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Postcranial remains of *Teraterpeton hrynewichorum* (Reptilia: Archosauromorpha) and the mosaic evolution of the saurian postcranial skeleton

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*Teraterpeton hrynewichorum* is an unusual archosauromorph reptile from the Upper Triassic (Carnian) Evangeline Member of the Wolfville Formation in Nova Scotia (Canada). Its long snout has transversely broad, cusped ‘molariform’ teeth posteriorly and lacks teeth anteriorly. The temporal region of the cranium is ‘euryapsid’ with large upper and closed lower temporal fenestrae. A previously undescribed specimen referable to *Teraterpeton* includes a nearly complete pelvic girdle and both hind limbs. The ilium has a long, dorsoventrally deep anterior process similar to that of derived rhynchosaurs. The pelvis has a well-developed thyroid fenestra, a feature shared only by Tanystropheidae among Archosauromorpha. Metatarsal V is proximodistally short, resembling the condition in Tanystropheidae. The pedal unguals of *Teraterpeton* are strongly flattened mediolaterally, dorsoventrally deep and weakly curved, much like the manual unguals. We performed a phylogenetic analysis of a matrix comprising 61 taxa of Permo-Triassic diapsid reptiles and 337 characters, which supports the position of *Teraterpeton* as the sister-taxon of *Trilophosaurus + Spinosuchus*. In the current phylogeny, parsimony-based character optimization of the aforementioned character-states in *Teraterpeton* indicate that all were acquired independently from other saurian lineages. The unusual combination of postcranial features in *Teraterpeton* underscores the critical importance of comprehensive taxon sampling for understanding the mode of character change among Triassic diapsid reptiles and careful apomorphy-based identifications to faunal analyses.

**Keywords:** Diapsida; Sauria; Archosauromorpha; Triassic; apomorphy-based identification

**Introduction**

Prior to the emergence of the archosaurian crown-group in the Early Triassic, a large number of lineages diverged from the archosaur stem in the Permian Period (Butler *et al.* 2011; Nesbitt *et al.* 2011; Ezcurra *et al.* 2014; Ezcurra 2016; Pritchard & Nesbitt 2017). Many of these lineages persisted through the Permo-Triassic Extinction (PTE) and diversified into a wide range of body plans and sizes in the Triassic Period. These non-archosauromorph archosauromorphs include herbivores with varied dental specializations, a variety of long-necked forms, and species with total body lengths ranging from 0.5 m to over 5 m. These taxa formed the first major ecomorphological diversification of Sauria in the fossil record (Foth *et al.* 2016; Ezcurra & Butler 2018).

Enormous variation also exists in the postcranial skeleton of non-archosauromorph archosauromorphs, such that many clear trends emerge within individual clades. These include elongation of the cervical vertebrae and cervical column in Tanystropheidae (Tschanz 1988; Li *et al.* 2004; Pritchard *et al.* 2015), increasing skeletal robustness in hyperodapedontine rhynchosaurs (Montefeltro *et al.* 2013; Ezcurra *et al.* 2016), and the transformation of the hind limb from a sprawling posture to a more upright crocodylian-like posture within Archosauriformes (Hutchinson 2001a; Nesbitt 2011; Ezcurra 2016). However, few clear and consistent trends have emerged among stem-archosaurs outside of Archosauriformes. This is possibly due to the limited known taxonomic diversity within many stem-archosaur clades, inadequate preservation of fossil material, or a high degree of homoplasy. More postcranial skeletons of non-archosauromorph archosauromorphs are needed to address these questions.

Sues (2003) described a distinctive new archosauromorph reptile, *Teraterpeton hrynewichorum*, on the basis of an excellently preserved, nearly complete skull associated with much of the postcranial skeleton (NSM 999GF041) from a poorly sorted red sandstone of the Evangeline Member exposed at Burntcoat Head in Hants...
County, Nova Scotia, Canada. The cranium of this taxon has a typically ‘euryapsid’ temporal configuration with large upper temporal fenestrae and imperforate, deep temporal bars (Sues 2003). The elongate premaxillae and anterior portions of the dentaries are devoid of teeth and possibly were covered by a keratinous beak in life (Sues 2003). The external naris is distinctly longer than the orbit. Both the maxillary and palatine teeth of Teraterpeton have crowns with bulbous bases, a single tall cusp and an anterior (mesial) “heel” (Sues 2003, p. 636). By contrast, the dentary teeth have the reverse configuration with a tall cusp and a posterior (distal) “heel” (Sues 2003, p. 636). The structure of the jaw joint and wear on the maxillary and palatine teeth indicate palinal jaw motion of the mandible (Sues 2003). Sues (2003) considered Teraterpeton most closely related to Trilophosaurus from the Upper Triassic (Carnian–Norian) of Arizona, New Mexico and Texas (Gregory 1945; Heckert et al. 2006; Spielmann et al. 2008). Comprehensive phylogenetic analyses by Pritchard et al. (2015), Nesbitt et al. (2015), and Sengupta et al. (2017) subsequently supported this hypothesis. Nesbitt et al. (2015) defined a new archosauromorph clade Allokotosauria, in which they placed Teraterpeton and Trilophosaurus along with Azendohsaurus, Pamelaria and Spinosuchus. We follow Nesbitt et al. (2015) and Sengupta et al. (2017) in considering Trilophosaurus (=Chinleogomphius) jacobi as a subjective junior synonym of Spinosuchus caseanus.

George P. Hrynewich, the discoverer (together with his son Sandy) of the holotype of Teraterpeton hrynewichorum, also collected a partial postcranial skeleton of a reptile from the type locality in June 1999. Upon preparation, this specimen also proved referable to this taxon (justified below). It preserves much of the pelvic girdle and hind limbs, which are only represented in the holotype by a fragment of the right ilium, part of the right femur and elements of two pedal digits (Sues 2003). The pelvis, hind limb and pes of T. hrynewichorum are strikingly different from those in more distantly related archosauromorph clades. We describe the new specimen and parallelism among saurian reptiles.

**Systematic palaeontology**

**Diapsida** Osborn, 1903

**Sauria** MacCartney, 1802

**Archosaurophora** Huene, 1946

**Allokotosauria** Nesbitt et al., 2015

**Trilophosauridae** Gregory, 1945

*Teraterpeton hrynewichorum* Sues, 2003

(Figs 1–6)

**Newly referred material.** NSM 018GF010.001, isolated partial cervical vertebra with fused right cervical rib (Fig. 1). NSM 018GF010.002, dorsoventrally somewhat crushed pelvic region of a postcranial skeleton with much of the pelvic girdle and seven proximal caudal vertebrae, associated left hind limb with articulated incomplete femur, tibia, fibula, tarsus and pes and right femur in articulation with partial right tibia and fibula (Fig. 2). The left hind limb appears to be in contact with the acetabulum and is flexed at the knee joint. In addition, two smaller blocks of sandstone preserve partial digits of another pes.

**Horizon and locality.** Evangeline Member of the Wolfville Formation (Upper Triassic, Carnian); Burntcoat Head, Hants County, Nova Scotia, Canada (Canada; Sues & Olsen 2015).

**Remarks on referral of NSM 018GF010.002 to *Teraterpeton hrynewichorum*.** Although there is only limited overlap between the bones of the holotype and NSM 018GF010.002, we confidently refer the latter to *Teraterpeton* based on a unique combination of diagnostic features (autapomorphies noted with *): (1) transversely flattened anterior process of ilium with convex margin anterodorsally; (2) anterior process of ilium extending well anterior to level of pubic peduncle; (3) transverse processes of caudal vertebrae extremely elongate (over six times longer than anteroposteriorly wide) and arcing posterolaterally along their lengths; and *4) presence of two, distinctive ungual morphotypes in both specimens. One morphotype exhibits a proximally

**Institutional abbreviations**

**AMNH:** American Museum of Natural History, New York, NY, USA; **BP:** Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; **IVPP:** Institute of Vertebrate Palentology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MCSN:** Museo Civico di Storia Naturali Milano, Milano, Italy; **NHMUK:** Natural History Museum, London, UK; **NMQR:** National Museum, Bloemfontein, Bloemfontein, South Africa; **NSM:** Nova Scotia Museum, Halifax, Nova Scotia, Canada; **PIMUZ:** Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland; **PIN:** Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **SAM PK:** Iziko South African Museum, Cape Town, South Africa; **SMNS:** Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TMM:** Texas Memorial Museum, Austin, TX, USA; **VMNH:** Virginia Museum of Natural History, Martinsville, VA, USA; **YPM:** Yale Peabody Museum of Natural History, New Haven, CT, USA.
tapering process extending from the proximodorsal surface of the proximal articular surface and a prominent flexor tubercle (preserved near the right humerus in the holotype: Sues 2003, fig. 7). The other is dorsoventrally tall and transversely flat, seemingly lacking the prominent flexor tubercle (preserved near the midline on the ventral surface of the abdominal block in the holotype).

Anatomical description

In addition to this anatomical description, we provide a table of measurements for select structures preserved in the referred specimens of *Teraterpeton hryniewichorum* (Supplemental material, Tables 1, 2).

Axial skeleton

Cervical region. In addition to the new partial postcranial skeleton, we also recognize a well-preserved isolated cervical vertebra (NSM 18GF010.001) that we refer to *Teraterpeton hryniewichorum* based on its close similarity to the cervical vertebrae in the holotype. These include an anteroposteriorly short centrum (length/height ratio = 1.34) relative to mid-cervical vertebrae in most early archosauromorphs (see Ezcurra 2016), a cervical rib indistinguishably fused to the centrum, and posteriorly pointed epipophyses that do not extend posteriorly beyond the level of the postzygapophyses. The specimen is missing the right zygapophyses, the tip of the neural spine, the right cervical rib and the posterior end of the left cervical rib (Fig. 1). The centrum is amphicoelous, compressed transversely at its anteroposterior midpoint and slightly less than twice as long as it is tall. The articular facets as preserved are subcircular.

The tuberculum and capitulum of the left cervical rib are fused to the diapophysis and parapophysis (Fig. 1C, F). Similar fusion occurs in *Avicanium renestoi* (Pritchard & Nesbitt 2017) and *Trilophosaurus buettneri* (TMM 31025-140). The dorsum of the diapophysis is positioned near the dorsoventral midpoint of the centrum, and the diapophysis and parapophysis are closely appressed to one another, as is common in Archosauromorpha (e.g. *Prolacerta broomi*, Gow 1975; *Tanystropheus longobardicus*, Wild 1973). Subtly convex laminae extend posteriorly from both diapophysis and parapophysis. They frame shallow fossae: one on the ventrolateral surface of the centrum, medial to the postparapophyseal lamina, and one on the lateral surface of the centrum, framed by the postparapophyseal lamina and the postdiapophyseal lamina.

The pedicel of the neural arch is approximately half as tall dorsoventrally as the centrum (Fig. 1A, B). The prezygapophyses are anteroposteriorly short, not extending further anteriorly beyond the anterior edge of the centrum. The prezygapophyseal facets are ovoid, with a transversely oriented long axis. A weak interzygapophyseal lamina extends between the pre- and postzygapophyses. The postzygapophyseal facets are ovoid with a posterolaterally oriented long axis. Posteriorly pointed epipophyses are present, which extend to the level of the postzygapophyseal facet (Fig. 1C). The development of the epipophyses is similar to that in *Trilophosaurus buettneri* (TMM 31025-140) and *Spinosuchus caseanus* (Spielmann et al. 2008) but not as pronounced as in *Tanystropheus longobardicus* (Wild 1973).

The two postzygapophyses were linked by a transversely narrow hypophyseal (following the definitions by Rauhut (2003) and Stefanič & Nesbitt (2018), which has a flat ventral margin (Fig. 1B). A deep, dorsoventrally high interspinous fossa is present dorsal to the hypophyseal. The configuration is similar.
to that in the mid-posterior cervical neural arches of *Trilophosaurus buettneri* (Spielmann et al. 2008), *Azendohsaurus madagaskarensis* (Nesbitt et al. 2015), and *Kuehneosaurus latus* (NHMUK PV R5972B). Anteriorly, the epipophyses are joined to the neural spine by a prominent spinopostzygapophyseal lamina.

The preserved cervical rib has a small anterior process, which extends anterior to the costal articulation (Fig. 1F). The shaft of the rib is oriented anteroposteriorly, in line with the long axis of the centrum. In these features, it closely resembles other early archosauromorphs (e.g. *Protorosaurus speneri*, Gottmann-Quesada & Sander 2009; *Proterosuchus alexanderi*, NMQR 1484). The
posterior margin of the rib shaft is weathered, such that
its full extent cannot be determined.

Sacrum. Portions of the sacrum are preserved in NSM
018GF010.002. The exposed portions of the first sacral
vertebra include a right pleurapophysis, right postzygapo-
physis and a portion of the right side of the centrum
that is missing its anterior articular face. The second
sacral is only represented by a partial neural spine and a
fragmentary right pleurapophysis (Fig. 2B, C).

The preserved portion of the centrum of the first sacral
vertebra is subcircular, with a slightly convex ventral sur-
face. The right postzygapophysis is transversely wide.
The right pleurapophysis is exposed on its posterior face,
which is fractured and weathered across much of its
surface. It is dorsoventrally tall and appears to taper post-
eroventrally (Fig. 3). In its current position, the first
pleurapophysis fits against the anterior process of the

Figure 3. Partial articulated manus? associated with the
postcranial skeleton of Teraterpeton hrynewichorum (NSM
018GF010.002) in A, lateral? and B, plantar views. Dashed
lines indicate broken or weathered surfaces on skeletal
elements. Black outlines are added to some bones to
differentiate them from surrounding matrix. Scale bar = 2 cm.

Figure 4. Pelvic region of the postcranial skeleton of
Teraterpeton hrynewichorum (NSM 018GF010.002) in A, right
lateral, B, ventral and C, anterior views. Dashed lines indicate
broken or weathered surfaces on skeletal elements. 
Abbreviations: am, inferred origin of M. ambiens; ap, anterior
process of ilium; c5, cervical vertebra 5; fe, femur; pp, posterior
process of ilium; pt, pubic tubercle; s1, sacral
vertebra 1; th, thyroid fenestra (preserved margin).
Scale bar = 2 cm.
ilium, anterior to the acetabulum. Its dorsal surface is largely flat and subtly concave, similar to the condition in *Trilophosaurus buettneri* (TMM 31025-140; Spielmann *et al.* 2008), *Tanystropheus longobardicus* (Wild 1973) and *Protosaurus speneri* (SMNS 55387; Gottmann-Quesada & Sander 2009). This contrasts with the condition in *Azendohsaurus madagaskarensis* (Nesbitt *et al.* 2015) and *Pamelaria dolichotrachela* (Sen 2003), in which the first sacral pleurapophysis has a deep concavity on its anterodorsal surface.

The pleurapophysis of the second sacral vertebra is unusual compared to those in most early Sauria (Fig. 2C). It is less than half the anteroposterior length of the first pleurapophysis. Its posteroverentral face is

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**Figure 5.** Hind limb elements of the postcranial skeleton of *Teraterpeton hrynewichorum* (NSM 018GF010.002). Right femur in A, extensor and B, flexor views. Left crus and pes in C, flexor view. Right crus in D, flexor and E, anterior (preaxial) views. Dashed lines indicate broken or weathered surfaces on skeletal elements. **Abbreviations:** ar, adductor ridge; fi, fibula; it, internal trochanter; mt, medial tibial condyle; pf, popliteal fossa; ti, tibia. Scale bar = 5 cm.
badly weathered and broken ventrally, such that much of its original extent may be missing. Its tapered distal tip fits against the ilium near its anteroposterior midpoint, dorsal to the position of the acetabulum. There is no apparent posterior process off the posterior surface of the pleurapophysis, a feature also absent in Protorosaurus speneri (SMNS 55387; Gottmann-Quesada & Sander 2009), Azendohsaurus madagaskaricensis (Nesbitt et al. 2015) and Tanytachelsos ahynis (YPM PU 8600; Olsen 1979).

Caudal region. The first four transverse processes of the caudal region are well exposed dorsally (Fig. 2C). The transverse processes and centra of the succeeding fifth, sixth and seventh caudal vertebrae are exposed ventrally (Figs 2B, 3). These three centra are unusually small relative to the size of the admittedly incomplete sacral centra – both in anteroposterior length and transverse breadth – compared to those in other early Sauria. By contrast, the equivalent caudal centra are subequal in size to the sacral centra in Protorosaurus speneri (Gottmann-Quesada & Sander 2009), Prolacerta broomi (BP/1/2676, SAM-PK 10802) and Trilophosaurus buettneri (TMM 31025-140, Gregory 1945). These features suggest an anteroposteriorly short tail relative to the size and breadth of the trunk, although it must be noted that the tail in NSM 018GF010.002 is incomplete (Fig. 3A, B). This rapid reduction in centrum size and length contrasts markedly from other many other early saurians, including Trilophosaurus buettneri (TMM 31025-140, Gregory 1945), Kuehneosaurus latus (TMM 41344-1) and Boreopricea funerea (PIN 3708/1). The only known non-archosaurian archosauromorphs that approach NSM 018GF010.002 in the shortening of the caudal vertebrae and tail are hyperodapedontine rhynchosaurs such as Hyperodapedon gordoni (Benton 1983) and H. huxleyi (Chatterjee 1974). In NSM 018GF010.002, there are subtle bilateral concavities in the ventrolateral surfaces of the exposed caudal centra. However, the centra are somewhat weathered and appear to have been transversely crushed, skewing them to the left side.

The preserved transverse processes are transversely elongate anteriorly, rapidly decreasing in length and robustness further posteriorly. Similarly elongate transverse processes occur in Tanytachelsos ahynis (e.g. VMNH 120049; Olsen 1979) and some basal sauropterygians (e.g. Li et al. 2014; Ji et al. 2016). No chevrons are apparent in NSM 018GF010.002 in the shortening of the caudal vertebrae and tail are hyperodapedontine rhynchosaurs such as Hyperodapedon gordoni (Benton 1983) and H. huxleyi (Chatterjee 1974). In NSM 018GF010.002, there are subtle bilateral concavities in the ventrolateral surfaces of the exposed caudal centra. However, the centra are somewhat weathered and appear to have been transversely crushed, skewing them to the left side.

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all Permo-Triassic diapsids, including the *Tropidostoma* Zone younginiform (SAM-PK 7710; Smith & Evans 1992), *Tanystropheus longobardicus* (PIMUZ T1277; Wild 1973), *Azendohsaurus madagaskarensis* (Nesbitt et al. 2015) and *Clevosaurus hudsoni* (NHMUK PV 36846; O’Brien et al. 2018). Unfused caudal ribs occur in non-diapsid eureptiles (e.g. *Eocaptorhinus laticeps*; Dilkes & Reisz 1986) and basal diapsids (e.g. *Araeoscelis gracilis*; Reisz et al. 1984).

**Forelimb**

**Manus?** NSM 018GF010.002 is associated with a series of small matrix blocks that contain parts of four digits. Each consists of articulated non-terminal phalanges and unguals (Fig. 3). One dissociated phalanx is slender and distinctly tapering between the proximal and distal articular ends. It has well-developed extensor pits in the sides of the distal articular end.

Penultimate phalanges are preserved in near-articulation with four of the ungual phalanges. Where completely preserved, these are proximodistally short and have almost no constriction between the proximal and distal articular ends (Fig. 3B). In proportions, they resemble the distal phalanges of hyperodapedontine rhynchosaurs (e.g. Benton 1983). The distal end is divided into distinct condylar surfaces, suggesting a hinge-like joint between the penultimate and ungual phalanges. It is not clear whether the distal phalangeal condyles converged dorsally as in *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (Nesbitt et al. 2015) and ‘*Chasmatosaurus*’ *yuani* (Young 1936).

The ungual phalanges are distinctive and differ markedly from those preserved on the articulated pes of NSM 018GF010.002. The exposed external surfaces of each ungual preserve proximodistally extending grooves (Fig. 4A), likely for vascular supply of the keratinous sheaths (e.g. Owen 1849; Baumel & Witmer 1993; Homberger et al. 2009). The exposed ventral surfaces of the unguals bear rugose flexor tubercles that extend ventrally relative to the proximal articular surfaces (Fig. 4B), similar to the condition in *Trilophosaurus buettneri* (TMM 31025-140; Spielmann et al. 2008) and *Azendohsaurus madagaskarensis* (Nesbitt et al. 2015). One of the best preserved unguals bears a strong, proximodorsally positioned process that arcs over the articular surface for the penultimate phalanx (Fig. 4A). One of the other unguals bears a broken surface where this extensor process would be positioned. The corresponding surface is flat in other archosauroomorphs (e.g. *Protorosaurus speneri*, Gottmann-Quesada & Sander 2009; *Azendohsaurus madagaskarensis*, Nesbitt et al. 2015; and *Tanystropheus longobardicus*, MCSN BES SC 1018, PIMUZ T/2817).

**Pelvis**

The pelvic girdle is articulated and generally well preserved on both sides (Fig. 4). The right side of the pelvis is well exposed both laterally and ventrally, whereas only the puboischiadic plate and posterior face of the ilium on the left side are well exposed. The margins of all elements are weathered, such that the extent and shape of the bones are not entirely clear. The right half of the pelvis is preserved in a position slightly dorsal to the left half.

**Ilium.** The iliac blade is well exposed on the left side. Its anterior and posterior margins are weathered, but much of the structure remains intact. The iliac blade possesses elongate anterior and posterior processes, extending well beyond the acetabulum (Fig. 4A). As preserved, the anterior process is subequal in length to the posterior process in sharp contrast to the small anterior tuberosity in *Trilophosaurus buettneri* (TMM 31025-73; Spielmann et al. 2008). The proportions of the processes resemble those in hyperodapedontine rhynchosaurs, such as *Hyperodapedon* (Benton 1983) and *H. huxleyi* (Chatterjee 1974). The anterior process is transversely flattened and squared-off anteriorly in lateral view, although the margins are heavily weathered. In the holotype, the anterior tip of the iliac blade is better preserved. There is a small, anteroventrally positioned tubercle. The blade curves anterodorsally from this tubercle, similar to the sloping condition seen in *Macrocnemus bassanii* (MCSN V 457; Peyer 1937), *Trilophosaurus buettneri* (TMM 31025-73; Spielmann et al. 2008) and *Prolacerta broomi* (NMQR 3763).

The posterior process of the ilium is transversely flattened and tapers dorsoventrally along its length. Its lateral surface lacks the posterodorsally extending crest in Tanystropheidae (e.g. Ezcurra 2016) and the ventrolateral depression in the posterior process as in *Mesosuchus brownii* (e.g. SAM-PK 6536) and *Prolacerta broomi* (e.g. BP/1/2676). The ventral base of the iliac blade tapers anteroposteriorly just dorsal to the acetabulum. There is a prominent supraacetabular buttress (*sensu* Romer 1956; =supraacetabular crest *sensu* Ezcurra 2016), but no lateral rugosity dorsal to the acetabulum. The acetabulum is oriented laterally and roughly circular, with a large contribution from the ilium that is heavily weathered at its deepest point. From lateral view, the ilium appears solidly co-ossified to both pubis and ischium (Fig. 4).

**Pubis.** The pubes are overall well preserved and exposed anterodorsally. The pubic symphysis only sits in an anteroposterior plane, lacking an anterior downturn (i.e. pubic ‘apron’ *sensu* Nesbitt et al. 2015) and Ezcurra (2016). It provided only a small contribution to the anteroventral face of the acetabulum (Fig. 4C). A prominent, dorsoventrally narrow crest extends
anteriorly from the acetabulum (Fig. 4B), which we homologize with the attachment of M. ambiens in other early Sauria (Romer 1922; Hutchinson 2001b). A similar, prominent crest is evident on the pubes of Prolacerta broomi (BP/1/2676, SAM-PK 6541), Azendohsaurus madagaskarensis (Nesbitt et al. 2015) and Mesosuchus browni (SAM-PK 6046; Dilkes 1998). In NSM 018GF010.002, the lateral face of the ambiens crest is badly weathered. The obturator foramen is positioned on the ventral surface of the pubis, inset medially relative to the crest.

Anteroventrally, the ambiens crest is continuous with another, anteroventrally inclined crest on the anterolateral face of the pubis. This we consider homologous with the pubic tubercle of other Sauria. It is anteroposteriorly expanded relative to the rest of the pubis (Fig. 4A, C). The ventral face of the tubercle is also heavily eroded, although it is unclear if there was a ventrally placed convexity similar to Prolacerta broomi (BP/1/2676, SAM-PK 6541; Gow 1975), ‘Chasmatosaurus’ yuani (IVPP V4067; Young 1936) and Proterosuchus alexanderi (NMQR 1484; Cruickshank 1972). Such a convex tubercle is absent in Trilophosaurus buettneri (TMM 31025-140; Gregory 1945) and Spinosaurus caseanus (NMMNH-P 50165; Spielmann et al. 2008).

Most of the ventral surface of the pubis is weathered away on both the left and right sides. The remaining bone is exceptionally thin on the right pubis, less than a millimetre in thickness. A small portion of the contact between pubis and ischium is preserved on the right side. It is a vertical contact just posterior to the obturator foramen.

Ischium. Both the right and left ischia are well preserved and exposed ventrolaterally. Compared to most non-archosauromorph archosauriforms, the bone is relatively short anteroposteriorly, with the posterior portion of the ischium sloping posteromedially from the acetabulum. Dorsally, the ischium contributes a small portion of the posteroventral face of the acetabulum (Fig. 4A).

Both ischia preserve a small, rounded margin medial to the puboischiadic contact, which we interpret as the ischial contribution to a fenestra (Figs 3B, 4B). We consider this homologous with the thyroid fenestra (sensu Romer 1956) because it manifests as a well-defined cavity within the puboischiadic plate as in Drepanosauromorpha (Renesto et al. 2010), Lepidosauria (e.g. Russell & Bauer 2008), Kuehneosauridae (AMNH FARB 2101, NHMUK PV R8172; Colbert 1970), Tanystropheidae (PIMUZ T/2817, T/2472; Wild 1973) and possibly Youngina capensis (BP/1/3859; Gow 1975). This stands in contrast to known allokotosaurs, such as Trilophosaurus buettneri (Spielmann et al. 2008), Pamelaria dolichotrachela (Sen 2003) and Azendohsaurus madagaskarensis (Nesbitt et al. 2015). In NSM 018GF010.002, it is unclear whether or not the thyroid fenestrae were continuous with one another along the midline, as much of the anteroventral surfaces of the ischia are badly broken and eroded (Fig. 4B).

The ischium does not have an elongate posterior extension beyond the acetabulum, in contrast to Trilophosaurus buettneri (e.g. Spielmann et al. 2008) and Protorosaurus speneri (e.g. Gottmann-Quesada & Sander 2009). It extends posteriorly to the same antero-posterior level as the posterior preserved margin of the iliac blade. Its posterior margin slopes relatively smoothly from the posterior margin of the acetabulum, similar to Azendohsaurus madagaskarensis (Nesbitt et al. 2015). The ischia meet along a straight, horizontal contact, despite the displacement of the right and left pelvis relative to one another (Fig. 4B).

Hind limb

Femur. The right femur is nearly complete, although the distal half is heavily eroded on its dorsal surface (Fig. 3B, C). Only the proximal half of the left femur is preserved (Figs 3, 4). At their proximal ends, both femora are crushed transversely along their long axes. Due to this distortion, the orientation and inclination of the shaft are difficult to assess. It is not clear if it had a sigmoid curvature similar to that in Trilophosaurus buettneri (TMM 31025-140; Spielmann et al. 2008) or Tanystropheus longobardicus (PIMUZ T/2817; Wild 1973).

The actual proximal surface of the femur is not exposed on either element. However, the bone clearly does not possess a proximal convexity or a curvature of the femoral head, resembling most non-archosauromorph archosauriforms (e.g. Trilophosaurus buettneri, TMM 31025-140, Spielmann et al. 2008; Mesosuchus browni, SAM-PK 6536; Proterosuchus alexanderi, NMQR 1484, Cruickshank 1972). The proximal half of the bone is marked by two proximodistally extending crests, one larger and one smaller (Figs 4A, 5).

The internal trochanter – the larger of the two crests – is positioned ventromedially and tapers distally (Fig. 5A), similar to the condition in lepidosaurs (e.g. Cleosaurus hudsoni, NHMUK PV R37030; Squamata, Russell & Bauer 2008) and early archosauromorphs (e.g. Azendohsaurus madagaskarensis, Nesbitt et al. 2015; Trilophosaurus buettneri, TMM 31025-140, Spielmann et al. 2008). It extends for one-third of the proximodistal length of the femur before merging into the main shaft. The internal trochanter is medially positioned relative to the proximomedial margin of the femur. On the postero-dorsal margin of the femur, there is a smaller proximodistally extending crest that we identify as the posterior
trochanter. In NSM 018GF010.002, this crest is only apparent in crosssection on the right side. Weakly developed posterior trochanters also occur in Tanystropheidae (e.g. Sennikov 2011; Pritchard et al. 2015).

The dorsal surface of the distal half of the femur is only partially preserved on the right side. It indicates that the bone was smoothly convex. The ventral surface of the femur exhibits a subtle, proximodistally extending ridge, which we identify as an adductor ridge (e.g. Romer 1956) and which extends from the distal tip of the internal trochanter to the popliteal fossa (Fig. 4B). It is only slightly raised from the femoral shaft and is more easily felt than seen. The adductor crest is slightly inclined towards the post-axial aspect of the popliteal fossa.

The popliteal fossa is visible on the right femur as a triangular, distally widened depression. It is shallow and demarcated by distally extending ridges just proximal to the distal condyles (Fig. 5B). If these correspond to muscle attachments it is likely the origins of M. gastrocnemius (Mivart 1867; Romer 1922). The dorsal surface of the distal femoral condyles are weathered away on both sides (Fig. 5A). The medial tibial condyle is strongly pointed, projecting far from the femoral shaft. This is similar to the condition of Prolacerta broomi (BP/1/2676; Gow 1975) and Azendohsaurus madagaskarensis (Nesbitt et al. 2015). It contrasts with the condition in Youngina capensis (BP/1/3859, Gow 1975) Tanystropheus sp. (SMNS 54627, Wild 1973). Only the ventral margin of the fibular condyle is preserved on the right side. It was quite large, occupying much of the ventromedial surface of the distal end of the femur as in Prolacerta broomi (BP/1/2676), Azendohsaurus madagaskarensis (Nesbitt et al. 2015) and ‘Chasmatosaurus’ yuani (IVPP V4067; Young 1936). The proximodistally short fossa between the fibular and lateral tibial condyles is marked by short, proximodistal striations.

Tibia. Partial tibiae are preserved on both sides (Figs 3, 5). The proximal articular surface is missing from the left bone and the distal articular surface is only partially exposed. The right element is heavily weathered, such that only its medial surface is preserved along much of its proximodistal length and only a tiny portion of the lateral surface is preserved at the distal end. On the left bone, the anteromedial surface is exposed.

Although the complete proximal articular surface is not preserved on either tibia, the preserved bone suggests that the element expanded only slightly at its proximal end (Fig. 5C, D, similar to the condition in the Tropidostoma Zone younginiform (SAM-PK 7710), Clevesaurus hudsoni (NHMUK R 36846; O’Brien et al. 2018), Trilophosaurus buettneri (TMM 31025-140; Spielmann et al. 2008), Macrocnemus bassanii (PIMUZ T/4822; Peyer 1937; Rieppel 1989) and Prolacerta broomi (BP/1/2676; Gow 1975). Some other Permo-Triassic diapsids exhibit marked dorsal expansion of the proximal end of the tibia (e.g. Azendohsaurus madagaskarensis, Nesbitt et al. 2015; Hyperodapedon gordoni, Benton 1983), a feature that correlates with the expansion of the femoral condyles. In NSM 018GF010.002, the tibial shaft is ovoid in crosssection, with a pointed margin along its medial surface. The anteromedial surface of the bone preserved on the left side is flattened and lacks distinct muscle scars (Fig. 5C).

The posteromedial surface is marked by proximodistally extending striations proximally, just distal to the articular surface on the tibia for the femoral condyles. A small, medially facing crest is preserved along the medial surface and may represent the insertion of M. pubiischiotibialis (Mivart 1867; Byerly 1926; Suzuki et al. 2011). At its distal end, the posteromedial surface of the tibia is rounded and convex, in contrast to the flattened lateral surface. The distal articular surface is not well exposed, but it appears to be relatively flat without a distinct ‘step’ as in many archosaurs (e.g. Nesbitt 2011; Ezcurra 2016).

Fibula. Portions of both fibulae are preserved, but both are fragmented into small pieces (Fig. 5). Most of the left fibula is preserved near its original articulation with the tibia. Its medial surface is exposed. The right fibula is only preserved as slender bone fragments alongside the distal end of the right tibia. The shaft of the fibula is sigmoidal (Fig. 5C), arcing posteromedially along its length. Sigmoidal fibulae are common to most Permo-Triassic diapsids, such as the Tropidostoma Zone younginiform (SAM-PK 7710; Smith & Evans 1992), Clevesaurus hudsoni (NHMUK R 36846; O’Brien et al. 2018) and Macrocnemus bassanii (PIMUZ T/4822; Peyer 1937; Rieppel 1989).

Tarsus

Astragalus. The astragalus is preserved on the left side distal to the tibial facet as a small, weathered sphere (Fig. 6). It is black in colour, without any finished surfaces and articular facets.

Lateral centrale. A small, distally tapering bone is preserved just distal to the astragalus on the left pes (Fig. 6). Its proximal surface is flattened and consists of finished bone. The remainder of the bone is roughened and irregular, lacking any finished bone surfaces. Separate centralia are not ubiquitous in early archosauromorphs (Nesbitt et al. 2015; Ezcurra 2016); they are absent in some Tanystropheidae (Wild 1973; Nosotti 2007).
**Calcaneum.** The left calcaneum is better preserved than the astragalus and centrale. The exposed plantar surface for the astragalus consists of weathered but finished bone. The facet for distal tarsal 4 is clear but embedded in matrix. The calcaneum had a lateral expansion (= tuber: *sensu* Thulborn 1980; Gauthier 1984; Gower 1996) that extends far laterally relative to the distal facet. However, the dorsal, lateral and ventral surfaces of this expansion are heavily weathered, obscuring the original shape of the bone (Fig. 6). It is not clear whether the ventrolateral margin of the calcaneum was concave as in *Azendohsaurus madagaskarensis* (Nesbitt et al. 2015) or convex as in *Trilophosaurus buettneri* (TMM 31025-140; Spielmann et al. 2008) and *Protorosaurus speneri* (Gottmann-Quesada & Sander 2009).

**Distal tarsal 4.** The fourth distal tarsal sits distal to the calcaneum on the left side (Fig. 6). It is an irregular bone. Its plantar and proximal surfaces are flattened, whereas the medial face is convex. The lateral surface of the tarsal has a small process that extends towards the proximal surface of the metatarsal III.

**Metatarsals I–IV.** The metatarsals are exposed in plantar view on the left side (Fig. 6B). Their proximal surfaces strongly overlap, with the medial elements overlying the lateral ones. The proximal articulating surfaces are heavily weathered on metatarsals I–IV, although they clearly expanded transversely at their proximal ends. The medial half of the first metatarsal is eroded, as are the distal ends of metatarsals I–IV.

The metatarsals increase in proximodistal length sequentially, with metatarsal I being the shortest (Fig. 6B). Metatarsal I, if its full proximodistal length is preserved, is less than one-third the length of metatarsal IV, similar to the condition in rhynchosaurs (e.g. Carroll 1976; Benton 1990; Dilkes 1998). In NSM 018GF010.002, the distal ends of the bones are transversely expanded.

**Metatarsal V.** The left metatarsal V is completely preserved and exposed in plantar view (Fig. 6B). It is ‘hooked’ (*sensu* Robinson 1975; Gauthier 1984), with the proximal articulation for distal tarsal 4 set at a right angle to the distal process for the phalanges. The lateral surface of the bone is thickened into a proximodistally elongate tuberosity (‘lateral plantar tubercle’: *sensu* Robinson 1975) that continues distally to the end of the bone. The distal process itself is very short proximodistally, barely extending beyond the level of the articulation with the distal tarsal. The proximolateral corner of metatarsal V is rounded, lacking a proximally projecting process (‘outer process’: *sensu* Goodrich 1942; Robinson 1975).

**Phalanges.** The digits on the left side of the pes remain in articulation with the metatarsals and one another in digits I–IV. Digit V does not preserve any phalanges. The phalanges are preserved in a hyperextended state, except at the distal interphalangeal joints. In digit IV – the only digit in which well-preserved phalanges are exposed ventrally – the phalanges are substantially shorter than metatarsal IV and decrease in proximodistal length distally. The unguals appear substantially longer than any of the other preserved phalanges. Only digit I is fully exposed, and it possesses two phalanges.

The unguals of pedal digits I–III are exposed in medial view (Fig. 2C). These were transversely compressed and tall. It is unclear whether they curved ventrally at their distal tips. It is also not clear whether or not they had prominent flexor tubercles ventral to the phalangeal articulation, but there is a very high extensor surface dorsal to the articulations. There is no distinct groove in the medial surfaces for a keratinous sheath, but the unguals are heavily weathered.

**Phylogenetic analysis**

We conducted phylogenetic analyses using both parsimony and Bayesian optimality criteria to both examine the impact of the new character data for *Teraterpeton hrynewichorum* and explore the distribution of selected postcranial anatomical traits among Permo-Triassic diapsid clades. We modified the character–taxon matrix of Pritchard et al. (2018), itself a modification of Pritchard et al. (2015), Nesbitt et al. (2015), Pritchard et al. (2016) and Pritchard & Nesbitt (2017). Details on matrix development, character additions and modifications are noted in Supplementary material, Appendix 1. The matrix used in this study comprises 337 characters and 61 diapsid taxa with *Petrolacosaurus kansensis* designated as the outgroup. The matrix is available as Project 3203 at the Morphobank data repository (www.morphobank.org).

Additionally, we incorporated two early archosauromorph taxa not present in previous modifications of the Pritchard et al. (2018) matrix. *Shringasaurus indicus* is a large-bodied azendohsaurid known from a substantial bonebed from the lower Middle Triassic Denwa Formation of India described by Sengupta et al. (2017). Aside from the bizarre, autopomorphic postorbital horns present in this species, *S. indicus* closely resembles *Azendohsaurus madagaskarensis* in nearly all respects.

The second species we integrate into the analysis is the bizarre, long-necked diapsid *Oziinek volans* from the Upper Triassic Krasiejów beds of Poland. This species was initially described by Dzik & Sulej (2016), who
included the species in Sharovipterygidae based on comparisons with *Sharovipteryx mirabilis* from the Upper Triassic Madygen Formation of Kyrgyzstan. In contrast to *S. mirabilis*, *O. volans* is known from a number of well-preserved skeletons including three-dimensionally preserved bones, and provides great potential for understanding its phylogenetic position and thus the possible position of Sharovipterygidae within Diapsida.

Figure 7. Strict consensus of six most-parsimonious trees (length = 1218 steps) resulting from a parsimony analysis of Diapsida in TNT v.1.5. The minimum length trees were hit in 4269 out of 10,000 replicates. Consistency index (CI) = 0.306, retention index (RI) = 0.656. Numbers above branches are frequency differences resulting from the jackknife analysis. Numbers below branches are Bremer supports.
For the parsimony analysis, we used the ‘Traditional Search’ option in TNT v.1.5 (Goloboff & Catalano 2016). We performed 10,000 replicates of Wagner trees using random addition sequences, followed by TBR branch swapping (10 trees held per replicate). The resultant trees were then subjected to an additional round of TBR branch swapping. We employed rule 1 of Coddington & Scharff (1994) for collapsing zero length branches. To explore branch support, we used the ‘Bremer Supports’ option in TNT to calculate decay indices, performing an additional round of TBR on the retained MPTs. We also performed jackknife resampling.
Figure 9. Schematized strict consensus phylogeny of Archosauromorpha based on the parsimony analysis featured in Figure 8, illustrating the distribution of key characters related to the anterior process of the ilium. Ambiguities between ACCTRAN and DELTRA optimizations are illustrated as grey branches. Ilia depicted are as follows: A, Azendohsaurus madagaskarensis (UA 9-5-98-448); B, Teraterpeton hrynewichorum (NSM 018GF010.002); C, Trilophosaurus buettneri (TMM 31025-73); D, Macrocnemus bassani (PIMUZ T/2477); E, Tanytrachelos athenis (AMNH FARF 7206); F, Prolacerta broomi (BP/1/2676); G, Erythrosuchus africanus (NHMUK PV R3592); H, Mesosuchus browni (SAM-PK 7416); and I, Hyperodapedon sanjuanensis (USNM PAL 452145). Note that Hyperodapedon gordoni was the member of the genus Hyperodapedon integrated into this phylogenetic analysis.

Figure 10. Schematized strict consensus phylogeny of Permo-Triassic Diapsida based on the parsimony analysis featured in Figure 8, illustrating the distribution of key characters related to the thyroid fenestra of the pelvis. Ambiguities between ACCTRAN and DELTRA optimizations are illustrated as grey branches. Puboischiadic plates depicted (in ventrolateral view) are as follows: A, Drepanosaurus unguicaudatus (MCSNB 5728); B, Gephyrosaurus bridensis (modified from Evans 1981); C, Protorosaurus speneri (illustrated based on SMNS cast of the Simon-Bartholomäus specimen and illustrations of IPB R535 in Gottmann-Quesada & Sander [2009]); D, Tanystropheus longobardicus (PIMUZ T/2482); E, Prolacerta broomi (BP/1/2676); F, Kuehneosaurus latus (NHMUK PV R8172); G, Azendohsaurus madagaskarensis (FMNH PR 2794); H, Teraterpeton hrynewichorum (NSM 018GF010.002); and I, Trilophosaurus buettneri (pubis, TMM 31025-79B; ischium, TMM 31025-78I).
on the matrix as well, performing 10,000 pseudoreplicates with a 20% removal probability. The strict consensus is presented in Figure 7.

For the Bayesian analysis, we used MrBayes v.3.2, employing the Mk model and a gamma distribution for rate variation across sites. We performed the analysis with a sampling frequency of 1000, two concurrent runs (nruns = 2) and four Metropolis-coupled chains (ncchains = 4). The analysis ran for 30,000,000 generations with a relative burn-in of 0.25. As the runs converged, the Potential Scale Reduction Factor (PSRF) hovered around 1.0, and the Effective Sample Size calculated in Tracer v.1.6 (Rambaut et al. 2014) was substantially greater than 200. We present the maximum clade credibility tree generated in TreeAnnotator v.1.8.4 (Rambaut & Drummond 2016) from the output of the MrBayes analysis in Figure 8. The only major distinction involves the position of Weigeltisauridae, which is the sister taxon of Drepanosauromorpha + Sauria in the Bayesian tree.

The addition of the new material of Teraterpeton hrynewichorum did not alter the position of the taxon relative to previous analyses (e.g. Sues 2003; Pritchard et al. 2015; Sengupta et al. 2017). As in Sengupta et al. (2017), Shringasaurus indicus is recovered as the sister taxon of Azendohsaurus spp. within Allokotosauria in both analyses. Ozimek volans is recovered as the sister taxon of Langobardisaurus + Tanytrachelos within Tanystropheidae in both analyses. We note that this result does not run counter to the conclusion of Dzik & Sulej (2016) that Ozimek volans and Sharovipteryx mirabilis are closely related. It is possible that both taxa are nested within Tanystropheidae and that the ecomorphological disparity of that clade is far greater than currently appreciated. As in Pritchard & Nesbitt (2017) and Pritchard et al. (2018), Kuehneosauridae are recovered nested deeply within Archosauromorpha, a position first suggested by Evans (1988).

Character evolution
We explored patterns of character change under both ACCTRAN and DELTRAN optimizations in PAUP* v.4.0 (Swofford 1998), rerunning the analysis under parsimony using 1000 replicates of random addition sequences and collapsing branches with a minimum length of 0. The six MPTs recovered were congruent with the MPTs from the TNT analysis. The analysis was run under ACCTRAN and DELTRAN optimizations to explore parsimonious character histories for several traits of interest in Teraterpeton hrynewichorum, which are presented in Figures 9–11. These illustrate a high degree of plasticity in a number of pelvic and hind limb characters that were previously restricted to a small number of clades or synapomorphic for specific clades of early Archosauromorpha.
Discussion

The discovery of a new fossil taxon inevitably increases the known diversity of body plans in the record. Each exhibits unique structures or a unique combination of structures, thereby increasing our perceptions of complexity and homoplasy within the inclusive clade. In effect, each new taxon represents a mosaic of morphological characters. However, the patterns of such anatomical mosaics are well worth considering for their implications for interpreting the fossil record.

A mosaic in the palaeontological sense may be divided into two intimately linked categories. The first involves a transitional mosaic: a combination of plesiomorphic and apomorphic traits that fit within an accepted hypothesis of morphological change within a particular lineage. Such mosaics inform a probable sequence of morphological change within a particular lineage. Such apomorphic traits that fit within an accepted hypothesis of morphological change within a particular lineage. Such transitional mosaics inform a probable sequence of morphological change within a particular lineage. Such mosaics inform a probable sequence of morphological change within a particular lineage.

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Mosaics and apomorphy-based diagnosis

The identification of isolated vertebrate bones and partial skeletons has long been informed by general anatomical comparisons with other vertebrates, known geographical distributions and temporal ranges (e.g. Estes et al. 1969; Heckert 2004; Heckert et al. 2012). Recently, stricter, phylogeny-driven criteria have been introduced to eliminate problems of circularity in using geographical or temporal preconceptions or shared primitive traits to make identifications. Bell et al. (2004) proposed the use of ‘reliable diagnostic features’ independent of distributional data, which has been refined to an apomorphy-based approach informed by modern phylogenetic analyses (e.g. Nesbitt et al. 2007; Nesbitt & Stocker 2008; Martz et al. 2012; Pritchard et al. 2015; Lessner et al. 2018).

Heckert et al. (2012) criticized the strict nature of apomorphy-based identification, citing the limited number of phylogenetic studies for certain taxa and perceived shortcomings of analyses. They specifically noted (1) the restricted distribution of characters selected for a particular phylogenetic data matrix and (2) the instability of topologies resulting from said phylogenetic analyses. The recognition of the mosaic nature of the skeleton of *Teraterpeton hrynewichorum* and its consequent complication of the distribution of apomorphies within early Sauria highlights an even greater consideration than topological inconsistency; even congruent topologies can have substantially different character optimizations, depending on the data and material incorporated into the codings.

Had the postcranial bones of *Teraterpeton hrynewichorum* been found in isolation, they would likely be assigned to a number of different early saurian clades using a strict apomorphy-based context: the ilium as that of a hyperodapedontine rhynchosaur, the fifth metatarsal as that of a derived tanystropheid or an erythrosuchid, and the pubis and ischium as belonging to one of a number of clades that possess a thyroid fenestra. The recognition of these features within a single specimen and the incorporation of the new material of *T. hrynewichorum* into a phylogenetic context is the necessary solution to this problem.

Nevertheless, we consider apomorphy-based identifications the best approach to refining identifications of isolated fossil elements, at least in taxa that have been subject to detailed phylogenetic analysis. However, those identifications must be recognized as provisional hypotheses requiring regular reassessments following new analyses and the description of new fossils. As noted by Nesbitt and Stocker (2008, p. 1070), “[a]pomorphies are tied to phylogenetic trees that are constantly being updated, changed, and revised”. Apomorphy-based identifications are inherently unstable, but they derive from phylogenetic frameworks that can be repeatably generated and tested.

The repeated testing of apomorphy-based identifications becomes more important in groups for which the phylogenetic framework is extremely labile, such as the Permo-Triassic diapsid reptiles analysed in this study.
The lineages analysed here appear to have diverged from one another and diversified morphologically very rapidly during the Permo-Triassic transition (e.g. Ezcurra 2016; Foth et al. 2016; Pritchard & Nesbitt 2017). This rapidity and the resultant homoplasy, coupled with the still sparse fossil record of diapsid reptiles from the late Permian and the first half of the Triassic in most continental deposits (Irmis & Whiteside 2012; Sues & Fraser 2010), make it unsurprising that the discovery of new taxa and more complete skeletons of known taxa would alter the distribution of apomorphies in the phylogenetic framework.

The character–taxon matrix employed to generate diagnostic apomorphies should sample as wide a range of different skeletal elements as possible and a broad sampling of taxa, ideally including incomplete forms with unique features. In terms of time intervals, the taxon sampling should also be as broad as possible, in the hope of breaking up the long branches that can confound phylogenetic signals (Nesbitt et al. 2007; Nesbitt & Stocker 2008; Martz et al. 2012; Pritchard et al. 2015). Most important of all, authors should discuss the specific analyses from which diagnostic apomorphies are derived or the absence of said apomorphies in prior analyses. This explicit context is critical to future testing of an apomorphy-based identification through revised phylogenetic studies.

**Functional implications**

During the Triassic Period, archosauromorphs underwent a major diversification of pelvic and hind limb morphologies. The most extensively studied part of this diversification is the three-phase transition from a sprawling, lizard-like posture in early archosauromorphs to a semi-erect posture within Archosauriformes (retained in modern Crocodylia) and finally to a fully erect hind limb posture within Avemetatarsalia (Charig 1972; Parrish 1986; Hutchinson 2001a, b; Sullivan, 2015). The ichnological record suggests that these transitions occurred rapidly in Archosauromorpha near the beginning of the Triassic (e.g. Kubo & Benton 2009), and many taxa representing all three postural categories co-occur throughout the period (e.g. Parrish 1986; Sullivan 2015). The anatomical evidence from the new specimen of *Teraterpeton hrynewichorum* strongly suggests it belongs to the sprawling grade of early archosauromorphs.

Based on the postural categories proposed by Charig (1972), Parrish (1986) defined three locomotor paradigms in Triassic archosauromorphs: sprawling gait, semi-erect gait and erect gait. The new material of *T. hrynewichorum* possesses many features that Parrish associated with the sprawling gait, including a femur lacking a distinct proximal head and a laterally oriented pes. It also possesses an “unexpanded” pelvis, in contrast to those of early ornithodirans with elongate pubic and ischiadic shafts (Parrish 1986, p. 25). As such, it likely would have maintained femoral flexors and extensors that would also have acted as long-axis rotators of the femur, akin to extant lepidosaurs (e.g. Sullivan 2015). *Teraterpeton hrynewichorum* also has a prominent internal trochanter and lacks a fourth trochanter, characters indicative of a sprawled posture (e.g. Hutchinson 2001a).

Although *T. hrynewichorum* fits well within the sprawling locomotor category of early archosauromorphs, details of its skeleton differ from other taxa within that same category. We suggest a number of muscle attachments related to these osteological correlates based on dissections and surveys of modern tetrapods (information from modern tetrapods from Mivart 1867; Romer 1922, 1923; Byerly 1926; Francis 1934; Walker 1973; Russell & Bauer 2008; Suzuki et al. 2011).

The tall, anteroposteriorly broad iliac blade with a relatively long anterior process differs from those of other early archosauromorphs, except for hyperodapedontine rhynchosaurs. This may have supported a larger attachment for the m. iliofemoralis, a muscle activated during the swing phase of locomotion in modern *Alligator* (Gatesy 1997). The puboischiadic plate in *T. hrynewichorum* is likewise relatively large, being proportionally transversely broader than in most early Archosauromorpha (e.g. Gregory 1935; Gottmann-Quesada & Sander 2009), supporting enlarged attachments for the m. puboischiofemoralis externus and m. puboischiofemoralis internus, muscles also activated in swing phase in *Alligator* (Gatesy 1997). The latter is also used at the transition between stance and swing phase and then throughout swing phase in the turtles *Trachemys* and *Apalone* (Blob et al. 2008). Finally, the extremely wide transverse processes of the anterior caudal vertebrae in *T. hrynewichorum* could have supported transversely broad and massive mm. caudifemoralis. Among the most studied of hind limb muscles, m. caudifemoralis longus is a major retractor of the thigh that is activated at the conclusion of swing phase and throughout stance phase in modern tetrapods (e.g. Reilly 1994–1995; Gatesy 1997; Higham & Jayne 2004).

The hypothesized enlargement of protractor and retractor muscles of the thigh relative to those in other archosauromorphs in *Teraterpeton hrynewichorum* and hyperodapedontine rhynchosaurs could suggest adaptations to more frequent walking than other sprawling archosauromorphs. Alternatively, Huene (1939) and Benton (1983) suggested that the pelvic and hind limb anatomy in stenaulorhynchine and hyperodapedontine rhynchosaurs was well suited to hind limb-mediated...
scratch digging. Benton (1983) supported this hypothesis based on the expanded surface area for muscle attachment of pelvic elements, the short pedal phalanges with well-developed articular surfaces, and the massive and curved pedal unguals – all features shared with *T. hrynewichorum*. However, hyperodapedontines also have massive hind limb bones with short shafts and wide, expanded articular surfaces, which Benton (1983) correlated with expanded flexors and extensors of the pes. The hind limb bones in *T. hrynewichorum* are comparatively slenderer, more akin to *Trilophosaurus buettneri* (e.g. Gregory 1945; Spielmann *et al.* 2008).

Specialist hind limb digging is rare in present-day tetrapods, largely restricted to some frog species (e.g. Kley & Kearney 2011). In some extant turtles and crocodylians, the hind limbs are preferred for digging only during nest excavation (e.g. Warner *et al.* 2006; Miller & Dinkelacker 2008; Kley & Kearney 2011). If *Teraterpeton hrynewichorum* and hyperodapedontines were specialist hind limb diggers, there would thus be no analogues among living quadrupedal reptiles (e.g. Kley & Kearney 2011). It is plausible that both the fore- and hind limbs in these Triassic taxa were capable of scratch digging, but it seems unlikely that the modifications to the pelvis can be explained solely in terms of digging. Although we have begun to recognize the high diversity of postcranial morphology within the sprawling lineages, the hind limbs are preferred for digging only in some extant turtles and crocodylians. Various anatomical features in the pelvis, hind limb and pes are shared in common with other Permo-Triassic diapsid lineages. Phylogenetic analysis demonstrates that these were convergently acquired, obscuring what were once considered unique synapomorphies of hyperodapedontine rhynchosaurids and derived tanystropheids. The patterns of homoplasy support the need for continued re-evaluation of apomorphy-based diagnoses of isolated skeletal remains, especially in clades with patchy fossil records. The expanded muscle attachments for the thigh indicate functional similarities with hyperodapedontines.

**Conclusions**

New specimens of the trilophosaur *Teraterpeton hrynewichorum* are described, including a partial postcranial skeleton preserving much of the hindquarters. Various anatomical features in the pelvis, hind limb and pes are shared in common with other Permo-Triassic diapsid lineages. Phylogenetic analysis demonstrates that these were convergently acquired, obscuring what were once considered unique synapomorphies of hyperodapedontine rhynchosaurus and derived tanystropheids. The patterns of homoplasy support the need for continued re-evaluation of apomorphy-based diagnoses of isolated skeletal remains, especially in clades with patchy fossil records. The expanded muscle attachments for the thigh indicate functional similarities with hyperodapedontines and Tim Fedak and Katherine Ogden (NSM) for assistance with curation of the specimens and further information on the holotype. We thank Diane Scott for her illustration of NSM 018GF010.002. We thank the two anonymous reviewers and the editors of the journal for their comments and critiques that substantially improved the manuscript.

**Supplemental data**

Supplemental material for this article can be accessed here: https://doi.org/10.1080/14772019.2018.1551249.

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Late Triassic dinosauromorph-bearing assemblages from Irmis, R. B. Palaeontology estimated from Permian and Triassic trackways.


