities are recovered in all the trees under IWs). The assessment of these different phylogenetic positions goes beyond the scope of this study and will be discussed elsewhere.

The enigmatic Triassic neodiapsids Feralisaurus corami and Elachistosuchus huenei were included in the CoArTreeP data set for the first time here (Fig. 9). Feralisaurus corami was recovered in previous phylogenetic analyses as a non-saurian neodiapsid or as a non-lepidosaurian lepidosauromorph, and the authors of the original description of this species preferred the latter hypothesis based on the morphology of the specimen (Cavicchini et al. 2020). Our results support the assignment of Feralisaurus corami to Lepidosauromorpha and outside Lepidosauria. However, under sub-optimal topological constraints, only one additional step forces the position of Feralisaurus corami as a non-saurian neodiapsid, but five steps are necessary to place this species within Archosauromorpha (as its earliest-branching member). In the case of Elachistosuchus huenei, previous analyses of its phylogenetic relationships recovered
conflicting results, as a pseudosuchian archosaur (Janensch 1949), a rhynchocephalian (Walker 1966), a non-lepidosaurian lepidosauromorph (as the sister taxon to Choristodera), a non-saurian neodiapsid or a non-archosauromorph archosauroomorph (Sobral et al. 2015). The results of our study favour the lepidosauroomorph hypothesis, but the branch support for the clade that includes Elachistosuchus huenei and other lepidosauroomorphs is very weak (minimum Bremer support and bootstrap frequencies <10% under eqWs). Indeed, only one additional step forces the placement of Elachistosuchus huenei as the earliest-branching archosauroomorph, and two extra steps places it as a choristoderan outside of Sauria. These alternative, slightly sub-optimal results are congruent with those recovered by Sobral et al. (2015). As a result, the phylogenetic relationships of both Feralisaurus corami and Elachistosuchus huenei remain extremely poorly supported in the context of our dataset, although the archosauroomorph affinities of the former species are definitely sub-optimal.

Is the skull of Sphodrosaurus pennsylvanicus autapomorphically large?

Our revision of the anatomy of Sphodrosaurus pennsylvanicus shows that this species can be easily distinguished from other archosauroomorphs (see Diagnosis). Our analyses also demonstrate that Sphodrosaurus pennsylvanicus does have a proportionately larger skull than the vast majority of Permo–Triassic diapsids (Figs 11A, C, 12A), considering the length either of the presacral vertebral series or of the femur as proxies for postcranial size, as claimed by previous authors (Colbert 1960; Sues et al. 1993). However, the condition of Sphodrosaurus pennsylvanicus is not unique among archosauroomorphs, as it is paralleled by hyperodapedontine rhynchosaurs (e.g. Chatterjee 1974; Benton 1983) and the proterochampsian Proterochampsia barrionuevoi (Trotteyn 2011) (Figs 11D, 12A). Although Sphodrosaurus pennsylvanicus and Proterochampsia barrionuevoi are found to be closely related to each other (both as members of Proterochampsia), most phylogenetic scenarios and optimization methods indicate that the two species developed unusually broad skulls independently (e.g. Fig. 11C). In addition, a considerably lower proportional skull width increase is also recovered at the base of Proterochampsia in several of our analyses. Nevertheless, if the genus Proterochampsia is the sister taxon to Doswelliidae, one possible scenario is that a skull as broad as that of Sphodrosaurus pennsylvanicus would be ancestral for this family and Doswellia kaltenbachi has an autapomorphically narrower skull. As a consequence, the results of our analyses indicate the most likely hypothesis is that the extremely broad skull of Sphodrosaurus pennsylvanicus is autapomorphic.

Do proterochampsid skull widths show positive interspecific allometry?

Regarding the relative size of the skull of proterochampsids (considering a monophyletic Proterochampsidae), Proterochampsia barrionuevoi is the largest known species and has the proportionally largest skull, whereas the smallest species, Tropicodus romeri and Pseudochampsa ischigualastensis, have proportionally smaller skulls. Thus, it can be argued that the relationship between skull width and presacral length has a positive allometry in proterochampsids. However, Cerritosaurus binsfeldi is one of the smallest known proterochampsids (Pradelli et al. 2022) and it seems to have a relatively large skull. The holotype and only known specimen of Cerritosaurus binsfeldi preserves a complete skull articulated to 15 presacral vertebrae (Trotteyn et al. 2013). The skull width is 52.7 mm and the preserved presacral vertebral length is 80.1 mm. If we assume a complete presacral vertebral series composed of 24 vertebrae, as in other proterochampsids (e.g. MCZ 4037), the estimated presacral length of Cerritosaurus binsfeldi would be c. 127 mm (based on the length of the preserved anterior-middle dorsal vertebrae). This estimate results in a skull width-presacral length ratio of 0.41, which is considerably higher than the ratio in Chanaresuchus bonapartei (0.20: PVL 4575, with skull width of 91.4 mm). The pGLS regressions between the skull width and presacral length of proterochampsids, including Cerritosaurus binsfeldi, are not significant (p = 0.2134 – 0.5452 using the three different mbl values), and Cerritosaurus binsfeldi and Proterochampsia barrionuevoi represent clear outliers above the regression lines (see Supplemental material 3). Indeed, the pGLS residual of Cerritosaurus binsfeldi in the regression using the time-calibrated tree with mbl of 1 My is considerably higher (0.12) than those of other proterochampsids (–0.08 to –0.32), with the exception of the very high value for Proterochampsia barrionuevoi (0.40). In the regression using an mbl of 0.1 My, the pGLS residual of Cerritosaurus binsfeldi (0.11) is very similar to that of Chanaresuchus bonapartei (0.09), and considerably lower than that of Proterochampsia barrionuevoi (0.61). In conclusion, we reject here the hypothesis of positive interspecific allometry in the skull size of proterochampsids. Instead, it seems that the earliest-branching proterochampsids (Proterochampsia barrionuevoi and Cerritosaurus binsfeldi) have proportionally larger skulls and that this has more to do with phylogeny than with scaling related to the overall body size of the species.
Implications for the taxonomic content and evolutionary history of Doswelliidae and Proterochampidae

The identification of *Sphodrosaurus pennsylvanicus* as a doswelliid adds a new species to this clade (Fig. 10). The first version of the phylogenetic dataset of the CoArTreeP recovered *Vancleavea campi* as the earliest-branching member of Doswelliidae (Ezcurra 2016), but analyses of more recent iterations of this data set found *Vancleavea campi* and its sister taxon, *Litorosuchus somnii*, within Proterochampsidae but outside the Doswelliidae + Proterochampidae dichotomy (e.g. Wynd et al. 2019; Ezcurra et al. 2020a; Trotteyn & Ezcurra 2020). An independent phylogenetic dataset alternatively recovered *Doswella kaltenbachi* as more closely related to Archosauria than to the clade *Vancleavea campi* + *Litorosuchus somnii* (Li et al. 2016). However, it should be noted that the character and taxon sampling of the latter matrix is poorer than that of the CoArTreeP for this part of the tree. As a result, the position of *Vancleavea campi* and *Litorosuchus somnii* within Doswelliidae seems unlikely based on current available information and is considerably sub-optimal in our analyses. The gracile and long-limbed reptile *Scleromochlus taylori* has been recently recovered as a doswelliid (Bennett 2020). However, this hypothesis has been found strongly sub-optimal in a more recent revision of its phylogenetic relationships, and *Scleromochlus taylori* has been recovered as the earliest-branching pterosauromorph (Ezcurra et al. 2020a). As a consequence, our study increases the known taxonomic richness of Doswelliidae to at least five nominal species: *Jaxtasuchus salomoni*, *Doswella kaltenbachi*, *Rugarhynchos sixmilensis*, *Ankylosuchus chinlegroupensis* and *Sphodrosaurus pennsylvanicus*.

The phylogenetic placement of *Proterochampsidae barrionuevoi* seems to be more problematic (Fig. 10). This species and *Proterochampsidae nodosa* have historically been grouped with *Cerritosaurus binsfeldi*, *Chanaresuchus bonapartei* and *Gualosuchus reigi* in a monophyletic *Proterochampidae* (see Trotteyn et al. 2013). However, recent studies have found an alternative hypothesis in which *Proterochampsidae* is the sister taxon to Doswelliidae, using a Bayesian inference analysis under rate heterogeneity (gamma distribution, with four rate categories, = Mk + G4 model; Wynd et al. 2019) and using a maximum parsimony analysis under IWS (Trotteyn & Ezcurra 2020); the maximum parsimony analyses under eqWs of these same datasets recovered a monophyletic *Proterochampidae*. Thus, downweighting the influence of homoplastic characters favours the position of the genus *Proterochampsidae* as the sister taxon to Doswelliidae under both maximum parsimony and model-based phylogenetic analyses.

Our phylogenetic analyses repeated the same results found by Trotteyn & Ezcurra (2020) under eqWs and IWS. However, in our phylogenetic analysis under IWS (k = 10), the absolute bootstrap frequencies of the clade *Proterochampsidae* + Doswelliidae remained virtually unchanged after the *a priori* exclusion of *Sphodrosaurus pennsylvanicus* (21% vs 25%), but the GC bootstrap frequencies changed from −25% to −16% after the inclusion of *Sphodrosaurus pennsylvanicus*. This indicates that the inclusion of *Sphodrosaurus pennsylvanicus* decreases the amount of conflicting information in support of the clade *Proterochampsidae* + Doswelliidae. Similarly, under equal weights, two additional steps are necessary to force the clade *Proterochampsidae* + Doswelliidae when including *Sphodrosaurus pennsylvanicus*, but three extra steps are required if *Sphodrosaurus pennsylvanicus* is excluded *a priori*. Thus, the anatomical information provided by *Sphodrosaurus pennsylvanicus* seems to reduce to some degree the anatomical gap between doswelliids and Proterochampsidae, and the non-monophyly of a traditional Proterochampidae seems to be more likely than before. However, additional information about doswelliid anatomy and early proterochampsians is needed to shed more light on the phylogenetic relationships of *Proterochampsidae*.

With the exception of *Jaxtasuchus salomoni* from the late Middle Triassic (late Ladinian) of Germany, all of the currently recognized doswelliid species are from late Triassic formations of the United States. The *Sphodrosaurus pennsylvanicus*-bearing Hammer Creek Formation is dated as late early to early middle Norian, thus being stratigraphically younger than the late Carnian strata that yielded the specimens of *Doswella kaltenbachi* (Dilkes & Sues 2009). *Ankylosuchus chinlegroupensis* is assigned to the Otischalkian land-vertebrate faunachron and thus dated close to the Carnian–Norian boundary (<221.76 ± 0.23 Ma, based on a date close to the base of the Blue Mesa Member of the Chinle Formation; Rasmussen et al. 2021). *Rugarhynchos sixmilensis* comes from the ‘Bluwater Creek Formation’, which correlates to the uppermost Blue Mesa Member up to the middle Sonsela Member of the Chinle Formation (Ramezani et al. 2014), and thus it is approximately constrained to 220.54 ± 0.96–215.67 ± 0.67 Ma (Rasmussen et al. 2020). As a result, the chronostratigraphic uncertainty of *Sphodrosaurus pennsylvanicus* probably overlaps those of *Ankylosuchus chinlegroupensis* and *Rugarhynchos sixmilensis*, the youngest known doswelliids (Fig. 10).
The biochron of *Proterochampsia barrionuevoi* is dated to within 231.4 ± 0.3 to 227.24 ± 1.27, –1.97 Ma (Rogers et al. 1993; Desojo et al. 2020) and, thus, it potentially overlaps the chronostratigraphic uncertainties of *Sphodrosaurus pennsylvanicus*, *Doswellia kaltenbachi* and *Ankylosuchus chinlegroupensis* (Fig. 10). If the genus *Proterochampsa* belongs to a traditionally monoplyhetic Proterochampsidae, this means that proterochampsids became extinct (or their currently known youngest records occur) at least five million years before the youngest doswelliid occurrence. On the other hand, if *Proterochampsa* is the sister taxon to Doswelliidae, its biochron would be congruent with those of doswelliids, but it would be the only evidence that the lineage that led to this clade also evolved in south-eastern Pangaea.

The anatomy of *Sphodrosaurus pennsylvanicus* in the context of the proterochampsian body plan

*Sphodrosaurus pennsylvanicus* and *Proterochampsia barrionuevoi* have broader skulls than other Permo–Triassic diapsids with a similar snout-vent length, and this should have important palaeobiological implications. For example, bite force correlates with head size in at least some extant reptiles (e.g. scincid and lacertid lizards; Verwaijen et al. 2002; Le Guilloux et al. 2020), and it has been reported that proportionally large heads might be advantageous during agonistic competitive intra-specific interactions (Wegener et al. 2019). However, the largely unknown skull structure of *Sphodrosaurus pennsylvanicus* prevents us from further discussing the possible function(s) of its broad skull. Regarding the rest of the body, the partially preserved postcranium of *Sphodrosaurus pennsylvanicus* also limits the number of comparisons that can be made with other taxa, being mostly restricted to the presacral vertebral series and hind limb. The morphospace plot shows that the body proportions of *Sphodrosaurus pennsylvanicus* are similar to those of *Proterochampsia barrionuevoi*, including the presence of a relatively short posterior stylodipodium and zeugopodium in relation to the presacral length and a longer femur than tibia in addition to the proportionally very broad skull (Fig. 12A).

Beyond the measurements included in the morphospace plot, the presence in *Sphodrosaurus pennsylvanicus* of a proportionally short pubis and an incipiently recurved and long pedal ungual also closely resembles the condition in *Proterochampsia barrionuevoi*. In particular, the only available pedal ungual of *Sphodrosaurus pennsylvanicus* (Fig. 8A, C) has been identified by the LDA as gryporial or much less likely scalporial among the functional categories of Thomson & Motani (2021). Gryporial unguals are adapted for hook-and-pull digging (extant examples are most anteaters and armadillos), whereas scalporial unguals are adapted for scratch-digging (extant examples are pangolins, meerkats and aardvarks) (Thomson & Motani 2021). As a consequence, the LDA robustly identifies the ungual of *Sphodrosaurus pennsylvanicus* as adapted for substrate processing (likely digging). A similar function could also be inferred for *Proterochampsia barrionuevoi* and other proterochampsids because of their pedal ungual morphology (see Trotteyn 2011), which is very similar to that of *Sphodrosaurus pennsylvanicus*.

Our observations and analyses indicate that *Sphodrosaurus pennsylvanicus* and *Proterochampsia barrionuevoi* probably occupied a similar ecological role in their respective palaeocommunities. *Proterochampsia barrionuevoi* has been historically interpreted as a semi-aquatic animal based on its cranial features (e.g. dorsally facing external nares and orbits, long rostrum, strongly ornamented external bone surfaces; Reig 1959; Sill 1967; Romer 1971) and this hypothesis is still broadly supported (Arcucci 2011; Trotteyn 2011; Trotteyn et al. 2013). In particular, the more recent description of a fairly complete skeleton of *Proterochampsia barrionuevoi* has confirmed the proportionally huge size of the skull (see Results; Trotteyn 2011) and may support the semi-aquatic hypothesis. As a result, semi-aquatic life habits could be hypothesized for *Sphodrosaurus pennsylvanicus* based on its similarities to *Proterochampsia barrionuevoi*. However, a more complete specimen of *Sphodrosaurus pennsylvanicus* is needed to test this hypothesis properly and shed more light on the mode of life of this species.

In conclusion, our results suggest that both *Sphodrosaurus pennsylvanicus* and *Proterochampsia barrionuevoi* could have been semi-aquatic reptiles that were able to swallow relatively large prey (if *Sphodrosaurus pennsylvanicus* was actually a predatory form) and were adapted for digging or at least using their hind limbs to process the substrate in some way. A semi-aquatic life habit is congruent with previous inferences for other proterochampsian species (Romer 1972; Bonaparte 1978; Weems 1980; Sues et al. 2013; Schoch & Sues 2014; Wynd et al. 2019). Nevertheless, a more terrestrial habit has been recently suggested at least for rhadinosuchine proterochampsids, because of the absence of clear evidence supporting a locomotor style associated to a semi-aquatic behaviour and palaeohistological features associated to semi-aquatic forms (Arcucci et al. 2019; Ezcurra et al. 2021c). There is a substantial disparity in the proterochampsian body plan: long-limbed (*Pseudochampsa ischigualastensis*) to short-limbed forms (*Chanaresuchus bonapartei*), species...
with a posterior zeugopodium as long as the stylodactylum (*Tropidosuchus romeri*) to ones with a proportionally very short zeugodactylum (*Sphodrosaurus pennsylvanicus* and *Proterochampsia barrionuevoi*), and large-headed forms (*Sphodrosaurus pennsylvanicus* and *Proterochampsia barrionuevoi*) to relatively small-headed forms (*Pseudochampsia ischiguastensis*) (Fig. 12A). Thus, it seems that there was a variety of lifestyle strategies among proterochampsians, possibly including different feeding behaviours and habitats ranging from semi-aquatic (e.g. *Proterochampsia* and *doswelliids*) to more terrestrial (e.g. *Tropidosuchus romeri* and rhadinosuchine proterochampsids).

### Supplemental material

Supplemental material for this article can be accessed here: https://doi.org/10.1080/14772019.2022.2057820. The data that support the findings of this study are openly available in Zenodo here: https://doi.org/10.5281/zenodo.5879789.

### Acknowledgements

The phylogenetic analysis was performed with TNT v. 1.5, a program made freely available through the Willi Hennig Society. This research was supported by Agencia Nacional de Promoción Científica y Tecnológica in the context of the Complete Archosauromorph Tree Project (CoArTreeP) [PICT 2018-01186 to MDE]. We thank Arjan Mann and Tom Dudgen for providing the files and code for the ungal category functional analysis. Peter Kroeher prepared the excellent latex peels of the holotype of *Sphodrosaurus pennsylvanicus*. We thank the reviewers Stephan Spiekman and Brenen Wynd and the editor Richard Butler for their suggestions and comments.

### ORCID

- **Martín D. Ezcurra** http://orcid.org/0000-0002-6060-6450
- **Hans-Dieter Sues** http://orcid.org/0000-0002-9911-7254

### References

Adams, D. C., Colyer, M. L., Kaliontzopoulou, A. & Balken, E. K. 2021. Geomorph: software for geometric morphometric analyses. *R* package version 4.0. Updated at: https://cran.r-project.org/package=geomorph, accessed 15 February 2022.

Akima, H. & Gebhardt, A. 2021. akima: interpolation of irregularly and regularly spaced data. *R* package version 0.6-2.2. Updated at: https://CRAN.R-project.org/package=akima, accessed 15 February 2022.

Arcucci, A. B. 1990. Un nuevo Proterochampsidae (Reptilia – Archosauriformes) de la fauna local de Los Chanares (Triásico Medio), La Rioja, Argentina. Ameghiniana, 27, 365–378.

Arcucci, A. B. 2011. Sistemática y filogenia de los proterochampsidos (Amniota, Diápida, Archosauriformes) del Triásico de América del Sur, y sus implicancias en el origen de Archosauromorpha. Unpublished PhD thesis, Universidad Nacional de San Luis, 302 pp.

Arcucci, A. B., Prevéria, M. E. & Mancuso, A. C. 2019. Ecomorphology and bone microstructure of Proterochampsia from the Chanares Formation. *Acta Palaeontologica Polonica*, 64, 157–170.

Baczko, M. B. von & Desojo, J. B. 2016. Cranial anatomy and palaeoneurology of the archosaur *Riojasuchus tenuisceps* from the Los Colorados Formation, La Rioja, Argentina. *PLoS ONE*, 11, e0148575. doi:10.1371/journal.pone.0148575

Baczko, M. B. von, Desojo, J. B. & Ponce, D. 2019. Postcranial anatomy and osteoderm histology of *Riojasuchus tenuisceps* and a phylogenetic update on Ornithosuchidae (Archosauria, Pseudosuchia). *Journal of Vertebrate Paleontology*, 39, e1693396. doi: 10.1080/02724634.2019.1693396

Baird, D. 1986. Some Upper Triassic reptiles, footprints, and an amphibian from New Jersey. *The Mosasaur*, 3, 125–153.

Bapst, D. W. 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, 3, 803–807.

Bennett, S. C. 2020. Reassessment of the Triassic archosauriform *Scleromochlus taylori* and a phylogenetic update on Ornithosuchidae (Archosauria, Pseudosuchia). *Palaeontologica Polonica*, 77, 153–170.

Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London B*, 302, 605–717.

Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84, 97–164.

Benton, M. J. & Walker, A. D. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zoological Journal of the Linnean Society*, 136, 25–47.

Bona, P., Fernandez Blanco, M. V., Ezcurra, M. D., Baczko, M. B. von, Desojo, J. B. & Pol, D. 2022. On the homology of crocodylian post-dentary bones and their macroevolution throughout Pseudosuchia. *The Anatomical Record*. doi:10.1002/ar.24873

Bonaparte, J. F. 1971. *Cerroitosaurus binsfeldi* Price, tipo de una nueva familia de tecodontes (Pseudosuchia – Proterochampsia). *Anais da Academia Brasileira de Ciências*, 43, 417–422.

Bonaparte, J. F. 1978. El Mesozoico de América del Sur y sus tetrapodos. *Opera Lilloana*, 26, 1–596.

Brusatte, S. L., Nesbitt, S. J., Irms, R. B., Butler, R. J., Benton, M. J. & Norell, M. A. 2010. The origin and
early radiation of dinosaurs. *Earth-Science Reviews*, 101, 68–100.

**Butler, R. J., Ezcurra, M. D., Liu, J., Sookias, R. B. & Sullivan, C.** 2019a. The anatomy and phylogenetic position of the erythrosuchid archosauriform *Guchengosuchus shiguaiensis* from the earliest Middle Triassic of China. *PeerJ*, 7, e6435. doi:10.7717/peerj.6435

**Butler, R. J., Sennikov, A. G., Dunne, E. M., Ezcurra, M. D., Hedrick, B. P., Maidment, S. C., Meade, L. E., Raven, T. J. & Gower, D. J.** 2019b. Cranial anatomy and taxonomy of the erythrosuchid archosauriform *Vjushkovia triplicostata* Huene, 1960, from the Early Triassic of European Russia. *Royal Society Open Science*, 6, 191289. doi:10.1098/rsos.191289

**Carroll, R. L.** 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London, B*, 293, 315–383.

**Cavicchini, I., Zaher, M. & Benton, M. J.** 2020. An enigmatic neodiapsid reptile from the Middle Triassic of England. *Journal of Vertebrate Paleontology*, 40, e1781143. doi:10.1080/07380590.2020.1781143

**Chatterjee, S.** 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London, B*, 267, 209–261.

**Chatterjee, S.** 1978. A primitive parasauchid (pterosaur) reptile from the Upper Triassic Maleri Formation of India. *Paleontologia africana*, 24, 99–168.

**Dalla Vecchia, F. M.** 2014. Gli pterosauri triassici. *Pubblicazione del Museo Friulano di Storia Naturale*, 54, 1–319.

**Desojo, J. B., Fiorelli, L. E., Ezcurra, M. D., Martinelli, A. G., Ramezani von, A. A., Baczko, M. B., Trotteny, M. J., Montefeltro, F. C., Ezpeleta, M. & Langer, M. C.** 2020. The Late Triassic Ichiguialast Formation at Cerro Las Lajas (La Rioja, Argentina): fossil tetrapods, high-resolution chronostratigraphy, and faunal correlations. *Scientific Reports*, 10, 12782. doi:10.1038/s41598-020-67854-1

**Dilkes, D. W. & Sues, H.-D.** 2009. Redescription and phylogenetic relationships of *Dodswilia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology*, 29, 58–79.

**Dilkes, D. W. & Arcucci, A. B.** 2012. Redescription of *Proterochampsia barinaveoi* (Archosauromorpha: Proterochampsidae) from the Late Triassic of Argentina and a new diagnosis of Proterochampsidae. *Palaeontology*, 55, 858–885.

**Evans, S. E.** 1980. The skull of a new eusauroid reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society*, 70, 203–264.

**Evans, S. E. & Jones, M. E. H.** 2010. The origins, early history and diversification of lepidosauriform reptiles. Pp. 27–44 in S. Bandyopadhyay (ed.) *New aspects of Mesozoic biodiversity*. Lecture Notes in Earth Science, 132. Springer, Berlin, Heidelberg.

**Ezcurra, M. D.** 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ*, 4, e1778. doi:10.7717/peerj.1778

**Ezcurra, M. D., Scheyer, T. M. & Butler, R. J.** 2014. The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. *PLoS ONE*, 9, e89165. doi:10.1371/journal.pone.0089165

**Ezcurra, M. D., Fiorelli, L. E., Martinelli, A. G., Rocher, S., Baczko, M. B. von, Ezpeleta, M., Taborda, J. R. A., Hechenleitner, E. M., Trotteny, M. J. & Desojo, J. B.** 2017. Deep faunistic turnovers preceded the rise of dinosaurs in southwestern Pangaea. *Nature Ecology & Evolution*, 1, 1477–1483.

**Ezcurra, M. D. & Butler, R. J.** 2018. The rise of the ruling reptiles and ecosystem recovery from the Permo–Triassic mass extinction. *Proceedings of the Royal Society B*, 285, 20180361. doi:10.1098/rspb.2018.0361

**Ezcurra, M. D., Gower, D. J., Sennikov, A. G. & Butler, R. J.** 2019. The osteology of the holotype of the early erythrosuchid *Garjainia prima* Ochnev, 1958 (Diapsida: Archosauromorpha) from the upper Lower Triassic of Europe Russia. *Zoological Journal of the Linnean Society*, 185, 717–783.

**Ezcurra, M. D., Nesbitt, S. J., Bronzati, M., Dalla Vecchia, F. M., Agnolin, F. L., Benson, R. B. J., Brignon Eglì, F., Cabreira, S. F., Evers, S. W., Gentil, A. R., Irmis, R. B., Martinelli, A. G., Novas, F. E., Roberto da Silva, L., Smith, N. D., Stocker, M. R., Turner, A. H. & Langer, M. C.** 2020a. Enigmatic dinosaur precursors bridge the gap to the origin of Pterosauria. *Nature*, 588, 445–449.

**Ezcurra, M. D., Fiorelli, L. E., Trotteny, M. J., Martinelli, A. G. & Desojo, J. B.** 2020b. The rhynchosaur record, including a new stenaulorhynchine taxon, from the Chaiares Formation (upper Ladinian–?lowermost Carnian levels) of La Rioja Province, north-western Argentina. *Journal of Systematic Palaeontology*, 18, 1907–1938.

**Ezcurra, M. D., Nesbitt, S. J., Fiorelli, L. E. & Desojo, J. B.** 2020c. New specimen sheds light on the anatomy and taxonomy of the early Late Triassic dinosauriforms from the Chaiares Formation, NW Argentina. *The Anatomical Record*, 303, 1393–1438.

**Ezcurra, M. D., Jones, A. S., Gentil, A. R. & Butler, R. J.** 2021a. Early archosauromorphs: the crocodile and dinosaur precursors. Pp. 175–185 in D. Alderton & S. A. Elias (eds) *Encyclopedia of geology. Volume 4*. Second Edition. Academic Press, London, UK.

**Ezcurra, M. D., Bandyopadhyay, S. & Gower, D. J.** 2021b. A new erythrosuchid archosauriform from the Middle Triassic Yerrapalli Formation of south-central India. *Amegebhiniana*, 58, 132–168.

**Ezcurra, M. D., Montefeltro, F. C., Pinheiro, F. L., Trotteny, M. J., Gentil, A. R., Lehmann, O. E. & Pradelli, L. A.** 2021c. The stem-archosaur evolutionary radiation in South America. *Journal of South American Earth Sciences*, 105, 102935.

**Ezcurra, M. D., Bandyopadhyay, S. & Sen K.** 2022. A new faunistic component of the Lower Triassic Panchet Formation of India increases the continental non-archosauromorph neodiapsid record in the aftermath of the end-Permian mass extinction. *Journal of Paleontology*, 96, 428–438.

**Ford, D. P. & Benson, R. B.** 2019. A redescription of *Orovenator mayorum* (Sauropsida, Diapsida) using high-resolution µCT, and the consequences for early amniote
phylogeny. *Papers in Palaeontology, 5*, 197–239. doi:10.1002/spp2.1236

Fraser, N. C. 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London, B*, 321, 125–178.

Fraser, N. C. & Rieppel, O. 2006. A new protorosaur (Diapsida) from the Upper Buntsandstein of the Black Forest, Germany. *Journal of Vertebrate Paleontology, 26*, 866–871.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences, 8*, 1–55.

Gauthier, J. A. 2020a. Archosauromorpha. Pp. 1183–1192 in K. de Queiroz, P. D. Cantino & J. A. Gauthier (eds) *Phylonyms: a companion to the PhyloCode*. CRC Press, Boca Raton.

Gauthier, J. A. 2020b. Archosauriformes. Pp. 1183–1185 in K. de Queiroz, P. D. Cantino & J. A. Gauthier (eds) *Phylonyms: a companion to the PhyloCode*. CRC Press, Boca Raton.

Gauthier, J. A., Kluge, A. G. & Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics, 4*, 105–209.

Gauthier, J. A. & de Queiroz, K. 2020. Diapsida. Pp. 1033–1040 in K. de Queiroz, P. D. Cantino & J. A. Gauthier (eds) *Phylonyms: a companion to the PhyloCode*. CRC Press, Boca Raton.

Gentil, A. R. & Ezcurra, M. D. 2022. Skull osteology of the holotype of the rhynchosaur *Hyperodapedon sanjuanensis* (Sill, 1970) from the Upper Triassic Ischigualasto Formation of Argentina. *The Anatomical Record, 305*, 1168–1200.

Goloboff, P. A., Farris, J. S., Källersjö, M., Oxelman, B., Ramirez, M. N. J. & Szumik, C. A. 2003. Improvements to resampling measures of group support. *Cladistics, 19*, 324–332.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics, 24*, 774–786.

Goloboff, P. A. & Catalano, S. A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics, 32*, 221–238.

Gottmann-Quesada, A. & Sander, P. M. 2009. A redescriptions of the early archosauromorph *Protosaurus sneri* (Meyer, 1832) and its phylogenetic relationships. *Palaeontographica Abteilung A, 287*, 123–220.

Gow, C. E. 1975. The morphology and relationships of *Yungania capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia africana, 18*, 89–131.

Gower, D. J. 1999. Cranial osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde, Series B, 280*, 1–49.

Gower, D. J. 2003. Osteology of the early archosauromorph reptile *Erythrosuchus africanus* Broom. *Annals of the South African Museum, 110*, 1–84.

Gower, D. J. & Sennikov, A. G. 1997. *Sarmatosuchus* and the early history of the Archosauria. *Journal of Vertebrate Paleontology, 17*, 60–73.

Gower, D. J. & Schoch, R. 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kuperzellenensis*. *Journal of Vertebrate Paleontology, 29*, 103–122.

Gower, D. J. Hancox, P. J., Botha-Brink, J., Sennikov, A. G. & Butler, R. J. 2014. A new species of *Garjainia Ochev*, 1958 (Diapsida: Archosauromorphes: Erythrosuchidae) from the Early Triassic of South Africa. *PLoS ONE, 9*, e111154. doi:10.1371/journal.pone.0111154

Heckert, A. B., Lucas, S. G. & Spielmann, J. A. 2012. A new species of the enigmatic archosauriform *Doswellia* from the Upper Triassic Bluewater Creek Formation, New Mexico, USA. *Palaeontology, 55*, 1333–1348.

Huene, E. von. 1935. Ein Rhynchocephale aus dem Rhät (Pachyostropheus n. g.). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abhandlungen, 74*, 441–447.

Huene, F. von. 1938. *Stenaulorhynchos*, ein Rhynchosauride der ostafrikanischen Obertrias. *Nova Acta Leopoldina, N.F.*, 6, 83–121.

Huene, F. von. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt, 65*, 268–275.

Hughes, B. 1963. The earliest archosauromorph reptiles. *South African Journal of Science, 59*, 221–241.

Ivakhnenko, M. F. 1979. [Permian and Triassic procolophons of the Russian Platform.] *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR, 164*, 1–80.

Jailil, N.-E. 1997. A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. *Journal of Vertebrate Paleontology, 17*, 506–525.

Janensch, W. 1949. Ein neues Reptil aus dem Keuper von Halberstadt. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte, B*, 1949, 225–242.

Jaquier, V. P., Fraser, N. C., Furrer, H. & Scheyer, T. M. 2017. Osteology of a new specimen of *Macrocenemus aff. M. fuyuanensis* (Archosauromorpha, Protosauroidia) from the Middle Triassic of Europe: potential implications for species recognition and paleogeography of tanystrophiae protorosaurs. *Frontiers in Earth Science, 5*, 91. doi:10.3389/feart.2017.00091

Jiang, D. Y., Rieppel, O., Fraser, N. C., Motani, R., Hao, W. C., Tintori, A., Sun Y.-L. & Sun, Z.-Y. 2011. New information on the protorosaurian reptile *Macrocenemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. *Journal of Vertebrate Paleontology, 31*, 1230–1237.

Keck F., Rimet F., Bouchez A. & Franc A. 2016. phylosignal: an R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution, 6*, 2774–2780.

Kischlat, E.-E. 2000. Tecdodôncios: a aurora dos arcosaurídeos no Triássico. Pp. 273–316 in M. Holz & L. F. De Ross (eds) *Paleontologia do Rio Grande do Sul. CIGOG/UFRGS, Porto Alegre*.

Kuhn, O. 1969. *Cotylosauria. Handbuch der Paläoherpetologie Teil 6* Gustav Fischer Verlag, Jena, 89 pp.

Langer, M. C., Ezcurra, M. D., Bittencourt, J. & Novas, F. E. 2010. The origin and early radiation of dinosaurs. *Biological Reviews, 85*, 55–110.

Le Guilloux, M., Miralles, A., Measey, J., Vanhooydonck, B., O’Reilly, L. J., Bowie, A. & Herrel, A. 2020. Trade-offs between burrowing and biting force in fossorial scincid lizards? *Biological Journal of the Linnean Society, 130*, 310–319.

Li, C., Wu, X. C., Zhao, L. J., Nesbitt, S. J., Stocker, M. R. & Wang, L. T. 2016. A new armored archosauromorph (Diapsida: Archosauromorpha) from the marine Middle Triassic of China, with implications for the
diverse life styles of archosauriforms prior to the diversification of Archosauria. The Science of Nature, 103, 95. doi:10.1007/s00114-016-1418-4

Lucas, S. G., Spielmann, J. A. & Hunt, A. P. 2013. A new doswelliid archosauromorph from the Upper Triassic of West Texas. Bulletin of the New Mexico Museum of Natural History and Science, 61, 382–388.

Maidment, S. C. R., Sennikov, A. G., Ezcurra, M. D., Dunne, E. M., Gower, D. J., Hedrick, B., Meade, L. E., Raven, T. J., Paschkenro, D. I. & Butler, R. J. 2020. The postcranial skeleton of the erythrosuchid archosauriform Garjainia prima from the Early Triassic of European Russia. Royal Society Open Science, 7, 201089. doi:10.1098/rsos.201089

Mann, A., Dudgeon, T. W., Henrici, A. C., Berman, D. S. & Pierce, S. E. 2021. Digit and ungual morphology suggest adaptations for scansoriality in the late Carboniferous eureptile Anthracodromeus longipes. Frontiers in Earth Science, 9, 440. doi:10.3389/feart.2021.657337

Montefeltro, F. C., Langer, M. C. & Schultz, C. L. 2010. Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida: Archosauromorpha) from the Upper Triassic of southern Brazil. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 101, 27–52.

Nesbitt, S. J. 2005. The osteology of the Middle Triassic pseudosuchian archosaur Arizonasaurus babbitti. Historical Biology, 17, 19–47.

Nesbitt, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. Bulletin of the American Museum of Natural History, 352, 1–292.

Nesbitt, S. J., Stocker, M. R., Small, B. J. & Downs, A. 2009. The osteology and relationships of Vancleavea campi (Reptilia: Archosauriformes). Zoological Journal of the Linnean Society, 157, 814–864.

Nesbitt, S. J., Brusatte, S. L., Desojo, J. B., Liparini, A., de França, M. A. G., Weinbaum, J. C. & Gower, D. J. 2013. Rausuchia. Pp. 241–274 in S. J. Nesbitt, J. B. Desojo & R. B. Irmis (eds) Anatomy, phylogeny and palaeobiology of early archosaurs and their kin. Geological Society of London, Special Publication, 379.

Nesbitt, S. J., Sidor, C. A., Angielczyk, K. D., Smith, R. M. H. & Tsuji, L. A. 2014. A new archosaur from the Manda Beds (Anisian, Middle Triassic) of southern Tanzania and its implications for character state optimizations at Archosauromorpha and Pseudosuchia. Journal of Vertebrate Paleontology, 34, 1357–1382.

Nesbitt, S. J., Flynn, J. J., Pritchard, A. C., Parrish, J. M., Ranivoharimanana, L. & Wyss, A. R. 2015. Postcranial anatomy and relationships of Azendohsaurus madagaskarensis. Bulletin of the American Museum of Natural History, 398, 1–126.

Nesbitt, S. J., Butler, R. J., Ezcurra, M. D., Barrett, P. M., Stocker, M. R., Angielczyk, K. D., Smith, R. M. H., Sidor, C. A., Niedzwiedzki, G., Sennikov, A. G. & Charig, A. J. 2017. The earliest bird-line archosaurs and the assembly of the dinosaur body plan. Nature, 544, 484–487.

Nesbitt, S. J., Langer, M. C. & Ezcurra, M. D. 2020. The anatomy of Asilisaurus kongwe, a dinosaurosaur from the Lifua Member of the Manda Beds (~Middle Triassic) of Africa. The Anatomical Record, 303, 813–873.

Nesbitt, S. J., Stocker, M. R., Ezcurra, M. D., Fraser, N. C., Heckert, A. B., Parker, W. G., Mueller, B., Sengupta, S., Bandopadhyay, S., Pritchard, A. C. & Marsh, A. D. 2022. Widespread azendohsaurids (Archosauromorpha, Allokotosauria) from the Late Triassic of western USA and India. Papers in Palaeoecology, 8, e1413. doi:10.1002/pal2.1413

Norman, D. B. 2020. Scelidosaurus harrisonii from the Early Jurassic of Dorset, England: cranial anatomy. Zoological Journal of the Linnean Society, 188, 1–81.

Norman, D. B., Crompton, A. W., Butler, R. J., Porro, L. B. & Charig, A. C. 2011. The Lower Jurassic ornithischian dinosaur Heterodontosaurus tucki (Crompton & Charig, 1962): cranial anatomy, functional morphology, taxonomy and relationships. Zoological Journal of the Linnean Society, 163, 182–276.

Olsen, P. E., Kent, D. V. & Whiteside, J. H. 2010. Implications of the Newark Supergroup-based astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 101, 201–229.

Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diapsitosaurs. Memoirs of the American Museum of Natural History, 1, 449–507.

Paradis, E. & Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics, 35, 526–528.

Parker, W. G., Nesbitt, S. J., Irmis, R. B., Martz, J. W., Marsh, A. D., Brown, M. A., Stocker, M. R. & Werning, S. 2021. Osteology and relationships of Revueltosaurus callenderi (Archosauria: Suchia) from the Upper Triassic (Norian) Chine Formation of Petrified Forest National Park, Arizona, United States. The Anatomical Record. doi:10.1002/ar.24757

Peecook, B. R., Smith, R. M. & Sidor, C. A. 2018. A novel archosauromorph from Antarctica and an updated review of a high-latitude vertebrate assemblage in the wake of the end-Permian mass extinction. Journal of Vertebrate Paleontology, 38, e1536664. doi:10.1080/07385809.2018.1536664

Peng, J.-H. 1991. A new genus of Proterosuchia from the Lower Triassic of Shaanxi, China. Vertebrata PalAsiatica, 29, 95–107.

Pinheiro, F. L., França, M. A., Lacerda, M. B., Butler, R. J. & Schultz, C. L. 2016. An exceptional fossil skull from South America and the origins of the archosauriform radiation. Scientific Reports, 6, 22817. doi:10.1038/srep22817

Pinheiro, F. L., De Simão-Oliveira, D. & Butler, R. J. 2020. Osteology of the archosauriform Teyuajagua paradoxus and the early evolution of the archosauriform skull. Zoological Journal of the Linnean Society, 189, 378–417.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. 2021. nlme: linear and nonlinear mixed effects models. R package version 3.1-152. Updated at: https://CRAN.R-project.org/package=nlme, accessed 15 February 2022.

Porro, L. B., Wittmer, L. M. & Barrett, P. M. 2015. Digital preparation and osteology of the skull of Lesothosaurus diagnosticus (Ornithischia: Dinosauria). PeerJ, 3, e1494. doi:10.7717/peerj.1494
Pradelli, L. A., Leard, J. M. & Ezcurra, M. D. 2022. Body size disparity of the archosauromorph reptiles during the first 90 million years of their evolution. Ameghiniana, 59, 47–77.

Price, J. W. 1956. A new locality for Upper Triassic vertebrate fossils in Lancaster County, Pennsylvania. Proceedings of the Pennsylvania Academy of Sciences, 30, 167–169.

Pritchard, A. C., Turner, A. H., Nesbitt, S. J., Irnis, R. B. & Smith, N. D. 2015. Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology, 35, e911186. doi:10.1080/02724634.2014.911186

Pritchard, A. C., Gauthier, J. A., Hanson, M., Bever, G. S. & Bhullar, B.-A. S. 2018. A tiny Triassic saurian from Connecticut and the early evolution of the diapsid feeding apparatus. Nature Communications, 9, 1213. doi:10.1038/s41467-018-03508-1

Pritchard, A. C. & Sues, H.-D. 2019. Postcranial remains of Teraterpeton brynewichorum (Reptilia, Archosauromorpha) and the mosaic evolution of the saurian postcranial skeleton. Journal of Systematic Palaeontology, 17, 1745–1765.

R Development Core Team. 2021. R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. Updated at: https://www.r-project.org/, accessed 15 February 2022.

Ramezani, J., Fastovsky, D. E. & Bowring, S. A. 2014. Revised chronostratigraphy of the lower Chinle Formation strata in Arizona and New Mexico (USA): high-precision U-Pb geochronological constraints on the Late Triassic evolution of dinosaurs. American Journal of Science, 314, 981–1008. doi:10.2475/06.2014.01

Rasmussen, C., Mundil, R., Irnis, R. B., Geisler, D., Gehrels, G. E., Olsen, P. E., Kent, D. V., Lepre, C., Kinney, S. T., Geissman, J. W. & Parker, W. G. 2021. U-Pb zircon geochronology and depositional age models for the Upper Triassic Chinle Formation (Petrified Forest National Park, Arizona, USA): implications for Late Triassic paleoecological and paleoenvironmental change. GSA Bulletin, 133, 539–558. doi:10.1130/B35485.1

Reig, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosauros del Triásico de Ischigualasto (San Juan, Argentina). Revista de la Asociación Geológica Argentina, 13, 257–270.

Reisz, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. University of Kansas Publications of the Museum of Natural History, 7, 1–74.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution, 3, 217–223.

Rogers, R. R., Swisher III, C. C., Sereno, P. C., Forster, C. A. & Monetta, A. M. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and 40Ar/39Ar dating of dinosaur origins. Science, 260, 794–797.

Romero, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. XI. Two new long-snouted thecodonts, Chanaresuchus and Galinosaur. Breiviora, 379, 1–22.

Romero, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XII. The postcranial skeleton of the thecodont Chanaresuchus. Breiviora, 385, 1–21.

Santa Luca, A. P. 1980. The postcranial skeleton of Heterodontosaurus tucki (Reptilia, Ornithischia) from the Stormberg of South Africa. Annals of the South African Museum, 79, 159–211.

Schoenly, T. M., Spiekmann, S. N., Sues, H.-D., Ezcurra, M. D., Butler, R. J. & Jones, M. E. 2020. Colobops: a juvenile rhynchocephalian reptile (Lepidosauromorpha), not a diminutive archosauromorph with an unusually strong bite. Royal Society Open Science, 7, 192179. doi: 10.1098/rsos.192179

Schoch, R. R. & Sues, H.-D. 2014. A new archosauriform reptile from the Middle Triassic (Ladinian) of Germany. Journal of Systematic Palaeontology, 12, 113–131.

Schoch, R. R. & Sues, H.-D. 2018. A new lepidosauromorph reptile from the Middle Triassic (Ladinian) of Germany and its phylogenetic relationships. Journal of Vertebrate Paleontology, 38, e1444619. doi:10.1080/02724634.2018.1444619

Sen, K. 2003. Pamelaria dolichorchaelcha, a new prolacertid reptile from the Middle Triassic of India. Journal of Asian Earth Sciences, 21, 663–681.

Sengupta, S., Ezcurra, M. D. & Bandopadhyay, S. 2017. A new horned and long-necked herbivorous stem-archosaur from the Middle Triassic of India. Scientific Reports, 7, 8366. doi:10.1038/s41598-017-08658-8

Sereno, P. C. 1994. The pectoral girdle and forelimb of the basal theropod Herrerasaurus ischigualastensis. Journal of Vertebrate Paleontology, 13, 425–450.

Siggogne-Russell, D. 1981. Étude ostéologique du reptile Simoedosaurus (Choristodera). 2e Partie: squelette postcrânien. Annales de Paléontologie (Vertébrés), 67, 61–140.

Siggogne-Russell, D. & Russell, D. E. 1978. Étude ostéologique du reptile Simoedosaurus (Choristodera). Annales de Paléontologie (Vertébrés), 64, 1–84.

Sill, W. D. 1967. Proterochampsia barroconuovo and the early evolution of the Crocodilia. Bulletin of the Museum of Comparative Zoology, Harvard University, 135, 415–446.

Simoes, T. R., Caldwell, M. W., Talanda, M., Bernardi, M., Palci, A., Vernygora, O., Bernardini, F., Mancini, L. & Nydam, R. L. 2018. The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. Nature, 557, 706–709.

Sobral, G., Sues, H.-D. & Müller, J. 2015. Anatomy of the enigmatic reptile Elachistosuchus huenei Janensch, 1949 (Reptilia: Diapsida) from the Upper Triassic of Germany and its relevance for the origin of Sauria. PLoS ONE, 10, e0135114. doi:10.1371/journal.pone.0135114

Sookias, R. B., Butler, R. J. & Benson, R. B. 2012. Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. Proceedings of the Royal Society of London B, 279, 2180–2187.

Sookias, R. B., Sullivan, C., Liu, J., Butler, R. J. 2014a. Systematics of putative euparkeriids (Diapsida: Archosauromorphes) from the Triassic of China. PeerJ, 2, e658 doi:10.7717/peerj.658

Sookias, R. B., Sennikov, A. G., Gower, D. J. & Butler, R. J. 2014b. The monophyly of Euparkeriidae (Reptilia: Archosauromorphes) and the origins of Archosauria: a revision of Dorosuchus neoequus from the Mid-Triassic of Russia. Palaeontology, 57, 1177–1202.

Spiekmann, S. N., Neenan, J. M., Fraser, N. C., Fernandez, V., Rieppel, O., Nosotti, S. & Scheyer, T. M. 2020. The cranial morphology of Tanystropheus hydroides
Re-assessment of the Triassic reptile Spododrosaurus

1677

(Tanystropheidae, Archosauromorpha) as revealed by synchrotron microtomography. PeerJ, 8, e10299. doi:10.7717/peerj.10299

Spiekmann, S. N., Fraser, N. C. & Scheyer, T. M. 2021. A new phylogenetic hypothesis of Tanystropheidae (Diapsida, Archosauromorpha) and other ‘protorosaurs’, and its implications for the early evolution of stem archosaurs. PeerJ, 9, e11143. doi:10.7717/peerj.11143

Spielmann, J. A., Lucas, S. G., Rinehart, L. F. & Heckert, A. B. 2008. The Late Triassic archosauriform Trilophosaurus. Bulletin of the New Mexico Museum of Natural History and Sciences, 43, 1–177.

Stockert, M. R., Zhao, L. J., Nesbitt, S. J., Wu, X. C. & Li, C. 2017. A short-snouted, Middle Triassic phytosaur and its implications for the morphological evolution and biogeography of Phytosauria. Scientific Reports, 7, 46028. doi:10.1038/srep46028

Sues, H.-D., Baird, D. & Olsen, P. E. 1993. Redescription of Sphodrosaurus pennsylvanicus Colbert, 1960 (Reptilia) and a reassessment of its affinities. Annals of Carnegie Museum, 62, 245–253.

Sues, H.-D., Desojo, J. B. & Ezcurra, M. D. 2013. Doswellicidae: a clade of unusual armoured archosauriforms from the Middle and Late Triassic. Pp. 49–58 in S. J. Nesbitt, J. B. Desojo & R. B. Irmis (eds) Anatomy, phylogeny and palaeobiology of early archosaurs and their kin. Geological Society of London, Special Publication, 379.

Sues, H.-D., Ezcurra, M. D. & Schoch, R. R. 2021. Efelsaurus triadicus Jaekel, 1904, a ‘forgotten’ reptile from the Upper Buntsandstein (Triassic: Anisian) of the Eifel region, Germany. PalZ, 96. doi:10.1007/s12542-021-00584-5

Thomson, T. J. & Motani, R. 2021. Functional morphology of vertebrate claws investigated using functionally based categories and multiple morphological metrics. Journal of Morphology, 282, 449–471.

Trotteyn, M. J. 2011. Material postcaneano de Protocochampsia barrionuevoi Reig 1959 (Diapsida: Archosauriformes) del Triásico Superior del centro-oeste de Argentina. Ameghinitana, 48, 424–447.

Trotteyn, M. J., Arcucci, A. B. & Raugust, T. 2013. Protocochampsia: an endemic archosauriform clade from South America. Pp. 59–90 in S. J. Nesbitt, J. B. Desojo & R. B. Irmis (eds) Anatomy, phylogeny and palaeobiology of early archosaurs and their kin. Geological Society of London, Special Publication, 379.

Trotteyn, M. J. & Ezcurra, M. D. 2014. Osteology of Pseudochoamphsia ischigualastensis gen. et comb. nov. (Archosauriformes: Proterochampsidae) from the early Late Triassic Iischigualasto Formation of northwestern Argentina. PLoS ONE, 9, e111388. doi:10.137/journal.pone.011388

Trotteyn, M. J. & Ezcurra, M. D. 2020. Redescription of the holotype of Chanaresuchus bonapartei Romer, 1971 (Archosauriformes: Proterochampsidae) from the Upper Triassic rocks of the Chañares Formation of north-western Argentina. Journal of Systematic Palaeontology, 18, 1415–1443.

Turner, A. H. & Nesbitt, S. J. 2013. Body size evolution during the Triassic archosauriform radiation. Pp. 573–597 in S. J. Nesbitt, J. B. Desojo & R. B. Irmis (eds) Anatomy, phylogeny and palaeobiology of early archosaurs and their kin. Geological Society of London, Special Publication, 379.

Venables, W. N. & Ripley, B. D. 2002. Modern applied statistics with S. Fourth Edition. Springer, New York, 495 pp.

Verwaijen, D., Van Damme, R. & Herrel, A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. Functional Ecology, 16, 842–850.

Walker, A. D. 1966. Elachistosuchus, a Triassic rhynchocephalian from Germany. Nature, 211, 583–585.

Weems, R. E. 1980. An unusual newly discovered archosaur from the Upper Triassic of Virginia, USA. Transactions of the American Philosophical Society, 70, 1–53.

Wegener, J. E., Mulder, K. P., Pringle, R. M., Losos, J. B. & Kolbe, J. J. 2019. Head size of male and female lizards increases with population density across island populations in the Bahamas. Breviora, 566, 1–9.

Wellnhofer, P. 2003. A Late Triassic pterosaur from the Northern Calcareous Alps (Tyrol, Austria). Pp. 5–22 in E. Buffetaut & J.-M. Mazin (eds) Evolution and palaeobiology of pterosaurs. Geological Society of London, Special Publication, 217.

Whitlatch, R. 2005. Phylogenetic relationship of Isalorhynchus genovefae, the rhynchosaur (Reptilia, Archosauromorpha) from Madagascar. Unpublished PhD dissertation, University of California, Santa Barbara, 276 pp.

Wild, R. 1979. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. Bollettino della Società Paleontologica Italiana, 17, 176–256.

Wynd, B. M., Nesbitt, S. J., Stocker, M. R. & Heckert, A. B. 2019. A detailed description of Bargarhynchus sixmilensis, gen. et comb. nov. (Archosauriformes, Proterochampsiis), and cranial convergence in snout elongation across stem and crown archosaurs. Journal of Vertebrate Paleontology, 39, e1748042. doi:10.1080/02724634.2019.1748042

Associate Editor Richard Butler