

# A late-surviving basal theropod dinosaur from the latest Triassic of North America

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The oldest theropod dinosaurs are known from the Carnian of Argentina and Brazil. However, the evolutionary diversification of this group after its initial radiation but prior to the Triassic–Jurassic boundary is still poorly understood because of a sparse fossil record near that boundary. Here, we report on a new basal theropod, *Daemonosaurus chauliodus* gen. et sp. nov., from the latest Triassic ‘siltstone member’ of the Chinle Formation of the *Coelophysis* Quarry at Ghost Ranch, New Mexico. Based on a comprehensive phylogenetic analysis, *Daemonosaurus* is more closely related to coeval neotheropods (e.g. *Coelophysis bauri*) than to Herrerasauridae and *Eoraptor*. The skeletal structure of *Daemonosaurus* and the recently discovered *Tawa* bridge a morphological gap between *Eoraptor* and Herrerasauridae on one hand and neotheropods on the other, providing additional support for the theropod affinities of both *Eoraptor* and Herrerasauridae and demonstrating that lineages from the initial radiation of Dinosauria persisted until the end of the Triassic. Various features of the skull of *Daemonosaurus*, including the procumbent dentary and premaxillary teeth and greatly enlarged premaxillary and anterior maxillary teeth, clearly set this taxon apart from coeval neotheropods and demonstrate unexpected disparity in cranial shape among theropod dinosaurs just prior to the end of the Triassic.

**Keywords:** Dinosauria; Theropoda; Late Triassic; Chinle Formation; New Mexico

## 1. INTRODUCTION

The oldest known theropod dinosaurs are Carnian in age [1–3]. The best-documented assemblage of basal theropods, from the Ischigualasto Formation of northwestern Argentina, already comprises at least three or four taxa (*Eodromaeus*, *Herrerasaurus*, *Sanjuansaurus*; the affinities of *Eoraptor* remain contentious [1,4,5]), which occur together with basal sauropodomorphs and an ornithischian [1,4–12]. Thus, the three principal lineages of dinosaurs originated before the Carnian. The Late Triassic record of theropods outside North America after their initial diversification is largely restricted to a few partial skeletons (e.g. *Lilienstermus*) and isolated bones from Europe or exceptional finds of rare taxa (e.g. *Zupaysaurus*) from other regions with poor chronostratigraphic control [9,10]. By contrast, North America has a rapidly growing theropod record in increasingly chronostratigraphically well-constrained strata extending up to the Triassic–Jurassic boundary in southwestern USA [13]. The Late Triassic record of dinosaurs from North America was long considered one of the most extensive [14]. However, a recent review, using an explicitly apomorphy-based approach to specimen identification, demonstrated that many of the published records were either based on incorrectly identified skeletal remains or on bones that were essentially indistinguishable from those

of the only well-documented Late Triassic theropod from North America, *Coelophysis bauri* [15]. Subsequently, a new taxon of basal theropod, *Tawa hallae*, from the late Norian Petrified Forest Member of the Chinle Formation at Ghost Ranch, New Mexico, established that theropod dinosaurs had a more complex evolutionary history prior to the origin of Neotheropoda than previously inferred [16]. With the exception of *Chindesaurus bryansmalli* [15], *T. hallae* [16], and an unnamed form from the Norian of western Texas [17], all other Norian-age theropods belong to Neotheropoda. Here, we report on a distinctive new taxon of basal theropod from the probably Rhaetian-age ‘siltstone member’ of the Chinle Formation [18] of the *Coelophysis* Quarry at Ghost Ranch that substantially adds to our knowledge of the early evolutionary history of this group.

## 2. SYSTEMATIC PALAEOLOGY

Dinosauria Owen 1842

Saurischia Seeley 1887

Theropoda Marsh 1881

*Daemonosaurus chauliodus* gen. et sp. nov.

### (a) *Etymology*

The generic nomen is derived from Greek *daimon*, evil spirit, and Greek *sauros*, reptile, in allusion to legends about evil spirits at Ghost Ranch, New Mexico. The specific epithet is derived from Greek *chauliodous*, with prominent teeth.

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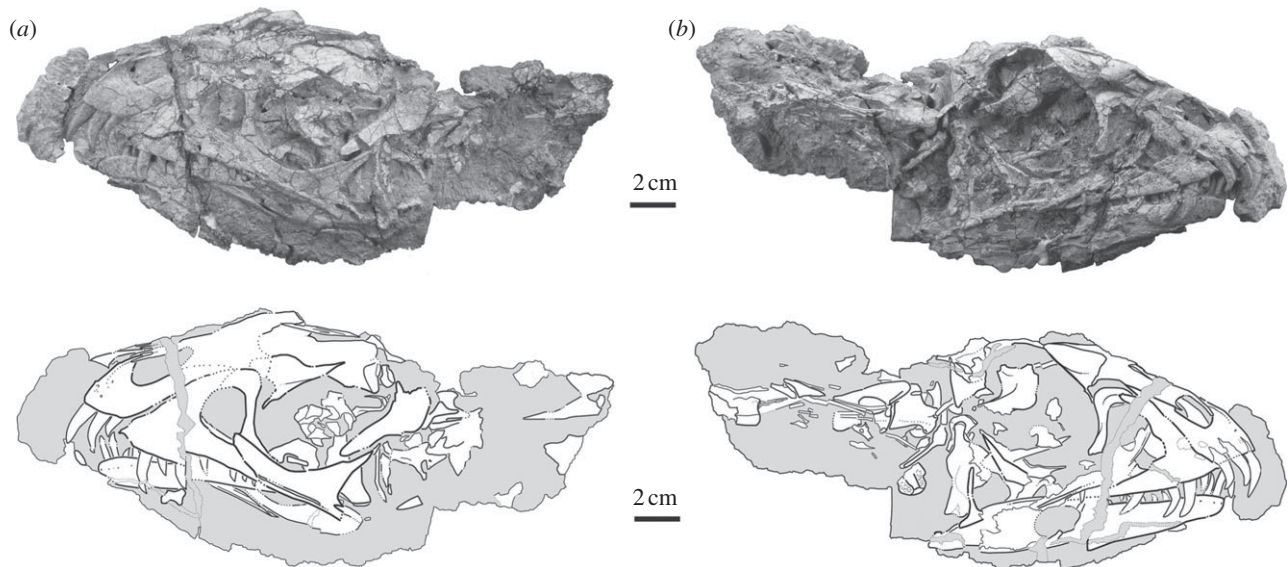


Figure 1. *Daemonosaurus chauliodus* gen. et sp. nov. (holotype; CM 76821), skull and anterior cervical vertebrae in (a) left lateral and (b) right lateral views. Lower row shows interpretative drawings with outlines of skeletal elements and with matrix indicated in grey.

#### (b) *Holotype*

CM (Carnegie Museum of Natural History) 76821, nearly complete but transversely crushed skull with mandible and associated anterior cervical vertebrae and ribs (figure 1). It is possible that additional postcranial bones will be retrieved during further preparation of the large block C-4-81 [19] in which CM 76821 was discovered in association with skeletal remains of *C. bauri*.

#### (c) *Locality and horizon*

*Coelophysis* Quarry [20], Ghost Ranch, 20 km northwest of Abiquiú, Rio Arriba County, New Mexico, USA. Geographical coordinates: latitude 36°20' N, longitude 106°27'30" E. 'Siltstone member' of the Chinle Formation [18]; Late Triassic (probably Rhaetian) [13,21].

#### (d) *Diagnosis*

Distinguished by the following unique combination of characters: skull proportionately deep and narrow, with short antorbital region; premaxillary and anterior maxillary teeth much enlarged relative to more posterior maxillary teeth; prefrontal large and occupies about 50 per cent of the dorsal margin of the orbit; ventral process of lacrimal with slender posterior projection extending along anterodorsal margin of jugal; dorsoventrally deep jugal with prominent lateral ridge; postorbital with anterolateral overhang over orbit; first two dentary teeth large and procumbent; alveolar margin of dentary downturned at symphysis; and third cervical vertebra with deep, rimmed, ovoid pleurocoel on the anterolateral surfaces of both centrum and neural arch. Possible autapomorphies of *Daemonosaurus* include long posterior process of premaxilla that almost contacts anterior process of lacrimal and antorbital fenestra nearly the same size as external naris. *Daemonosaurus* differs from *Herrerasaurus ischigualastensis* [6,22] in having a much anteroposteriorly shorter antorbital fenestra, a posteroventral process of lacrimal that extends along the anterodorsal margin of the jugal, and much enlarged premaxillary teeth. *Daemonosaurus* differs from *Eodromaeus murphi* [1]

in the absence of a distinct ridge on the lateral side of the maxilla, the proportionately much smaller antorbital fossa, presence of much enlarged premaxillary teeth, presence of a posteroventral process of the lacrimal that extends along the anterodorsal margin of the jugal, and greater dorsoventral expansion of the jugal. *Daemonosaurus* differs from *Eoraptor lunensis* [4] in the presence of much enlarged premaxillary and anterior maxillary teeth and a much more restricted antorbital fossa on the maxilla. *Daemonosaurus* differs from *T. hallae* [16] and the neotheropod *C. bauri* [19,21,23,24] especially in the presence of a dorsoventrally deep premaxilla, a slight subnarial gap and a proportionately larger prefrontal. *Daemonosaurus* differs from *Chindesaurus bryansmalli* [14,15] in the presence of an ovoid deep depression on the anterior portion of the centra of postaxial cervical vertebrae (postaxial cervical vertebrae are the only bones currently known for both taxa).

#### (e) *Ontogenetic age*

It is difficult to assess the ontogenetic stage of CM 76821. To date, no postcranial bones other than a few cervicals for this specimen have been recovered; histological data from these elements are typically used to assess individual age [25]. The proportionately large orbit, short snout and lack of fusion between the constituent elements of the braincase in CM 76821 are commonly considered indicators of somatic immaturity among theropod dinosaurs [26]. However, the neurocentral sutures between the centrum and neural arch on the axis and third cervical vertebra of CM 76821 are closed. The sequence of closure of these sutures (anterior to posterior versus posterior to anterior) in theropods is poorly understood, and both sequences of closure are present in that group [27]. In Crocodylia and other suchian archosaurs, closure of the neurocentral sutures proceeds from posterior to anterior [27,28]. If the latter pattern was present in *Daemonosaurus*, CM 76821 might represent a skeletally more mature individual, with the apparently juvenile features being autapomorphies of this taxon.

**(f) Comments**

Post-burial compaction of the enclosing mudstone matrix led to transverse flattening of the skull of CM 76821 and extensive fracturing of individual bones. As a result of this damage, identification of some sutures is difficult, and there has also been loss of bone in a number of places. Many of the cranial bones were separated and displaced from neighbouring elements. The paired bones comprising the skull roof were disarticulated along the midline so that their dorsal surfaces now face towards their respective sides. Much of the postorbital region of the skull, including much of the braincase, has disintegrated. The bones of the palate are partially obscured by other cranial elements. The mandibular rami were disarticulated at the symphysis and displaced. The right side of the snout incurred some damage when an inexperienced volunteer first uncovered the skull. Careful mechanical preparation subsequently exposed the more completely preserved left side of the skull. Examination of both sides of the skull now permits identification and interpretation of most cranial features.

**3. DESCRIPTION**

The lightly built skull is narrow and relatively deep with a proportionately large orbit (figures 1 and 2). It has a length of about 140 mm (measured from the tip of the premaxilla to the posterior margin of the quadrate on the right side), of which the antorbital region comprises only about 50 per cent. The external narial fenestra is elliptical, with its long axis extending anteroventrally, and faces laterally; its greatest length (on the right side) is 20 mm. The orbit is proportionately large (with an estimated anteroposterior diameter of 50 mm on the left side) and appears to be subcircular rather than oval as is typical for Neotheropoda [26]. Part of a collapsed ring of scleral ossicles is preserved in the left orbit. The infratemporal fenestra is shorter anteroposteriorly than tall dorsoventrally. The subtriangular antorbital fenestra (anteroposterior length of 19 mm; left side) is much smaller than the orbit and comparable in size to the external naris. The premaxilla has a roughly quadrangular, posteriorly inclined and dorsoventrally deep body similar to that of *Herrerasaurus* [6]. It holds three much enlarged teeth, which decrease in size from the first to the third and are slightly procumbent. The broad posterior process of the premaxilla extends back beyond the posterior margin of the external naris, which is located well dorsal to the alveolar margin as in *Herrerasaurus*. It excludes the maxilla from participation in the posterior margin of the external naris and almost reaches the anterior process of the lacrimal. The anteroventral margin of the external narial fenestra is bordered by a shallow fossa. A small foramen opens in this depression. Posteriorly, the dorsal (nasal) processes of the premaxillae insert between two anterior processes of each nasal, forming an elongated W-shaped suture between these elements across the slender internarial bar. The anteriorly tall maxilla has a gently convex alveolar margin, which curves somewhat dorsally near the suture with the premaxilla. Its dorsal process diverges from the tooth-bearing ramus at a steep angle and is confluent with the anterior edge of the maxilla. Although both sides of the snout are slightly damaged in this region there is no unequivocal evidence for a

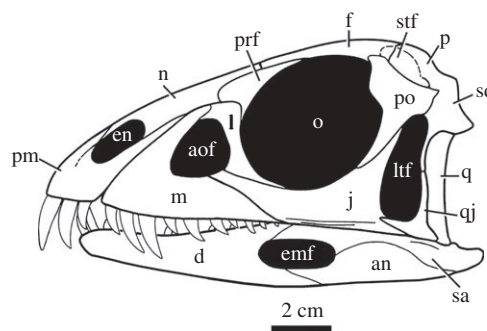


Figure 2. *Daemonosaurus chauliodus* gen. et sp. nov., outline reconstruction of the skull in left lateral view (based on CM 76821). Abbreviations: an, angular; aof, antorbital fenestra; d, dentary; emf, external mandibular fenestra; en, external narial fenestra; f, frontal; l, lacrimal; ltf, lower temporal (infratemporal) fenestra; m, maxilla; n, nasal; o, orbit; p, parietal; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; stf, supratemporal fossa.

subnarial foramen on the suture between the premaxilla and maxilla. A slight subnarial gap is present in the upper alveolar margin, similar to the condition in *Eoraptor* [5] but not nearly as extensive as in *Tawa* [16] and basal neotheropods [19,26]. The maxilla lacks a longitudinal ridge extending above and parallel to the alveolar margin, unlike in *C. bauri* [19] and *Eoraptor* [1,4]. It holds only nine or 10 maxillary teeth, the lowest number observed among known Triassic theropods, including *Eodromaeus*, which has 11 maxillary teeth [1], and short-snouted juveniles of *C. bauri*, which have 18 maxillary teeth [23]. The upper tooth row extends posteriorly beyond the anterior margin of the orbit. The anterior maxillary teeth, especially the second and third, have tall crowns. As in *Herrerasaurus* [6] and *Tawa* [16], the antorbital fossa is restricted to the dorsal process of the maxilla and largely concealed in lateral view. The lateral edge of the nasal is rounded as in *Herrerasaurus* [6]. The nasal does not enter into the dorsal margin of the antorbital fenestra. The lacrimal is slightly anterodorsally inclined and shaped like an inverted L, with slender anterior and ventral processes. There is no pneumatic recess or lateral overhang in the posterodorsal corner at the junction between the anterior and ventral processes as there is in neotheropods, such as *C. bauri*. The ventral process of the lacrimal is slightly expanded near its contact with the jugal and has a slender posterior extension along the ventral portion of the orbit. Its anterolateral surface forms the posteroventral portion of the antorbital fossa. The prefrontal occupies about 50 per cent of the dorsal margin of the orbit and forms a slender process extending ventrally along the posteromedial edge of the lacrimal. Anterolaterally, the triradiate postorbital forms a distinct overhang over the orbit, as in *Eoraptor*, *Herrerasaurus*, *Tawa* and basal neotheropods [4,16,26]. The supratemporal fossa extends anteriorly onto the posterodorsal surface of the more or less quadrangular frontal where it is delimited by an arcuate rim. The frontal contributes to the dorsal margin of the orbit. The anterior process of the jugal is rather deep ventral to the lacrimal and enters into the posteroventral margin of the antorbital fenestra. As in *Eodromaeus* [1], *Eoraptor* [1,4],

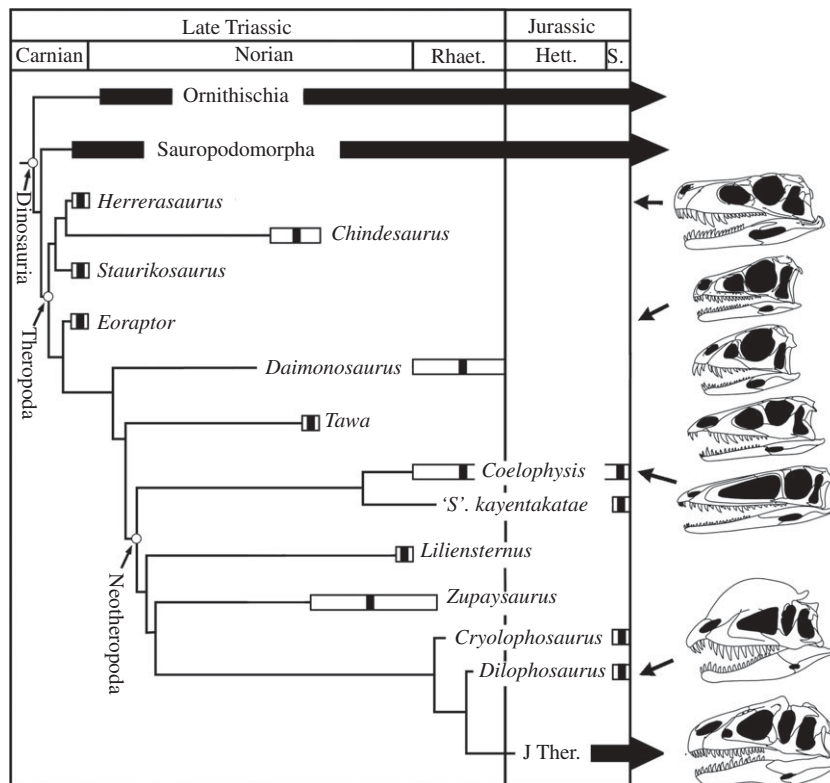


Figure 3. Temporally calibrated phylogeny of basal theropod dinosaurs based on the phylogenetic analysis presented in this paper (see the electronic supplementary material for character–taxon matrix). Diagrams illustrate reconstructed skulls of representative theropod taxa (based on [16,26]). Abbreviations: Hett., Hettangian; J Ther., more derived Jurassic theropods (exemplified by *Allosaurus fragilis*); Rhaet., Rhaetian; S., Sinemurian. 'S'. *kayentakatae* is '*Syntarsus*' *kayentakatae* [24,26] and '*Syntarsus*' *rhodesiensis* is referred to *Coelophysis* following [31].

*Herrerasaurus* [6] and some neotheropods (e.g. *C. bauri*), a prominent longitudinal ridge extends just above the ventral margin on the lateral surface of the jugal. The slender anterior process of the L-shaped quadratojugal extends anteriorly to the posterior edge of the dorsal process of the jugal, as in *Tawa* and neotheropods [16]. The quadrate has a small proximal head and a tall shaft with a slightly concave posterior margin. The basioccipital is large and the exoccipitals are clearly separated along the midline as in all dinosaurs [5]. As in *Tawa* [16], the descending process of the opisthotic is laterally extensive and not concealed in posterior view as in neotheropods. The paroccipital process projects laterally and somewhat posteriorly and lacks a dorsal or ventral expansion. It is relatively long and has a somewhat convex ventral margin. The braincase of *Daemonosaurus* was apparently not as pneumatized as that of *Tawa* because the anterior portion of the basioccipital is formed by solid bone. The dentary is relatively long and shallow, with nearly parallel dorsal (alveolar) and ventral margins. Its symphyseal portion is not expanded dorsoventrally. Anteriorly, the alveolar margin of the dentary descends slightly towards the ventral margin.

The dentition of *Daemonosaurus* is distinctly heterodont. The premaxillary and anterior maxillary teeth are much enlarged. The premaxillary teeth projected anteriorly and below the ventral margin of the dentary. The first and second dentary teeth are larger than the others and procumbent. Both the premaxillary and anterior dentary teeth are rounded in transverse section. The maxillary and more posterior dentary teeth have

labiolingually compressed crowns with finely serrated mesial and distal carinae. Five cervical vertebrae, the first three of which are partially or fully exposed, are preserved in articulation with the skull. The centra of the axis and third cervical lack ventral keels. The length of the preserved cervicals and long, slender cervical ribs that extend parallel to the centra suggests that the neck was rather long like that of *Tawa* [16]. The prezygapophyses are anteriorly elongated. The postzygapophyses bear posteriorly elongated epiphyses as in all dinosaurs [5]. The anterolateral surface of the third cervical vertebra has a deep, rimmed and oval pneumatic fossa that lies at the junction of the centrum and the neural arch. This opening occupies 40–50% of the length of the centrum. The pneumatic fossa on the third cervical vertebra of *Daemonosaurus* represents a previously unknown type of pneumatic feature among basal theropods and demonstrates disparity in the formation of such features on the cervical vertebrae in basal theropods. For example, the cervical vertebrae of *Tawa* [16] and *C. bauri* [19,26] share a rimmed, posteriorly opening fossa on the anterior portion of the centrum, just medial to the parapophysis. Furthermore, *C. bauri* [19,26] also possesses a rimmed fossa on the posterior portion of the centrum. On the postaxial cervicals of *Dilophosaurus* [29], two oval pneumatic fenestrae occupy the same position as the anterior and posterior pneumatic fossae of *C. bauri*. The only known cervical of *Chindesaurus* has a small ovoid foramen without a distinct rim in the anterior portion of the centrum [14]. The differences in the form (fossae versus fenestrae), position (centrum versus centrum and neural

arch) and number (one versus two) of pneumatic features among basal theropods show the mosaic acquisition of pneumatic features in the cervical vertebrae of these dinosaurs.

#### 4. PHYLOGENETIC ANALYSIS AND DISCUSSION

In order to assess the phylogenetic position of *D. chauliodus*, we added character state scorings for this taxon as well as four new characters to the character–taxon matrix from [16] (see the electronic supplementary material). The revised matrix comprises 42 taxa and 319 characters. We did not include the very recently described *Eodromaesus murphi* [1] because we have not yet examined the original material. The character–taxon matrix was analysed using PAUP\*, v. 4.0b10 for Macintosh PPC [30] (for details refer to the electronic supplementary material).

The analysis generated three most parsimonious trees, each with a length of 899 steps, a Consistency Index of 0.418, and a Retention Index of 0.704. Our analysis places *Daemonosaurus* as more derived than Herrerasauridae and *Eoraptor* and more basal than the clade *Tawa* + Neotheropoda (see the electronic supplementary material for details; figure 3). *Daemonosaurus* is referable to Dinosauria and Saurischia based on the presence of a distinct narial fossa on the premaxilla (character state 12.1), the deeply bifurcated posterior process of the jugal (54.3), the separation of the exoccipitals on the floor of the braincase (78.1), the extension of the supratemporal fossa onto the posterodorsal surface of the frontal (90.1) and the presence of epipophyses on the cervical vertebrae (127.1). *Daemonosaurus* is most closely related to the clade *Tawa* + Neotheropoda based on the presence of an anterior process of the quadratojugal that extends to the posterior border of the dorsal process of the jugal (52.1), deep pneumatic fossae on the postaxial cervical vertebrae (128.1), and parapophyses and diapophyses that are nearly in contact on the anterior cervical vertebrae (124.1).

The structure of the skull of *Daemonosaurus* further bridges the morphological gap between that of the basal theropods *Herrerasaurus* and *Eoraptor* and the clade *Tawa* + Neotheropoda. *Daemonosaurus* still retains a few plesiomorphic character states present in *Herrerasaurus* including the large body of the premaxilla (1.0) and limited lateral exposure of the antorbital fossa (317.1). This transitional suite of character states of *Daemonosaurus* and *Tawa* further supports placement of *Eoraptor* and Herrerasauridae as basal theropods [4,6,9,16,22,26] rather than as basal saurischians [5,10,12] or, in the case of *Eoraptor*, as a basal sauropodomorph [1].

The phylogenetic position of *Daemonosaurus* indicates that its lineage was among the first theropod dinosaurs that diversified during the early Late Triassic (figure 3). *Daemonosaurus* demonstrates that members of this initial dinosaurian radiation persisted until near the end of the Triassic. Neotheropods are apparently the only group of theropod dinosaurs to survive the end-Triassic extinction event [26]. *Daemonosaurus* differs from other known early Mesozoic theropods in its dentition and cranial proportions. Coeval coelophysids, such as *C. bauri* [19,24], and other basal neotheropods [26] have distinctly elongated snouts with loosely articulated premaxillae

and more numerous, rather small premaxillary and maxillary teeth. A comparison of ratios of snout length versus skull length (see the electronic supplementary material) shows that *Daemonosaurus* diverges from the trend in neotheropods, most of which have snouts longer than 50 per cent of the total length of the skull. Short-snouted forms are uncommon among toothed theropods [1,26]. In the present case, differences in snout proportions and shape may have allowed coexisting theropod taxa to exploit different trophic sources, as is the case among extant crocodylians [32]. Of the material examined by us, only the holotype of *Eoraptor lunensis* [1,4] has a ratio of snout length versus skull length comparable to that for *Daemonosaurus*, but its ratio of lacrimal height versus snout length is more similar to that for *C. bauri*. The greatly enlarged premaxillary and anterior maxillary teeth, the low maxillary tooth count and possibly the proportions of the snout in *Daemonosaurus* suggest greater ecological diversification of snout shape and tooth shape among theropod lineages during the latest Triassic than previously assumed.

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