A new Early Permian reptile and its significance in early diapsid evolution

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The initial stages of evolution of Diapsida (the large clade that includes not only snakes, lizards, crocodiles and birds, but also dinosaurs and numerous other extinct taxa) is clouded by an exceedingly poor Palaeozoic fossil record. Previous studies had indicated a 38 Myr gap between the first appearance of the oldest diapsid clade (Araeoscelidia), *ca* 304 million years ago (Ma), and that of its sister group in the Middle Permian (*ca* 266 Ma). Two new reptile skulls from the Richards Spur locality, Lower Permian of Oklahoma, represent a new diapsid reptile: *Orovenator mayorum* n. gen. et sp. A phylogenetic analysis identifies *O. mayorum* as the oldest and most basal member of the araeoscelidian sister group. As Richards Spur has recently been dated to 289 Ma, the new diapsid neatly spans the above gap by appearing 15 Myr after the origin of Diapsida. The presence of *O. mayorum* at Richards Spur, which records a diverse upland fauna, suggests that initial stages in the evolution of non-araeoscelidian diapsids may have been tied to upland environments. This hypothesis is consonant with the overall scant record for non-araeoscelidian diapsids during the Permian Period, when the well-known terrestrial vertebrate communities are preserved almost exclusively in lowland deltaic, flood plain and lacustrine sedimentary rocks.

Keywords: diapsida; evolution; phylogeny; Permian; reptile

1. INTRODUCTION

Diapsids were the most conspicuous and numerically dominant vertebrates (e.g. dinosaurs, ichthyosaurs, pterosaurs) of land, sea and air environments during the Mesozoic Era (252.4–65.5 Ma), and continued to be significant components of Cenozoic communities (squamates, crocodiles, birds). However, this obvious evolutionary success is belied by a poor fossil record in the preceding Palaeozoic Era. Numerous attempts to document Palaeozoic diapsids have not met with any significant success, with many taxa being reindentified as small synapsids [1–3]. Based on sister-group comparison of the two diapsid subclades [4,5], non-araeoscelidian diapsids must have originated by the end of the Kasimovian Stage of the Carboniferous Period, *ca* 303.9 Ma ago, but definitive fossils first appear only in Middle Permian strata (i.e. in rocks slightly older than 266 Ma), with *Lanthanolania ivakhnenkoi* currently the oldest known non-araeoscelidian diapsid [6]. Diapsids remained rare throughout the rest of the Permian, and only in the Early Triassic, after the end-Permian extinction, did they become common elements of vertebrate communities.

The overwhelming majority of Palaeozoic localities that yield terrestrial vertebrates represent near-water lowland environments, including deltaic, lacustrine, riparian and floodplain sites [2,7]. The Lower Permian upland sediments from the Dolese Quarry near Richards Spur, OK, USA, are the exception, and they preserve what is arguably the richest terrestrial vertebrate fauna of Late Palaeozoic age [8–10].

Collecting at Richards Spur has been ongoing and a recent visit to the locality resulted in the discovery of two partial diapsid skulls. These specimens share a characteristic lacrimal bone morphology, which distinguishes them from other reptiles and supports their identification as a new taxon. Parietal and jugal morphology is indicative of the presence of the upper and lateral temporal fenestrae that are diagnostic of diapsids. Accordingly, we describe the new Richards Spur material here as a new genus and species of diapsid reptile, and investigate the phylogenetic relationships of this new taxon in order to evaluate its impact on diapsid phylogeny and on the earliest chapter of diapsid evolution.

2. MATERIAL

The study material (figure 1) comprises two partial skulls that are reposited in the collections of the Sam Noble Oklahoma Museum of Natural History as OMNH 74606 and 74607. The skulls were prepared mechanically using pin vises. A scanning electron microscope (JEOL NeoScope JCM-5000) was used to examine the parabasisphenoid for denticles. We also examined the parietal described by Carroll [11], which is reposited in the Peabody Museum of Yale University as YPM 4926.

We assign OMNH 74606 and 74607 to the same species because they share a unique lacrimal bone morphology: the lacrimal narrows anteriorly, making a tiny contribution to the external naris, and the bone is curved in the transverse plane for all but its posteriormost approximately 30 per cent (figure 2b,c). OMNH 74606 and 74607 clearly represent a diapsid on the basis of jugal morphology, of which the triradiate shape (figure 2a) is indicative of an unequivocal lateral temporal fenestra, and by parietal morphology (figure 2d), which is indicative of the unequivocal presence of an upper
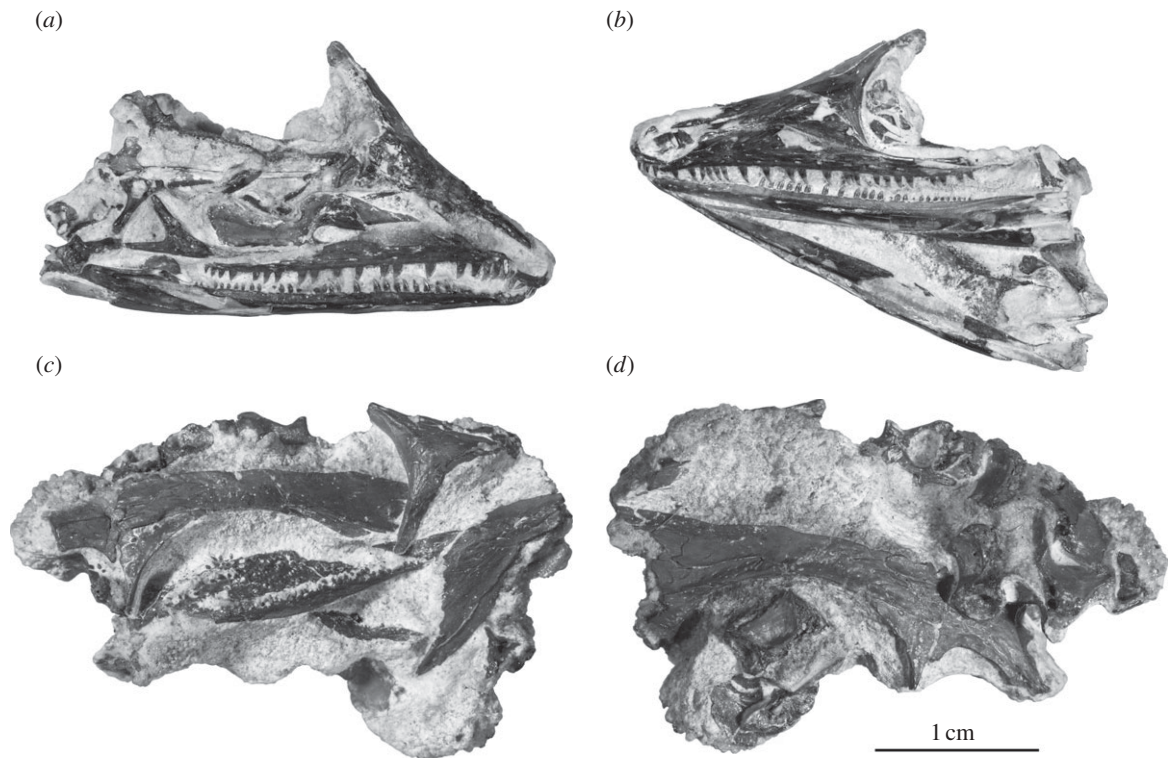
Figure 1. *Orovenator mayorum* n. gen. et sp. Photographs. (*a*) OMNH 74606, holotype, skull in right lateral view, with palatal elements and parabasisphenoid in dorsal view. (*b*) OMNH 74606 in left lateral view, with right pterygoid and parabasisphenoid in palatal view and right mandibular ramus in medial view. (*c*) OMNH 74607, referred specimen, right side of skull roof in dorsal view and right pterygoid in palatal view. (*d*) OMNH 74607, left side of skull roof in dorsal view, with cervical vertebrae in left lateral view and caudal vertebra in posterior view.
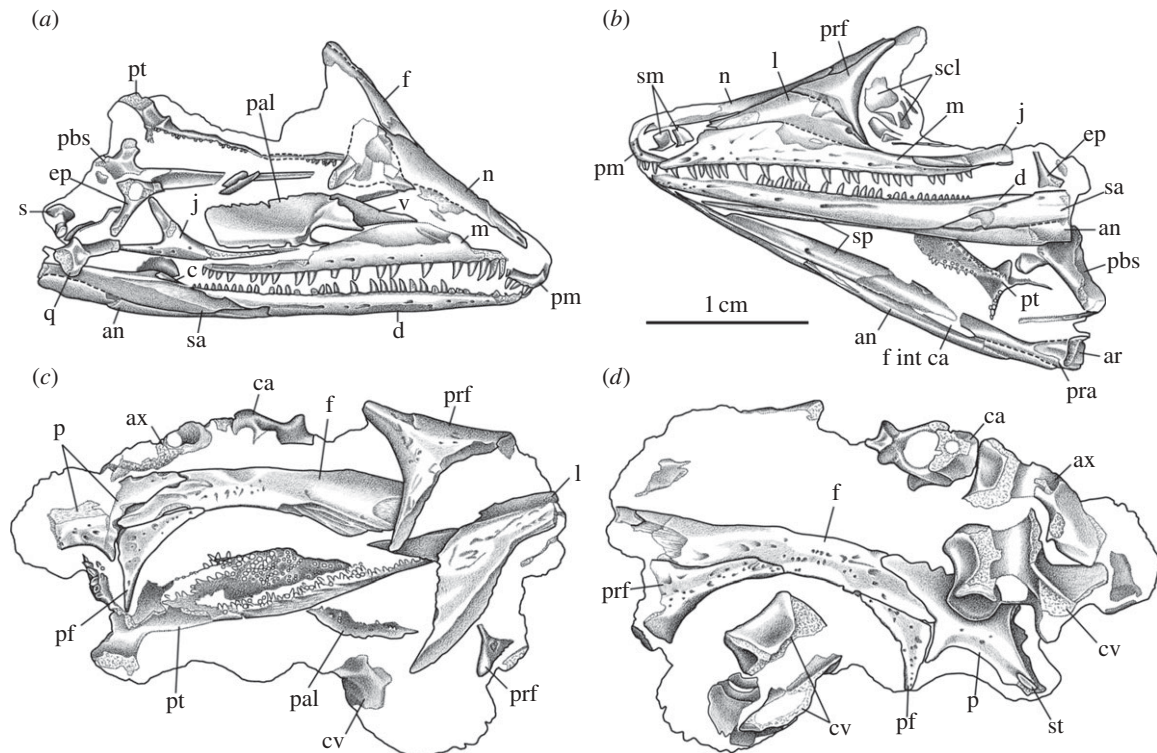

Figure 2. *Orovenator mayorum* n. gen. et sp. Interpretive drawings. (*a*) OMNH 74606, holotype, in right lateral view. (*b*) OMNH 74606 in left lateral view. (*c*) OMNH 74607, referred specimen, right side in dorsal view. (*d*) OMNH 74607, left side in dorsal view. Abbreviations: an, angular; ar, articular; ax, axis; c, coronoid; ca, caudal vertebra; cv, cervical vertebra; d, dentary; ep, epipterygoid; f, frontal; f int ca, foramen intermandibularis caudalis; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pbs, parabasisphenoid; pf, postfrontal; pm, premaxilla; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; s, stapes; sa, surangular; scl, scleral ossicles; sm, septomaxilla; sp, splenials; st, supratemporal; v, vomer.

temporal fenestra. Based on its maxillary morphology (figure 2a,b), with its lack of caniniform teeth and its anteriorly high dorsal lamella (forming most of the posterior margin of the external naris, like this element in *L. ivakhnenkoi*, and unlike the condition seen in captorhinids, araeoscelidians and other basal eureptiles), the new Richards Spur diapsid probably belongs to the sister group of Araeoscelidia. The name Eosuchia, originally erected by Broom [12] as a suborder for the family Youngindae, was attached to the araeoscelidian sister group by Laurin [4]. This reconception of Eosuchia was adopted by a few studies [3,13,14]. However, considering that Eosuchia was long classified as an order of 'primitive lepidosaurians' in pre-cladistic classifications [15], other studies eschewed Eosuchia as a converted clade name [5,6,16]. Regardless, the araeoscelidian sister group is a cohesive group, despite the weak or uncertain interrelationships of its basal (predominantly Palaeozoic) members. It is useful and expedient to attach a formal name to this clade, and towards this purpose we redefine Benton's [17] name Neodiapsida as a stem-based group, as *Youngina capensis* Broom, 1914 [12] and all species more closely related to it than to *Petrolacosaurus kansensis* Lane, 1945 [18]. Laurin [4] did create a phylogenetic definition for Neodiapsida, but his definition is compromised by the use of Younginiformes as a reference taxon, because Younginiformes is probably an artificial grouping [16] (this study). In addition to employing the preferred method of using species as reference taxa, our definition captures Benton's [17] original concept of Neodiapsida as a major clade of diapsids exclusive of *P. kansensis* and other araeoscelidians.

For our phylogenetic analysis, we used the characters and data matrix of Müller [5] as augmented by Bickelmann *et al.* [16]. We recoded some taxa for certain characters (see the electronic supplementary material for data matrix and summary of character coding changes). We deleted the following taxa from our analysis: *Galesphyrus*, *Kenyasaurus*, *Palaeagama*, *Saurosternon* and Testudines. We excluded *Galesphyrus*, *Kenyasaurus* and *Saurosternon* because these three taxa are known from one or two specimens each that preserve only postcrania; we exclude *Palaeagama* because it is known only from a single, badly crushed skeleton [19]. We also excluded Testudines because the relationships of turtles continue to remain contentious [20] and are beyond the scope of this study. We performed a heuristic analysis with a simple-addition sequence and tree bisection, and reconnection branch swapping in PAUP v. 4.0b10. We also conducted a bootstrap analysis (300 replicates). Finally, a Bremer decay analysis was performed using the heuristic algorithm in PAUP, by relaxing parsimony a single step at a time and generating strict consensus trees until resolution was completely lost in the ingroup (Diapsida).

3. SYSTEMATIC PALAEONTOLOGY
Diapsida Osborn, 1903
Neodiapsida Benton 1985 (*sensu* this study).
Orovenator mayorum n. gen. et sp.

(a) Etymology
The generic name is from Classical Greek *oro* for 'mountain', alluding to the Richards Spur locality, which is interpreted to be an exhumed Permian hill [21], and
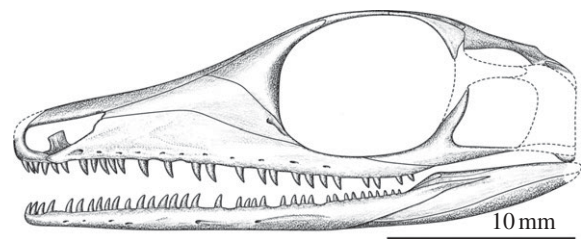
Figure 3. *Orovenator mayorum* n. gen. et sp. Reconstruction of skull roof and mandible in left lateral aspect. Based mainly on OMNH 74606, with information on posterior of skull table from OMNH 74607.

Latin *venator* for 'hunter'. The specific epithet honours Bill and Julie May of Norman, OK, USA, for their contributions to the palaeontology of Oklahoma.

(b) Material
OMNH 74606, holotype, a partial skull preserving snout, parabasisphenoid, palate and mandible (figure 1a,b); and OMNH 74607, referred specimen, a partial skull preserving most of the skull roof, palatal elements and vertebrae (figure 1c,d).

(c) Locality and horizon
Fissure fills at Richards Spur, OK, USA. The fissures have long been regarded as Early Permian in age on the basis of biostratigraphic comparisons with classic continental faunal elements from localities of the surrounding redbed strata [8]. Speleothems from the fissures have been dated to 289 Ma [22], indicating a Sakmarian age for the Richards Spur fauna.

(d) Diagnosis
Small diapsid reptile distinguished by an elongate external naris, a transversely curved lacrimal, a parietal that extends anteriorly along the midline as far as the anteriormost point of the postfrontal, an elongate dentary that extends posteriorly to a point directly ventral to the inferred midpoint of the lateral temporal fenestra, and a surangular that forms a dorsal shelf above the adductor fossa and anteriorly forms a trough receiving the posterodorsal process of the coronoid.

4. DESCRIPTION
OMNH 74606 (figures 1a,b and 2a,b) represents an individual that is slightly smaller than OMNH 74607 (figures 1c,d and 2c,d). Four vertebrae are preserved in the latter specimen, of which three are cervicals and the fourth is a caudal. The cervical vertebrae exhibit the sharp ventral keel that is characteristic of early diapsids [23]. This evidence, together with the observation that the vertebrae are of a size expected for a diapsid of this skull size, suggests to us that the cervicals are correctly associated with the skull. The closed neurocentral sutures of the cervicals indicate that OMNH 74607 is an adult. A reconstruction of the skull roof and mandible in left lateral aspect is shown in figure 3.

(a) Skull roof
OMNH 74606 retains the alveolar portions of both premaxillae (figure 2a,b). Each bone has five isodont,

homodont teeth, which resemble slightly recurved cones with sharp tips. The maxilla is an elongate element (figure 2*a*,*b*). The subnarial process is long and low, indicating that the external naris was anteroposteriorly elongate. The alveolar region is surmounted by a low dorsal process. The maxilla, however, is relatively higher anteriorly than in araeoscelidians [24,25], as evidenced by its contribution to the posterior end of the external naris, and the maxilla exhibits the same approximate outline anteriorly as that restored for the maxilla of *Y. capensis* [26]. There are 31 maxillary tooth positions on the left side of OMNH 74606, of which 10 are empty. The anterior five or six teeth resemble the premaxillary teeth, but are slightly larger. Teeth in the succeeding seven or eight tooth positions are distinctly larger, but they do not form a caniniform region, nor is any one tooth large enough to be identified as a caniniform.

What is preserved of the incomplete nasals indicates that each was a long, slightly curved sheet of bone. Both septomaxillae are visible in the left naris of OMNH 74606 (figure 2*b*). Each is a polygonal bone with a thickened anterior margin that would have formed the posterior margin of the nostril proper.

The lacrimal is highly distinctive in *Orovenator* (figure 2*b*,*c*). Unlike the flat or faintly curved lacrimals of other early reptiles, the lacrimal of this diapsid can be divided into a laterally facing posterior portion and a dorsally facing anterior portion. The two distinct external surfaces of the lacrimal meet along a narrowly curved region that extends from the contact with the dorsal margin of the maxilla, posteriorly across the central portion of the lacrimal and onto the prefrontal. Anteriorly the lacrimal narrows to make a relatively small contribution to the external naris.

The prefrontal is a conspicuously triradiate element. The facial portion has a distinct dorsal exposure, which transitions ventrally to a convex lateral exposure. OMNH 74607 preserves a complete, relatively slender frontal (figure 2*c*,*d*). It extends posteriorly as far as the posteriormost margin of the postfrontal. The postfrontal is a distinctly triangular element that forms the posterodorsal corner of the orbit. It is excluded from the upper temporal fenestra by the parietal and the postorbital, and there is no excavation or fossa associated with the fenestra along the posterior region of the bone, as seen in *Y. capensis* [27].

OMNH 74607 preserves a nearly complete left parietal and a fragmentary right element. Comparisons with other taxa and YPM 4926 are complicated because the pineal foramen is obscured by a cervical vertebra. The parietal extends nearly as far anteriorly as the anteriormost tip of the postfrontal (figure 2*c*,*d*). The free lateral margin of the parietal contributing to the upper temporal fenestra is more deeply embayed than that of *Petrolacosaurus* [24], such that the fenestra extends medially almost to a plane that is parasagittal to the medial margin of the postfrontal. However, the upper temporal fenestra does not excavate the parietal quite as deeply as in *Y. capensis* [26], where the fenestra is restored as extending as far medially as the postfrontal. The posterior margin of the parietal of *O. mayorum* is emarginated more deeply than in *Y. capensis*, such that the posterior margin of the skull table would have featured a bilateral emargination (as restored for YPM 4926 by Carroll [11]). Extending posteroventrally from the

posterior margin of the skull table is a relatively deep occipital flange (foreshortened in figure 2*d*). The occipital flange is largely smooth, apart from fine, shallow parasagittal grooves that may represent roughened surfaces for contact with the postparietal and the tabular (neither of which is preserved). The parietal receives the supratemporal in a small, dorsal furrow on its posterolateral process. A small fragment of the supratemporal is preserved in this position on the left side.

The jugal is a slender, triradiate element with a long suborbital process, and a long, overlapping suture with the maxilla (figure 2*a*). The slender subtemporal process attenuates posteriorly, but the tip is covered by the quadrate, and we are unable to determine whether the jugal would make contact with the quadratojugal or if it ends freely posteriorly, as this element does in many later diapsids [6,16].

(b) *Palate and braincase*

The palate is represented by all elements, whereas the braincase is represented only by the parabasisphenoid and the right stapes. Vomers are exposed only in dorsal aspect and little is visible beyond what is shown in figure 2*a*. The palatine has a distinctly rectangular outline, much like that of *P. kansensis*, but it also has a relatively long vomerine process, as in *Y. capensis*, suggesting that the choana extended relatively farther posteriorly than in *P. kansensis* [24]. It has a transversely narrow maxillary pedicel for contacting the skull roof, and a relatively long, straight lateral edge for the medial margin of a narrow suborbital fenestra (figure 2*a*). The ventral surface of the palatine bears at least two clusters of small conical teeth. The pterygoid is an elongate element with three clusters of small teeth, one bordering the interpterygoid vacuity, another forming half of the pterygo-palatine cluster and the third on the transverse flange. The tooth-bearing posterior margin of the transverse flange is oriented perpendicular to the midline, as in *Y. capensis* [26]. The ectopterygoid (not shown) is a relatively broad element reminiscent of that in *P. kansensis*.

Both elements of the palatoquadrate complex are preserved. The epipterygoid consists of a transversely thick triangular base and a narrow columella (figure 2*a*,*b*). A tiny, lenticular facet positioned anteroventrally on the medial surface of the base indicates that the epipterygoid made a minor contribution to the basicranial recess. The quadrate (figure 2*a*) is a relatively small, compact element that resembles that of *Acerosodontosaurus piveteaui* [16], with a conspicuous shelf on its posterior margin for the reception of the paroccipital process. The posterior margin of the dorsal lamella is straight and there is no conch. The condyle is not preserved, but what remains of the condylar base suggests that the condyles were anteroposteriorly narrow.

The parabasisphenoid is characterized by an elongate cultriform process (figure 2*a*,*b*). The anterolaterally oriented basipterygoid process exhibits a bifaceted articulating surface. Ventrally there is a conspicuous vidian sulcus. The bases of tiny denticles are present on a roughened portion of the crista ventrolateralis, and a few denticles are present centrally on the ventral surface (of which all but one are obscured by the left angular in figure 2*b*). The stapes consists of an expanded footplate
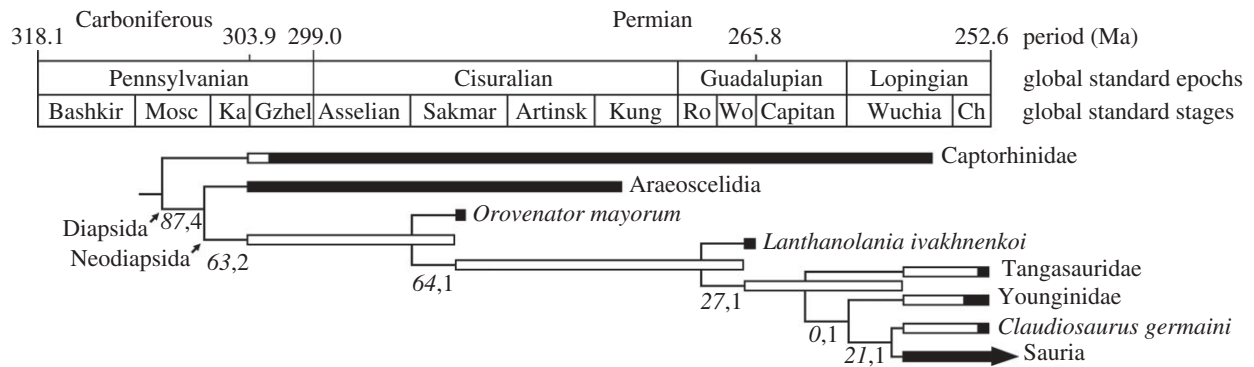
Figure 4. Temporal calibration of single optimal tree discovered in a PAUP heuristic analysis of Diapsida [31]. Black bars are known ranges, open bars are ghost taxa and ghost lineages. Tree length = 873, consistency index (CI) = 0.4605, CI excluding informative characters = 0.4586, retention index = 0.5802, rescaled CI = 0.2672. Clade support indicated by numbers subtending branches (italic numbers = bootstrap support values; roman numbers = Bremer decay values). Neodiapsida is diagnosed by the following unambiguous synapomorphies: lower temporal fenestra is present but open ventrally (character 17, state 2); caniniform teeth absent from maxilla (character 39, state 1); subtemporal process of jugal is slender/narrow (character 91, state 1). Some clades have been condensed into the following taxa (with included terminal taxa): Sauria (Archosauromorpha + Lepidosauromorpha); Tangasauridae (*Tangasaurus* (*Acerosodontosaurus* + *Hovasaurus*)); Younginidae (*Thadeosaurus* + *Youngina*).

that narrows into a short, robust columella, from which extends a short dorsal process.

(c) Mandible
The dentary is an astonishingly slender element. The slightly eroded right mandibular ramus exhibits an extensive sutural surface on the angular for the dentary, and shows that the latter bone extended relatively far posteriorly, to a point directly ventral to the inferred midpoint of the lateral temporal fenestra (figures 2a and 3). This is in strong contrast to the condition documented for araeoscelidians, in which the dentary extends no farther posteriorly than the back of the orbit [24,25], but not that different from Carroll's [26] reconstruction of *Y. capensis*, in which the dentary extends posteriorly to a level just behind the postorbital bar. There are 42 tooth positions in the right dentary of OMNH 74606, a few of which are empty. This is the highest known complement of marginal teeth in a Palaeozoic neodiapsid, but may be matched by *A. piveteaui*, which preserves at least 34 tooth positions in its incomplete dentary [16,28]. The teeth are smaller versions of the upper marginal series. The splenial is remarkably slender. The posterior end of the right splenial is preserved as an impression, and appears to form the anterodorsal margin of a well-developed foramen intermandibularis caudalis.

Only the posterodorsal end of the coronoid is exposed (figure 2a), and it is nestled in a dorsal trough formed by the surangular. It forms the anterior end of a relatively low coronoid eminence. The surangular is a relatively low element with a narrow shelf that forms the dorsal margin of the adductor fossa. The similarly low angular appears to be little more than a narrow, gently curving sheet of bone with a conspicuous ventral ridge. The angular forms most of the ventral margin of the foramen intermandibularis caudalis. The posterodorsal margin of this foramen is formed by the prearticular, which also forms the medial rim of the adductor fossa. The expanded end of this bone sheaths the ventral surface of the articular, of which only the anterior end is

preserved (figure 2b). As this is surrounded by other mandibular elements and the quadrate, the articular is exposed only in sectional view and no anatomical detail is visible.

(d) Vertebrae
Three cervical vertebrae and a single caudal are preserved in OMNH 74607 (figure 2d). All are deeply amphicoelous. The caudal is definitely notochordal (the cervicals are presumably so). Each cervical exhibits a sharply keeled centrum that is approximately 70 per cent as high as it is long and fused to its neural arch. The anterior of the semi-articulated cervicals exhibits an anteroposteriorly longer neural spine than the other, allowing us to identify it as the axis. Unfortunately, the dorsal region of its neural spine is missing and little more can be said of this structure beyond the observation that the posterior edge is slightly convex. The cervicals are clearly not as elongate as are those of araeoscelidians [24,25]. The proportions of the best-preserved vertebra, cervical 3, are similar to those of cervical vertebrae of *Y. capensis* [29]. Neither the mamillary processes described in araeoscelidians [24,25] nor the extra intervertebral processes described in *Y. capensis* and other 'younginiforms' [29,30] are present. The caudal vertebra, which is smaller than the cervicals, exhibits an open neurocentral suture (figure 2d). Its association with the skull is less certain than the cervicals, and its ontogenetic stage is different from that of the cervicals.

5. DISCUSSION
Our phylogenetic analysis positions *O. mayorum* as the most basal neodiapsid (figure 4). Support for Neodiapsida is moderate, with bootstrap and Bremer support values of 63 per cent and 2, respectively. More than half of the clades within Neodiapsida collapse with a single extra step, and all but four clades collapse with two extra steps. Diapsida is the strongest ingroup clade in our analysis, with bootstrap and Bremer support values of 87 per cent and 4, respectively. Overall weakness of

the phylogeny is not unexpected because Palaeozoic neo-diapsids could not be scored for 39 to 89 per cent of the characters (versus 1–42% for Mesozoic neodiapsids). Overall, the range of Bremer values found in this analysis does not differ greatly from those discovered for most clades in other recent analyses of Permo-Triassic taxa [32–34].

The neodiapsid identification of *O. mayorum* and its presence at Richards Spur has important implications for early diapsid evolution. This fossil locality is famous for producing thousands of skeletal elements of small ter-restrial vertebrates, which represent more than 30 tetrapod species [35]; in eight decades of collecting, only a single aquatic vertebrate fossil (a shark tooth [8]) has been recovered from the locality. Accordingly, palaeontologists have traditionally regarded the Richards Spur vertebrate assemblage to represent an upland tetra-pod fauna [7,9,10], one that differs significantly in composition with the lowland tetrapod faunas of the sur-rounding redbed localities of the southwestern USA. This view of the Richards Spur fauna dovetails well with the geological interpretation of the locality as an exhumed Permian hill [21], preserving a unique preservational set-ting for the Palaeozoic. *Orovenator* is the latest addition to this late Palaeozoic upland tetrapod fauna.

Following recent work that dates the Richards Spur fauna to 289 Ma [22], it is evident that *Orovenator* signifi-cantly reduces the ghost taxon for Neodiapsida (figure 4). Neodiapsids are otherwise absent from the Lower Per-mian and most of the Middle Permian. They are not found in lowland localities, unlike their araeoscelidian relatives [24,25], until *ca* 266 Ma. We suggest that this is because of ecological partitioning: the separation of diapsids into araeoscelidian and neodiapsid lines may have resulted in araeoscelidians having adapted to low-land environments, whereas neodiapsids adapted to upland habitats, which are usually not preserved except under extraordinary conditions, such as those at Richards Spur. This hypothesis is supported by a relatively rich fossil record for araeoscelidians (at least 44 specimens known from eight formations) with respect to neodiapsids (three specimens, all from Richards Spur) during the first 30 Myr of diapsid history (see the electronic supplemen-tary material). Whereas we recognize that our hypothesis draws greatly on negative evidence (i.e. the absence of neodiapsid fossils at lowland localities), the record of 14 specimens (individuals) of *Araeoscelis* from three different formations of the Lower Permian of north-central Texas [25,36], a region that has been well sampled by palaeon-tologists over the past 140 years and consists of numerous localities that preserve small vertebrates [37], supports our view that the lack of neodiapsid fossils in southwes-tern USA is not attributable to poor preservation potential for diapsids.

The disappearance of araeoscelidians at the end of the Early Permian might have allowed neodiapsids to expand their ranges to the lowlands, which would account for the preservation of later neodiapsids such as *Lanthanolania* in the Mezen Basin of eastern Europe and *Youngina* in the Karoo Basin of southern Africa. Neodiapsids, however, continued to be relatively small, rare members of terres-trial vertebrate ecosystems until the appearance of archosauriforms (*Archosaurus rossicus*) at the very end of the Palaeozoic Era.

Thus, the remarkable scarcity of late Palaeozoic neo-diapsids suggests that they occupied more upland environments. Only two localities of this time are inter-preted as preserving an upland tetrapod fauna. One of these, the Bromacker Quarry in the Tambach Basin of Germany, has yielded a small, diverse Early Permian fauna of amphibians, diadectomorphs, synapsids and rep-tiles [38], but has yet to produce a diapsid fossil. Bromacker, however, represents a high-altitude basin and, in addition to preserving a different tetrapod com-munity, it differs substantially geologically from the Dolese Quarry. Notably, the most common members of Bromacker are diadectomorphs and seymouriamorph amphibians, tetrapods that are very rare at Richards Spur.

YPM 4926, an isolated diapsid parietal described by Carroll [11], probably belongs to another neodiapsid species. It is slightly larger than the parietal of OMNH 74607, but exhibits definite morphological differences, such as the relative size and shape of the posterolateral process, and the size and shape of the temporal flange, which we believe are taxonomic. Recent collecting efforts at the Richards Spur locality have been successful in dis-covering new, superbly preserved terrestrial vertebrates, and we expect that this ongoing work will yield more data on early diapsid evolution.

The exhumed Palaeozoic hills (Dolese Quarry and the Slick Hills) of Oklahoma, therefore, represent a unique window into the evolution of terrestrial vertebrate com-munities at a time when diapsid reptiles, such as *Orovenator*, were rare elements of those communities, before neodiapsids came into their dominant role during the Mesozoic Era.

REFERENCES

1 Reisz, R. R. & Dilkes, D. W. 2003 *Archaeovenator hamiltonensis*, a new varanopid (Synapsida: Eupelyco-sauria) from the Upper Carboniferous of Kansas. *Can. J. Earth Sci.* **40**, 667–678. (doi:10.1139/E02-063)

2 Reisz, R. R. & Modesto, S. P. 2007 *Heleosaurus scholtzi* from the Permian of South Africa: a varanopid synapsid, not a dia-psid reptile. *J. Vert. Paleontol.* **27**, 734–739. (doi:10.1671/0272-4634(2007)27[734:HSFTPO]2.0.CO;2)

3 Reisz, R. R., Laurin, M. & Marjanovic, D. 2010 *Apsisaurus witteri* from the Lower Permian of Texas: yet another small varanopid synapsid, not a diapsid. *J. Vert. Paleontol.* **30**, 1628–1631. (doi:10.1080/02724634.2010.501441)

4 Laurin, M. 1991 The osteology of a Lower Permian eosu-chian diapsid from Texas and a review of diapsid phylogeny. *Zool. J. Linnean Soc.* **101**, 59–95. (doi:10.1111/j.1096-3642.1991.tb00886.x)

5 Müller, J. 2004 The relationships among diapsid reptiles and the influence of taxon selection. In *Recent advances in the origin and early radiation of vertebrates* (eds G. Arratia, M. V. H. Wilson & R. Cloutier), pp. 379–408. Munich, Germany: Verlag Dr. Friedrich Pfeil.

6 Modesto, S. P. & Reisz, R. R. 2003 An enigmatic new diapsid reptile from the Upper Permian of Eastern Europe. *J. Vert. Paleontol.* **22**, 851–855. (doi:10.1671/0272-4634(2002)022[0851:ANEDRF]2.0.CO;2)

7 Sullivan, C., Reisz, R. R. & May, W. J. 2000 Large dissorophoid skeletal elements from the Lower Permian Richards Spur fissures, Oklahoma, and their paleoecological implications. *J. Vert. Paleontol.* **20**, 456–461. (doi:10.1671/0272-4634(2000)020[0456:LDSEFT]2.0.CO;2)

8 Olson, E. C. 1991 An eryopoid (Amphibia: Labyrinthodontia) from the Fort Sill fissures, Lower Permian, Oklahoma. *J. Vert. Paleontol.* **11**, 130–132. (doi:10.1080/02724634.1991.10011379)

9 Evans, D. C., Maddin, H. C. & Reisz, R. R. 2009 A re-evaluation of sphenacodontid synapsid material from the Lower Permian fissure fills near Richards Spur, Oklahoma. *Palaeontology* **52**, 219–227. (doi:10.1111/j.1475-4983.2008.00837.x)

10 Reisz, R. R., Schoch, R. R. & Anderson, J. S. 2009 The armoured dissorophid *Cacops* from Early Permian of Oklahoma and the exploitation of the terrestrial realm by amphibians. *Naturwissen* **96**, 789–796. (doi:10.1007/s00114-009-0533-x)

11 Carroll, R. L. 1968 A diapsid (Reptilia) parietal from the Lower Permian of Oklahoma. *Postilla* **117**, 1–7.

12 Broom, R. 1914 A new thecodont reptile. *Proc. Zool. Soc. Lond.* **1914**, 1072–1077. (doi:10.1111/j.1469-7998.1914.tb07729.x)

13 deBraga, M. & Reisz, R. R. 1995 A new diapsid reptile from the uppermost Carboniferous (Stephanian) of Kansas. *Palaeontology* **38**, 199–212.

14 Senter, P. 2004 Phylogeny of Drepanosauridae (Reptilia: Diapsida). *J. Syst. Palaeont.* **2**, 257–268. (doi:10.1017/S1477201904001427)

15 Romer, A. S. 1956 *Osteology of the reptiles*. Chicago, IL: Chicago University Press.

16 Bickelmann, C., Müller, J. & Reisz, R. R. 2009 The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Upper Permian of Madagascar and the paraphyly of 'younginiform' reptiles. *Can. J. Earth Sci.* **46**, 651–661. (doi:10.1139/E09-038)

17 Benton, M. J. 1985 Classification and phylogeny of the diapsid reptiles. *Zool. J. Linnean Soc.* **84**, 97–164. (doi:10.1111/j.1096-3642.1985.tb01796.x)

18 Lane, H. H. 1945 New Mid-Pennsylvanian reptiles from Kansas. *Trans. Kansas Acad. Sci.* **47**, 1–3. (doi:10.2307/3625454)

19 Carroll, R. L. 1977 The origin of lizards. In *Problems in vertebrate evolution* (eds S. M. Andrews, R. S. Miles & A. D. Walker), pp. 359–396. Linnean Society Symposium Series 4.

20 Lyson, T. R., Bever, G. S., Bhullar, B.-A. S., Joyce, W. G. & Gauthier, J. A. 2010 Transitional fossils and the origin of turtles. *Biol. Lett.* **6**, 830–833. (doi:10.1098/rsbl.2010.0371)

21 Donovan, R. N. 1986 Geology of the Slick Hills. In *The Slick Hills of southwestern Oklahoma—fragments of an Aulacogen?* (ed. R. N. Donovan), pp. 1–12. Norman, OK: Oklahoma Geological Survey (Guidebook 24).

22 Woodhead, J., Reisz, R., Fox, D., Drysdale, R., Hellstrom, J., Maas, R., Cheng, H. & Lawrence Edwards, R. 2010 Speleothem climate records from deep time? Exploring the potential with an example from the Permian. *Geology* **38**, 455–458. (doi:10.1130/G30354.1)

23 Laurin, M. & Reisz, R. R. 1995 A reevaluation of early amniote phylogeny. *Zool. J. Linnean Soc.* **113**, 165–223. (doi:10.1111/j.1096-3642.1995.tb00932.x)

24 Reisz, R. R. 1981 *A diapsid reptile from the Pennsylvanian of Kansas*, vol. 7, pp.1–74. (Special Publication Museum of Natural History). Lawrence, KS: University of Kansas.

25 Reisz, R. R., Berman, D. S. & Scott, D. 1984 The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. *J. Vert. Paleontol.* **4**, 57–67. (doi:10.1080/02724634.1984.10011986)

26 Carroll, R. L. 1981 Plesiosaur ancestors from the Upper Permian of Madagascar. *Phil. Trans. R. Soc. Lond. B* **293**, 315–383. (doi:10.1098/rstb.1981.0079)

27 Reisz, R. R., Modesto, S. P. & Scott, D. 2000 *Acanthotoposaurus bremneri* and the origin of the Triassic archosauromorph reptile fauna of South Africa. *S. Afr. J. Sci.* **96**, 443–445.

28 Currie, P. J. 1980 A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Can. J. Earth Sci.* **17**, 500–511. (doi:10.1139/e80-046)

29 Currie, P. J. 1981 The vertebrae of *Youngina* (Reptilia: Eosuchia). *Can. J. Earth Sci.* **18**, 815–818.

30 Currie, P. J. & Carroll, R. L. 1984 Ontogenetic changes in the eosuchian reptile *Thadeosaurus*. *J. Vert. Paleontol.* **4**, 68–84. (doi:10.1080/02724634.1984.10011987)

31 Osborn, H. F. 1903 On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* **17**, 275–276. (doi:10.1126/science.17.424.275-b)

32 Dilkes, D. W. 1998 The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Phil. Trans. R. Soc. Lond. B* **353**, 501–541. (doi:10.1098/rstb.1998.0225)

33 Fröbisch, J. 2007 The cranial anatomy of *Kombuisia frerensis* Hotton (Synapsida, Dicynodontia) and a new phylogeny of anomodont therapsids. *Zool. J. Linnean Soc.* **150**, 117–144. (doi:10.1111/j.1096-3642.2007.00285.x)

34 Modesto, S. P., Scott, D. M., Botha-Brink, J. & Reisz, R. R. 2010 A new and unusual procolophonid parareptile from the Lower Triassic Katberg Formation of South Africa. *J. Vert. Paleontol.* **30**, 715–723. (doi:10.1080/02724631003758003)

35 Reisz, R. 2007 Terrestrial vertebrate fauna of the Lower Permian cave deposits near Richards Spur Oklahoma with emphasis on dissorophoids. *J. Vert. Paleontol.* **27**(Suppl. 3), 133A.

36 Vaughn, P. P. 1955 The Permian reptile *Araeoscelis* restudied. *Bull. Mus. Comp. Zool.* **113**, 305–469.

37 Heaton, M. J. 1979 Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian [of] Oklahoma and Texas. *Okla. Geol. Surv. Bull.* **127**, 1–84.

38 Eberth, D. A., Berman, D. S., Sumida, S. S. & Hopf, H. 2000 Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, central Germany): the upland Holy Grail. *Palaios* **15**, 293–313. (doi:10.1669/0883-1351(2000)015<0293:LPTPAV>2.0.CO;2)