The last diadectomorph sheds light on Late Palaeozoic tetrapod biogeography

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Diadectomorpha is a clade of Late Palaeozoic vertebrates widely recognized as the sister group of crown-group Amniota and the first tetrapod lineage to evolve high-fibre herbivory. Despite their evolutionary importance, diadectomorphs are restricted stratigraphically and geographically, with all records being from the Upper Carboniferous and Lower Permian of North America and Germany. We describe a new diadectomorph, *Alveusdectes fenestralis*, based on a partial skull from the Upper Permian of China. The new species exhibits the derived mechanism for herbivory and is recovered phylogenetically as a deeply nested diadectid. Approximately 16 Myr younger than any other diadectomorph, *Alveusdectes* is the product of at least a 46 Myr ghost lineage. How much of this time was probably spent in Russia and/or central Asia will remain unclear until a specimen is described that subdivides this cryptic history, but the lineage assuredly crossed this region before entering the relatively isolated continent of North China. The discovery of *Alveusdectes* raises important questions regarding diadectomorph extinction dynamics including what, if any, ecological factors limited the diversity of this group in eastern Pangea. It also suggests that increased sampling in Asia will likely significantly affect our views of clade and faunal insularity leading up to the Permo-Triassic extinction.

1. Introduction

For a radiation that is only moderately diverse (13 recognized species [1]) and failed to survive the Palaeozoic, Diadectomorpha is central to discussions of Late Palaeozoic vertebrate evolutionary history. It is the first and most diverse example of high-fibre herbivory among Permo-Carboniferous tetrapods and thus critical to the origin of modern terrestrial communities [2]. Diadectomorpha is also widely accepted as the sister taxon to crown-group Amniota ([3]; but see [4]), giving it significant influence on our understanding of amniote origins. Here we describe a new diadectomorph based on a partial skull recovered from the Upper Permian Jiyuan Fauna of northern China [5]. The new taxon is the first record of a diadectomorph outside North America or Germany and the first evidence that Diadectomorpha survived the Lower Permian. A possible diadectomorph was recently reported from the Upper Permian of Brazil; however, the poor preservation of the specimen does not support a clear diagnosis [6]. We explore the phylogenetically contextualized implications of this extralimital status for the geographical and stratigraphic dynamics of this important group.

2. Systematic palaeontology

Diadectomorpha Watson 1917  
Diadectidae Cope 1880  
*Alveusdectes fenestralis* gen. et sp. nov.
(a) Etymology
Generic name from the Latin alveus, meaning reservoir and referring to the type locality near Xiaolangdi Reservoir, and decies, biter. Specific epithet from the Latin fenestratus, meaning windows and referring to the characteristically large suborbital fenestrae.

(b) Holotype
IVPP V 20127, partial skull with lower jaws.

(c) Type locality and age
Shangshihzei (Upper Shihhotse) Formation, Henan Province (field locality 63 [24]; Jiuyuan fauna correlates roughly with Cistecephalus assemblages of South Africa [7], which is dated as Wuchiapingian, Upper Permian, roughly 256 Ma [8].

(d) Diagnosis
Diadectid diadectomorph distinguished by three autapomorphies: large suborbital fenestra, large fourth dentary tooth, and especially elongate and posteriorly positioned Meckelian fenestra. Diagnosed to Diadectomorpha based on long Meckelian fenestra, labial parapet of dentary, and procumbent teeth in anterior portion of mandible [9]. Diagnosed to Diadectidae based on heterodont dentition with transversely oriented molariform teeth with labial and lingual cusps. Differs from Dicaleptus (spp.) and D. fenestratus in having a slender lower jaw [10]; from Dicaleptus ammiguldeusis and Orobates pabsti in having a secondary palatal shelf [11,12]; from Ambedus pusillus in having marginal teeth whose roots are longer than the height of their crowns [9]. Further differs from Ambedus, Desmatodon, Dicaleptus absitus, and possibly D. ammiguldeusis in having as many as four lower incisiform teeth [9,10,12–14]. The largest preserved dentary tooth has a similar breadth to that of Desmatodon but is not as long [9,10]. Differs from all diadectids, besides Dicaleptus, in possessing cheek teeth whose crown height is less than half crown width [9,10]. See the electronic supplementary material for further discussion.

3. Description
The fragmentary skull (figure 1) includes portions of the left jugal, palatine, ectopterygoid, epipterygoid, pterygoid, parabasiphenoid and both maxillae. The left maxilla houses three deeply ankylosed and nearly complete marginal teeth that remain labial to the lower teeth during jaw adduction. The anterior two teeth exhibit transversely elongate crowns, whereas that of the third is more oval with a strong central ridge flanked by shallow basins and a moderately developed shoulder. The root of the reciprocal third tooth is distinctly longer than the height of its crown. The jugal overlaps the maxilla to form the ventral orbital margin. The edentate palatine includes a secondary shelf that articulates with the maxilla above the alveolar margin and may have served as an occlusal surface for the lower teeth [15,16]. The palatine, jugal and pterygoid together define a suborbital fenestra whose distinctly large size reflects a retraction of the pterygoid (figure 16). The pterygoid includes an edentulous transverse flange whose lateral end lies at the level of the maxillary tooth row and, with the ectopterygoid, defines a pterygoideus depression. The tiny interpterygoid vacuity is closed posteriorly by the block-like basal process of the pterygoid and is partially divided sagittally by the broken cultriform process. The basicranial joint is closed and inflexible.

The relatively well-preserved mandibles (figure 1; electronic supplementary material, figure S2) are slender, with a lateral surface dominated by a dentary that meets the angular along an extensive contact and the surangular at its postero-dorsal terminus. The dentary possesses approximately 15 teeth arranged along a sigmoid line in dorsal view. The crowns are lost but the oval and procumbent roots indicate the anterior four teeth were incisiform. Tooth 4 is comparably robust to the largest dentary tooth of Desmatodon [9,10]. The roots at positions 2 and 3 are mediolaterally compressed, whereas that of position 5 exhibits slight transverse expansion. All the posterior teeth are molariform with low, transversely oriented crowns, which are distinct from their constricted base, but whose surface details are poorly preserved. The dorsal surface of the dentary extends, as a platform, to a low parapet and lateral to the tooth row.

The medial surface of the mandible includes a large sphenial that meets the prearticular and the slanting surface of the angular posteriorly. Anteriorly, the splenial contributes to an expanded mandibular symphysis and runs just below a small foramen near the midline that may correspond to the anterior dentary fenestra of Dicaleptus lentus [13] and D. absitus [14]. The prearticular narrows as it extends anteriorly, but it still forms most of the medial wall of the Meckelian canal. The canal opens ventrally via a long and narrow fenestra formed between prearticular and angular. The fenestra’s anterior margin approximates the third cheek tooth, which is well posterior to that of other diadectids.

4. Phylogenetic analysis
The following characters distinguish this animal as a diadectomorph in early tetrapods: heterodont dentition with anterior procumbent anterior teeth, transversely expanded, molariform cheek teeth and presence of parapet (see the electronic supplementary material for more comparison). We were able to score Alveusdectes fenestratus for 14 of the 36 characters used by Kissel & Reisz [9] (electronic supplementary material, table S1) to resolve the relationships within Diadectomorph. Our analysis (see the electronic supplementary material text) recovered two most-parsimonious trees with Alveusdectes nested deep within Diadectomorpha in an unresolved relationship with Desmatodon and a Dicaleptus–Dipsactus clade (figure 2; see electronic supplementary material, table S2 for synapomorphy list).

5. Discussion
Previous diadectomorph records range from the Upper Carboniferous to the Early Permian and are from either North America or Germany (electronic supplementary material, table S3; figure 2; [1])—areas that, in the Late Paleozoic, were closely associated geographically and formed the western and central regions of the Laurasian portions of Pangea [18]. Although the holotype of Alveusdectes is poorly preserved, it provides strong evidence that Diadectomorph survived the Early Permian with a geographical range that included the eastern margin of Pangea. The
Figure 1. The photos and illustrations of skull and mandibles of Alveusdectes fenestratus (IVPP V 20127). Dorsal (a), ventral (b) and (f) left lateral views; section showing two teeth (c); right lower jaw in medioventral (d) and medial (g) views; rearmost left maxillary tooth in occlusal view (e). a, angular; ad.f, adductor fossa; a.f, anterior dentary fenestra; art, articular; c, coronoid; cul.p, cultriform process (parabasisphenoid); d, dentary; ec, ectopterygoid; ep, epipterygoid; j, jugal; m, maxilla; M.f, Meckelian fenestra; pl, palatine; pra, prearticular; ps, parabasisphenoid; pt, pterygoid; q.pt, quadrate process of pterygoid; sa, surangular; so.f, suborbital fenestra; sp, splenial. Scale bars, 1 cm. (Online version in colour.)
deeply nested phylogenetic position of the Carboniferous Desmatodon [1,10] indicates a significant undiscovered early history of the group. Alveusdectes extends the upper end of diadectomorph chronology by approximately 16 Ma. The length of its ghost lineage depends on its unresolved relationships with Desmatodon and the Diadectes–Diasparactus radiation, but conservatively IVPP V 20127 represents a diadectid lineage that originated in the Carboniferous and had been evolving independently for more than 46 Myr.

During the Upper Carboniferous, the northern end of the Palaeo-Tethys Sea separated the eastern margin of Pangea from North China [18,19]. The relative isolation of North China ended in the Middle Permian when a northern connection was established with what are now central Asia and the Siberian region of Russia [20]. Given that North China had no direct connection with central (Europe) and western (North America) Laurasia—the unequivocal site of origin for the Alveusdectes–Desmatodon–Diadectes clade—the Alveusdectes lineage must have entered North China after crossing Russia/central Asia. The absence of published Russian/central Asian records obscures how much of its ghost lineage was spent in these intervening regions.

A similar dispersal pattern is found among early amniotes [21]. For example, both Bolosauridae (parareptiles) and Captorhinidae (early eureptiles) had entered North China by the Middle Permian [20,22]. Unlike Alveusdectes, these Chinese specimens have closely related forms in the Russian Permian [23–27]. Absence of a Russian record suggests diadectomorphs were scarce in eastern Pangea and probably underwent no significant diversification in that part of the supercontinent. The derived mechanism for processing high-fibre plants certainly was in place at the origin of the Alveusdectes lineage. Whether this functional complex placed some ecological constraint on the eastern diadectids or whether other factors were more limiting—perhaps competition with the increasingly diverse amniotes—remains unclear, but the undersampled Palaeozoic record of Asia may yet illuminate this point. Rapidly increasing research...
efforts in China hopefully will spark more interest in the Late Palaeozoic of other areas of eastern Pangea (e.g. central Asia). The fruit of such labours is likely to significantly alter current views of clade and faunal insularity shortly before the Permian–Triassic extinction.

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