New basal synapsid supports Laurasian origin for therapsids

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The distant evolutionary ancestry of mammals is documented by a rich therapsid fossil record. While sphenacodontid synapsids are considered the sister-group of therapsids, the place of origin of therapsids is an enigma, largely because of a long standing morphological and temporal gap (Olson's Gap) in their fossil record. We describe a new large predatory synapsid, *Raranimus dashankouensis* gen. et sp. nov., from the Middle Permian of Dashankou in China which has a unique combination of therapsid and sphenacodontid features. This specimen is of great significance as it is a basal therapsid which is the sister taxon to all other therapsids. The fact that it was found in association with Early Permian tetrapods (*Anakamacops* and *Belebey*) suggests that it is the oldest therapsid and provides the first evidence of therapsid-bearing rocks which cover Olson's Gap. It further supports that therapsids may have had a Laurasian rather than Gondwanan origin.

Key words: Therapsida, Dashankou, Permian, Laurasia, China.

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Introduction

A rich, nearly continuous 315 million year fossil record documents the evolutionary history of a diverse clade of synapsid amniotes that includes extant mammals and their stem-group, often called "mammal-like reptiles" (Rubidge and Sidor 2001; Kemp 2005). One of the major remaining problems in synapsid research is the presence of a morphological and temporal gap (so-called Olson's Gap) between the earliest therapsids and their supposed sphenacodontian-grade ancestors (Hopson 1991; Sidor and Hopson 1998; Kemp 2005). Even at their first appearance in the fossil record therapsids had already diversified into several distinct groups including small and large herbivores and predators (Chudinov 1983; Rubidge 1995).

The Middle Permian Dashankou fauna from Gansu Province, China is known to have produced a wide variety of basal tetrapod fossils (Battail 2000; Li 2001). Recently a remarkable new specimen, comprising the partial snout of a tetrapod, was discovered at the Dashankou locality and contributes to the diversity of this fauna. Although fragmentary, the fossil reveals a unique combination of therapsid and sphenacodontid features. This find helps us understand the morphological transition from sphenacodonts to therapsids and provides new insight into the long-standing debate on whether basal therapsids had a Laurasian or Gondwanan origin.

Institutional abbreviations.—BPI, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; IGCAGS, Institute of Geology, Chinese Academy of Geological Sciences; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

Geological setting

The Dashankou locality is located about 20 km southwest of Old Yumen City, 50 km west of Jiayuguan City, 2500 m above the sea level. It lies on the north side of the Qilian Mountains. This single locality produced all known tetrapods of the Dashankou Fauna. The Dashankou Fauna, including the taxon described in this paper, is from the Xidagou Formation. The Xidagou Formation is fluvial deposit which is characterized by a reddish medium to coarse sandstone containing pebbles, but the vertebrate fossils occur in a red mudstone in the upper part of the unit.

Material and methods

The skull, which is preserved in a red mudstone, was excavated in 1998. The specimen was prepared mechanically using an air-driven engraver fitted with a tungsten carbide stylus.

A phylogenetic analysis was performed with PAUP 4.0b10 (Swofford 2001). See Appendices 1, 2 for the list of characters, sources and data matrix.

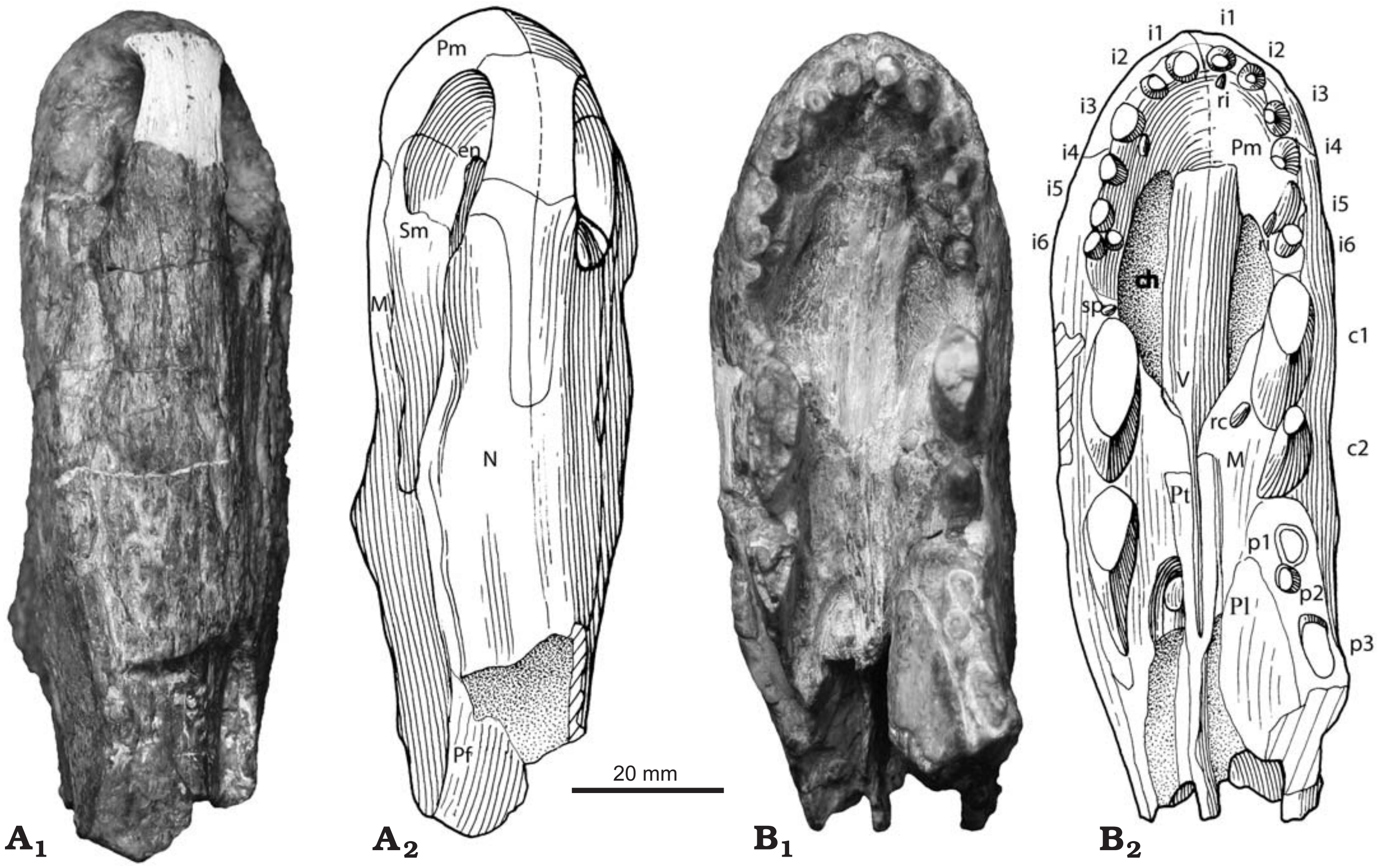

Fig. 1. Partial skull of the basal therapsid *Raranimus dashankouensis* gen. et sp. nov., IVPP V15424 (holotype) from Middle Permian Xidagou Formation, Dashankou, Xumen, Gansu, China, in dorsal (**A**) and ventral (**B**) views. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2). Abbreviations: c1–2, canine 1–2; ch, choana; en, external naris; i1–6, incisor 1–6; M, maxilla; N, nasal; p1–3, postcanine 1–3; Pf, prefrontal; Pl, palatine; Pm, premaxilla; Pt, pterygoid; rc, replacement canine; ri, replacement incisor; Sm, septomaxilla; sp, small precanine maxillary tooth; V, vomer.

Systematic palaeontology

Therapsida Broom, 1905

Genus *Raranimus* nov.

Etymology: From Latin *raro-* (rare) and *animus* (soul, spirit).

Type species: *Raranimus dashankouensis* sp. nov.

Diagnosis.—As for the type species by monotypy.

Raranimus dashankouensis gen. et sp. nov.

Figs. 1, 2.

Etymology: Specific name from Dashankou, the name of the fossil locality.

Holotype: IVPP V15424.

Type locality: Dashankou Locality, Yumen, Gansu Province, China.

Type horizon: Xidagou Formation, Middle Permian (Li et al. 2004).

Diagnosis.—A plesiomorphic therapsid characterised by: choana short, with the posterior margin lying at the level of the first pair of canines; long facial process of septomaxilla; presence of one precanine and two functional linguo-labially compressed canines on maxilla; six incisors.

Description.—The specimen consists of a well preserved though slightly laterally crushed, slender snout (length of 100 mm, height of 65 mm, width between canines 33 mm) with a marginal tooth series comprising incisors, precanines, canines and the roots of three postcanines (Figs. 1B, 2). Recurved and slender incisor teeth and the presence of serrations on the posterior edge of the second canine suggest that it belonged to a large predator with the complete skull probably exceeding 16 cm in length.

A large oval external naris (Figs. 1A, 2) is positioned close to the anterior margin of the snout. The dorsal process of the premaxilla makes up most of the internarial bar, and terminates posteriorly beyond the posterior margins of the external nares where it is overlapped by the nasals. Paired nasals extend backwards from the posterodorsal margin of the external naris to meet the prefrontal posteriorly, and ventrally form a long sutural contact with the maxilla and septomaxilla. The latter bone comprises the floor of the external naris with its posterodorsal process wedged between the maxilla and the nasal and extending further posteriorly on the snout than the dorsal process of the premaxilla. While the posteriormost extent of the maxilla is not preserved, it contacts the nasal dorsally and the prefrontal posterodorsally. Anteriorly the vertical suture between the maxilla and the premaxilla descends from the front of the external naris to a point between the third and fourth incisor, and continues posteriorly along the ventral edge labial to the incisors before turning medially to reach the

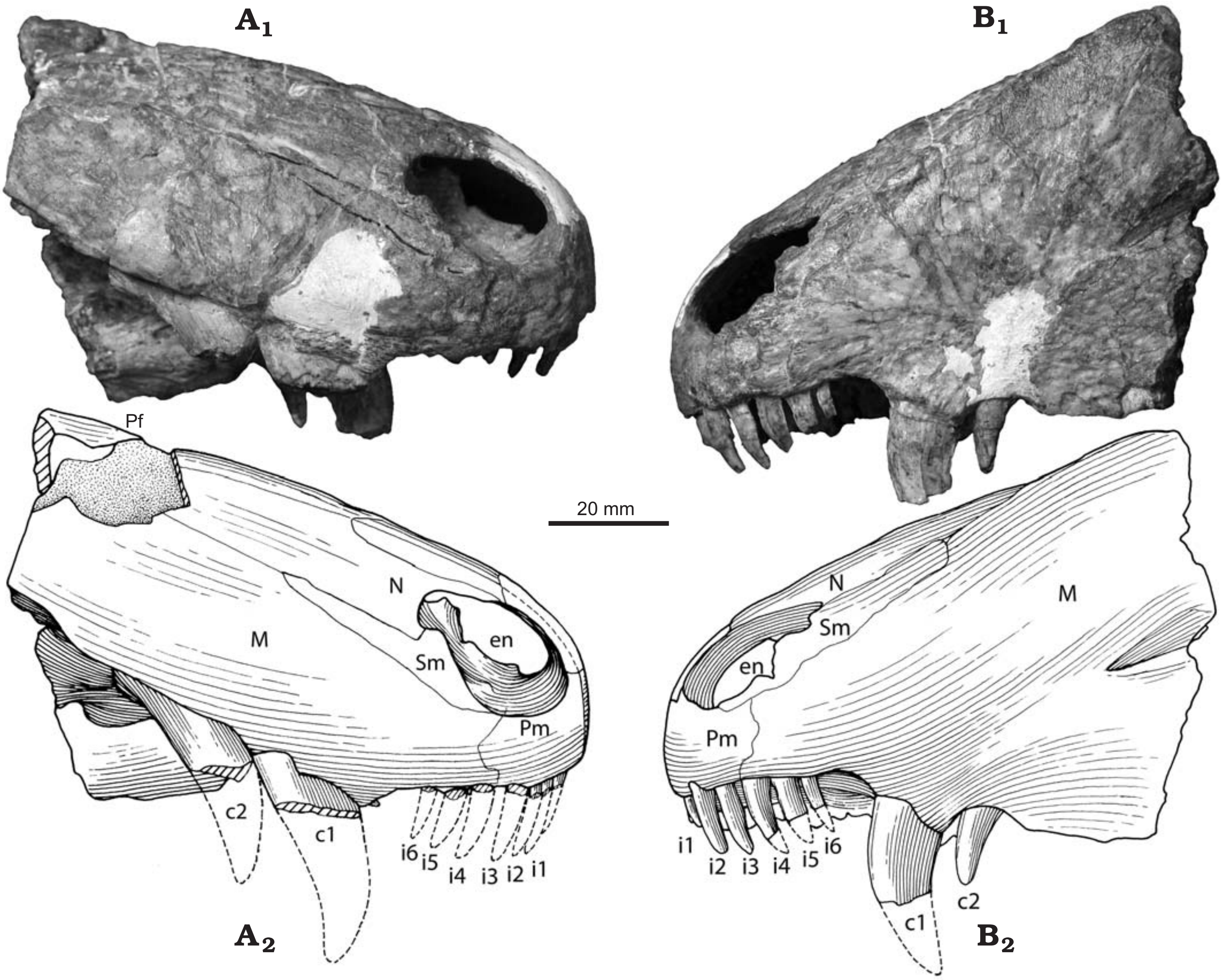

Fig. 2. Partial skull of the basal therapsid *Raranimus dashankouensis* gen. et sp. nov., IVPP V15424 (holotype) from Middle Permian Xidagou Formation, Dashankou, Xumen, Gansu, China in right lateral (**A**) and left lateral (**B**) views.. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2). Abbreviations: c1–2, canine 1–2; ch, choana; en, external naris; i1–6, incisor 1–6; M, maxilla; N, nasal; p1–3, postcanine 1–3; Pf, prefrontal; Pl, palatine; Pm, premaxilla; Pt, pterygoid; rc, replacement canine; ri, replacement incisor; Sm, septomaxilla; sp, small precanine maxillary tooth; V, vomer.

choana in front of the precanine. In lateral view the ventral margin of the maxilla turns sharply downwards forming a notch between the last incisor and canine. Bone sculpturing is present on the snout with small pits on the anterior surface of the premaxilla and radial striations converging on the concave area above the root of the canine on the maxilla, while longitudinal striations occur on the rest of the snout.

In palatal view the premaxilla forms the anterior and most of the lateral margin of the choana up to the level of the precanine, while being anteroventrally overlain by the anterior process of the vomer as in dinocephalians. Long, thin and edentulous paired vomers form the medial border of the choana. Their ventral surface is flat with the anterior section being slightly ventrally convex and the lateral edges of the posterior interchoanal portion forming weak ridges. The choanae are short, extending from the level of the fourth incisor to that of the first canine, a character unknown in other therapsids. Only the anterior part of the left palatine is preserved. It underlies the maxilla, possibly contacts the vomer medially, and extends anteriorly to the level of the first postcanine. No palatine teeth are evident and only the anterior portions of the pterygoids are present.

Six incisors were present on each premaxilla. Those with preserved crowns show them to be similar in size, recurved and unserrated, and therefore resembling the morphology of those of most theriodont therapsids (Fig. 1B). A diastema is present between the last incisor and the first canine on the left side and the last incisor and precanine on the right. Two recurved canines, ovoid in cross section, are present in each maxilla. The complete left second canine (c2 in Fig. 2B) is considered to be newly erupted as it only partially occupies its alveolus. No serrations are preserved on the first canine, but they do exist on the posterior ridge of the right second canine. A small replacement tooth, lingual to the left first canine indi-

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cates that the two canines are not simply replacements of one another, but functioned simultaneously. This makes *Raranimus* the only therapsid with two functional canines, a condition reminiscent of the caniniform teeth seen in the large predatory sphenacodontids (Romer and Price 1940; Reisz 1986). These canines, despite being doubled as in basal synapsids, have a more derived therapsid morphology in being quite slender and compressed linguo-labially, rather than having the massiveness seen in similarly sized sphenacodontids.

A small precanine with fine serrations on its anterior ridge is present in the maxilla anterior to the right first canine (Fig. 1B) and is reminiscent of the small precanine teeth known in *Dimetrodon* (Romer and Price 1940) and *Tetraceratops* (Laurin and Reisz 1996). Roots of three postcanines are preserved in the left maxilla but the rest of this bone is missing. Judging by root diameter, the postcanines vary in size but are all much smaller than the canines.

Discussion

To explore the phylogenetic position of *Raranimus* and to examine the effects of the new data upon current hypotheses of relationships amongst basal synapsids and therapsids, we built upon the data matrices from Sidor and Hopson (1998), Sidor and Rubidge (2006), and Rubidge et al. (2006). Therocephalians and cynodonts are excluded from this analysis because their position as advanced therapsids is confirmed in the primary analyses. *Haptodus* is used as the outgroup, and the alleged basalmost therapsid *Tetraceratops* is also included. Laurin and Reisz (1996) stated that the interpterygoid vacuity is closed posteriorly by an additional posteromedian flange of pterygoid. As we are unable to verify this we have coded character 41 as unknown. From all the characters used in analysis, *Tetraceratops* has only two derived states (Appendix 2) and our analysis supports that *Tetraceratops* is better considered as a sphenacodontid as suggested by Conrad and Sidor (2001). Our phylogenetic analysis shows *Raranimus* to be the most basal therapsid as it is closely allied to other well known therapsids (Fig. 3). *Raranimus* retains a number of plesiomorphic sphenacodontid characters (vomerine process of premaxilla absent, more than one functional canine, concave diastema with postero-ventrally sloping alveolar margin of the premaxilla, and nearly parallel-sided internarial portion of vomer) (Romer and Price 1940; Reisz 1986) which are unknown in any other therapsid. However, the presence of a greatly elongated dorsal process of the premaxilla, septomaxilla with a long facial process, maxilla which is increased in height so as to contact the prefrontal, and ventral surface of the vomer with lateral ridges and median trough distinguish *Raranimus* as a therapsid (Hopson and Barghusen 1986; Hopson 1991; Sidor and Hopson 1998). The very short choana which extends posteriorly only as far as the anterior margin of the canine, and six incisors are considered as autapomorphies.

While Broom (1910) pointed out the similarities between "pelycosaurs" and therapsids, there has always been a morphological gap between the two groups (Kemp 2005, 2006). Pelycosaurian-grade synapsids are known predominantly from Carboniferous–Middle Permian rocks of North America, Europe and Asia, while therapsids are known predominantly from Middle Permian or younger rocks of South Africa and Russia, with little temporal overlap between them apart from some varanopid relicts in Russia and South Africa (Dilkes and Reisz 1996; Modesto et al. 2001; Botha-Brink and Modesto 2007), and caseids in Russia (Reisz 1986). Because the earliest Russian therapsid faunas are more primitive than those from the *Tapinocephalus* Assemblage Zone of South Africa it was considered that therapsids had their origin in Russia (Laurasia) and arrived in southern Africa (Gondwana) by overland dispersal (Boonstra 1969). More recent discovery of a basal therapsid fauna from the underlying *Eodicynodon* Assemblage Zone of South Africa resulted in the opposite proposal of a Gondwanan origin for several therapsid clades (Rubidge 1995; Modesto and Rubidge 2000; Modesto and Rybczynski 2000; Abdala et al. 2008). Unfortunately, although the oldest

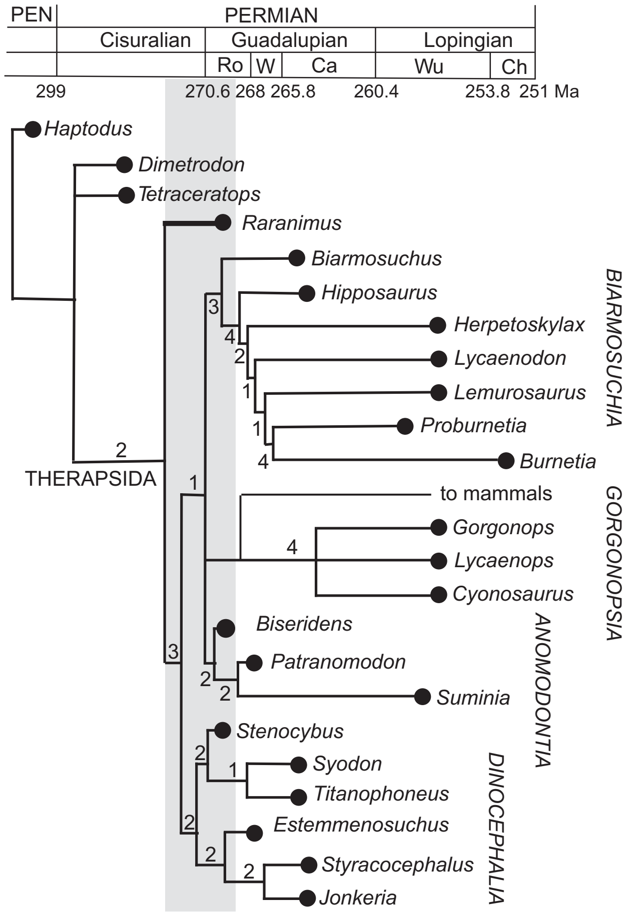

Fig. 3. Phylogeny of *Raranimus* among basal therapsids. Tree (tree length = 169, consistency index = 0.54, retention index=0.75) is the strict consensus tree of four shortest trees resulting from our PAUP analysis (version 4.0b10, branch and bound search, with unordered multistate characters) of 71 cranial and dental characters. Numbers on tree indicate decay index of the respective clade. Shaded area indicates "Olson's Gap". Abbreviations: Ca, Capitanian; Ch, Changhsingian; Ma, Million years; PEN, Pennsylvanian; Ro, Roadian; W, Wordian; Wu, Wuchiapingian.

and most basal therapsid faunas are known from Russia, South Africa and China (Battail 2000; Modesto and Rybczynski 2000; Li 2001; Kemp 2005), the current lack of reliable radiometric dates limits accurate age correlation of these geographically spaced faunas.

Roadian tetrapod faunas from North America are very different from the oldest faunas from South Africa, Russia, and China with the major difference being the lack of therapsids in the North American faunas (Reisz and Laurin 2001; Lucas 2002, 2004, 2006). *Tetraceratops* from the Early Permian of Texas, has been considered the oldest therapsid (Laurin and Reisz 1996) but its therapsid identity has since been questioned (Sidor and Hopson 1998; Conrad and Sidor 2001) and our analysis shows it to be more basal than *Raranimus* (Fig. 3). Lack of a therapsid record in the early Roadian and their first appearance as an already diverse group at the Roadian–Wordian transition, suggests a gap (dubbed Olson's Gap) in the early therapsid fossil record (Lucas 2004; Ivakhnenko 2005), a crucial interval in which the initial evolution of this group must have occurred (Abdala et al. 2008).

One of the great remaining unsolved problems in synapsid history is the sphenacodontid-therapsid transition and the early diversification of therapsids. It has been suggested that the origin and early diversification of the main therapsid lineages occurred either by a rapid process of apomorphy accumulation, or by gradual acquisition of apomorphies during an extended temporal interval of up to 35 Ma (Kemp 2006; Abdala et al. 2008). Choosing between these two scenarios is possible only if therapsid-bearing rocks from Olson's Gap are found. The presence of *Raranimus* at Dashankou, the basalmost Middle Permian therapsid known, in association with the dissorophoid *Anakamacops,* the bolosaurid *Belebey* (both families occur together only in the Early Permian) and the very primitive therapsids *Biseridens*, *Stenocybus,* and *Sinophoneus* (known only from China, Li et al. 1996; Cheng and Li 1997; Li and Cheng 1997; Li 2001), support the hypothesis of an early Roadian age for this locality, and helps to fill in Olson's Gap. In addition, the discovery of a new basal Laurasian therapsid which cannot be assigned to any major therapsid clade, suggests that the initial evolutionary radiation of therapsids occurred in Laurasia.

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Appendix 1

List of characters and character states used to construct the cladogram. The number preceding the character definition corresponds to that of the columns in the data matrix. Most of the characters are cited from SH: Sidor and Hopson (1998); SR: Sidor and Rubidge (2006); RSM: Rubidge et al. (2006). When an asterisk follows the citation, it denotes that the character definition has been modified or character state(s) has been added/deleted. Coding of characters is based on the coding of selected characters in original references, sources listed in the end of character list, and personal observation.

1. Dorsal surface of snout: oblique convex (0), near straight and flat (1). (SH: 46*)
2. Snout width/height ratio: height greater than width (0), height equal to width (1), height less than width (2). (SH: 45)
3. External nares: terminal (0), retracted (1). (RSM: 4)
4. Length of dorsal process of premaxillae: short (0), long, reaching to a level posterior to that of the upper canine (1). (SH: 1*; SR: 2; RSM: 2)
5. Premaxilla alveolar margin shape: downturned (0), horizontal or slightly upturned (1), greatly upturned (2). (SH: 2*; SR: 3*; RSM: 3*)
6. Antorbital region: long (0), short (1). (SR: 4)
7. Septomaxilla: contained within external naris (0), escapes to have a short (1) or long facial exposure (2). (SH: 6; SR: 5*, 6*; RSM: 5)
8. Maxilla contacts prefrontal: absent (0), present (1). (SH: 8; SR: 8; RSM: 7)
9. Shape of dorsal surface of nasals: flat (0), with median boss (1). (SR: 9; RSM: 9*)
10. Supraorbital margin: thin (0), moderately to greatly thickened (1). (SR: 12; RSM: 12)
11. Orbit size smaller than that of the temporal fenestra: absent (0), present (1)
12. Adductor musculature originates on lateral surface of postorbital: absent (0), present (1), on both postorbital and postfrontal (2). (SR: 13*, 17*; RSM: 13*)
13. Postorbital bar: thin (A-P length less than one-third of height) (0), thickened such that A-P length is greater than 40% of its height (1). (RSM: 16)
14. Length of posterior process of postorbital: stops above lateral

temporal fenestra (0), descends onto posterior margin of lateral temporal fenestra (1). (RSM: 14)
15. Boss above postorbital bar: absent (0), present (1). (RSM: 15)
16. Postfrontal: without (0) or with (1) posterior extension along its medial contact with the frontal. (SR: 16; RSM: 18)
17. Shape of dorsal surface of parietal surrounding parietal foramen: flat (0), low and diffuse swelling (1), forms well-defined chimney (2). (SH: 21*; SR: 18; RSM: 19)
18. Temporal fenestra: small (0), expanded posterodorsally (1) so that adductor musculature origination on squamosal visible in dorsal view. (SH: 14*; SR: 19; RSM: 20)
19. Intertemporal region: wider (0) or narrower (1) than interorbital region. (SH: 18*; SR: 20; RSM: 21)
20. Ventral surface of zygomatic arch and suborbital bar: smooth (0), with bosses (1). (SR: 21, RSM: 22)
21. Zygomatic arch elevated above margin of upper tooth row so as to fully expose quadrate and quadratojugal in lateral view: absent (0), present (1). (SR: 22)
22. Anterior extension of anterior ramus of squamosal: stops under temporal fenestra (0), beyond the anterior margin of the temporal fenestra (1). (SR: 23*; RSM: 23*)
23. Squamosal external auditory meatus groove: absent (0), present (1) (SH: 52*)
24. Preparietal: absent (0), present (1). (SH: 48; SR: 24; RSM: 24*)
25. Supratemporal: present (0), absent (1). (SH: 22; SR: 25; RSM: 25)
26. Tabular: contacts paroccipital process of opisthotic (0), restricted dorsally (1). (SH: 54*; SR: 26*)
27. The position of the posterior border of choana: close to the incisor (0), far behind the incisor (1)
28. Length of vomerine process of premaxilla: short (0); long, extending posteriorly and forming part of the medial margin of the inner choana (1); absent in ventral view (2) so that vomer abuts body of premaxilla. (SH: 3*; SR: 1*; RSM: 1*)
29. Vomer: paired (0), unpaired (1). (SH: 25*, 26*; SR: 27; RSM: 26)
30. Vomer internarial part: nearly parallel-sided or slightly expanded backward (0), widest nearly middle (1), strongly constraining backwards (2). (SH: 23*)
31. Interchoanal portion of vomer where it meets the postchoanal portion: broad (0), forms median ridge (1). (SH: 23*; RSM: 27)
32. Vomer ventral surface: flat to convex (0), lateral ridges and median trough (1). (SH: 24*)
33. Choanal and postchoanal portions of vomer: meet at similar level on palate (0), choanal portion is offset ventrally from postchoanal portion (1). (SR: 28)
34. Lateral margin of the choana formed by the palatine: less than 1/3 (0), over 1/3 (1)
35. Two palatines: separated by the vomer and pterygoid (0), join in midline (1)
36. Palatine dentition: broadly distributed (0), restricted to small area (1), absent (2). (SH: 36*; SR: 29; RSM: 28*)
37. Dentition on palatal ramus of pterygoid: present (0), absent (1). (SH: 37; SR: 33)
38. Row of teeth on transverse flange of pterygoid: present (0), absent (1). (SR: 30*; RSM: 29)
39. Position of transverse flange of pterygoid: under posterior half of orbit (0), under anterior half of orbit (1), preorbital (2). (SH: 73*; SR: 31; RSM: 30)
40. Pterygoid: without (0) or with (1) shelf posterior to its transverse flange. (SR: 32; RSM: 31)
41. Basicranial rami of pterygoids: broadly separated (0), narrowly separated with median trough formed (1), broadly contacting anterior to basicranium (2). (SR: 34; RSM: 32)
42. Medial edge of pterygoid basicranial ramus forms parasagittal ridge on ventral surface: absent (0), present (1). (RSM: 33)
43. Basipterygoid articulation located: high above primary palate (0), just dorsal to basicranial ramus of pterygoid (1), at level basicranial ramus (i.e., suture visible in ventral view) (2). (SR: 35)
44. Ectopterygoid teeth: present (0), absent (1). (SH: 39; SR: 36; RSM: 34)
45. Shape of postparietal: wider than tall (0), approximately square (1), or taller than wide (2). (SR: 37; RSM: 35)
46. Forward rotation of occiput: none (0), moderate (= vertical) (1), pronounced (2). (SH: 42; SR: 38; RSM: 36)
47. Paroccipital process orientation: strongly posteroventral and lateral (0), moderately posteroventral and lateral (1), transverse (2) (SH: 65)
48. Quadrate contact: primarily paroccipital process (0), about equal paroccipital process and squamosal (1), mostly squamosal (2) (SH: 58*)
49. Stapedial foramen: present (0), absent (1). (SH: 76; SR: 39; RSM: 37) [this foramen is present in *Scylacops*, and coded as 0 for all taxa of Gorgonopsia here]
50. Dentary height in canine versus anterior postcanine regions: nearly equivalent (0), shows pronounced difference (1). (SH: 79*; SR: 40; RSM: 38)
51. Dentary: coronoid eminence (0), coronoid process (1) (SH: 80)
52. Dentary-angular suture: runs diagonally across lateral surface of mandible (0), posterior margin of dentary deeply incised (1). (SR: 41; RSM: 39)
53. Coronoid (posterior): present (0), absent or greatly reduced (1). (SH: 91*; SR: 47)
54. Lateral mandibular fenestra: absent (0), present (1). (SH: 93, 94*; SR: 46)
55. Angular reflected lamina dorsal notch: near articular (0), midway between articular and dentary (1), close to dentary (2) (SH: 97)
56. Angular with pattern of ridges and fossae on its lateral surface: absent (0), present (1). (SH: 98*; SR: 42; RSM: 40)
57. Dorsal edge of surangular just posterior to dentary with laterally projecting ridge: absent (0), or present (1). (SR: 43; RSM: 41)
58. Foramen between prearticular and angular (sometimes bordered by splenial as well) on medial surface of lower jaw: absent (0), present (1). (SR: 44; RSM: 42)
59. Articular dorsal process: absent (0), present (1). (SR: 45; RSM: 43)
60. Differentiation of upper tooth row: more than one caniniform teeth (0), one canine (1), barely differentiated (1). (SR: 48*)
61. Premaxillary teeth number: 5 (0), 4 or less (1), 6 (2)
62. Upper and lower incisors intermesh: absent (0), present in anterior incisors (1), present in all incisors (2). (SH: 105*;SR: 49; RSM: 44)
63. Incisor heels: absent (0), present (1) (SH: 106)
64. Upper incisors: much larger (0) or roughly equivalent in size to postcanines (1). (SR: 50; RSM: 46)
65. Precanine maxillary teeth: present (0), absent (1) (SH: 110)
66. Lower canine: fits into choana (0), or into fossa roofed by premaxilla and maxilla (1), or passes anterior and external to upper canine (2). (SR: 51; RSM: 47)

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67. Upper and lower canines: without heels (0) or small heels present (1). (SR: 52; RSM: 45)
68. Postcanine diastema on upper jaw: absent (0), present (1)
69. Number of upper postcanines: twelve or greater (0), fewer than 12 (1). (SH: 112; SR: 53; RSM: 48)
70. Postcanine teeth with triangular crown bearing coarse serrations along both anterior and posterior carinae: absent (0), present (1). (SH: 113*; SR: 56; RSM: 51)
71. Upper postcanine teeth confluent with upper incisor row medial to canine: absent (0), present (1). (SR: 55; RSM: 50)

Taxa included and the coding basis:

Haptodus (Currie 1977; Laurin 1993)
Dimetrodon (Romer and Price 1940)
Tetraceratops AMNH4526 (Laurin and Reisz 1996; Conrad and Sidor 2001)
Raranimus IVPP V15424
Biarmosuchus (Chudinov 1960; Ivakhnenko 1999)
Hipposaurus (Sigogneau 1970; Sigogneau-Russell 1989)
Herpetoskylax (Sidor and Rubidge 2006)
Lycaenodon (Sidor 2003)
Lemurosaurus (Sidor and Welman 2003)
Proburnetia and *Burnetia* (Rubidge and Sidor 2002)
Syodon and *Titanophoneus* (Orlov 1958)
Stenocybus IGCASGS V361 (Cheng and Li 1997)
Styracocephalus (Rubidge and van den Heever 1997)
Jonkeria (Boonstra 1936)
Estemmenosuchus (Chudinov 1960; Ivakhnenko 2000)
Biseridens IGCAGS V 632, IVPP V 12009 (Li and Cheng 1997)
Patranomodon (Rubidge and Hopson 1996)
Suminia (Rybczynski 2000)
Gorgonops, *Lycaenops*, and *Cyonosaurus* (Sigogneau 1970)

Appendix 2

Character matrix used to analyze the phylogenetic position of *Raranimus*

Taxon	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Haptodus	0000000000	0000000000	00000??000	0000000000	0000?0000-	0000-00000	00000?0000	0
Dimetrodon	0000000000	0000000000	0000000000	0000000000	?000000000	0000-00000	1000010000	0
Tetraceratops	000000000?	??0000????	??????00?	????00000	?0?1?????0	?0?0??0??0	1000000?0	0
Raranimus	**00010?2100**	**??????????**	**??????0000**	**01000?????**	**??????????**	**?????????0**	**2?0?0?00?0**	**?**
Biarmosuchus	0001102100	0100002000	00101000?1	??10?00010	20?1111101	00?0011??1	0?011?0110	0
Hipposaurus	0001102100	000101200?	0?11101??1	111??00010	1021111111	0(01)0001?111	01011?0110	0
Herpetoskylax	0000102100	000?012000	(01)111101?1?	?111?10110	10211111?1	0100011011	01011?0110	0
Lycaenodon	00001?2100	000?012?0?	???1??1111	1111010110	11?1??????	?????????1	0?011?011?	0
Lemurosaurus	000??02101	00010?2001	011??01??1	1111?10110	11?1111111	01?00110?1	?1011?0110	0
Proburnetia	0000111?11	000?1?1001	011??111?0	11?1010110	11211112?1	?100?1???1	?1011?0?10	?
Burnetia	00???1??11	100?1?1001	0?1??111?1	?1?1010?10	11?1?11???	?????????1	????1?????	?
Syodon	0111201100	1210002110	0010101201	0101?10?10	2011211100	0100100101	0210111010	0
Titanophoneus	0111201101	1210002110	0010101201	0101011010	2011211100	00001001?1	0210111010	0
Stenocybus	0001201100	0210002110	00101?????	??????00?0	20??211??0	?0?010???1	02101?1?10	0
Styracocephalus	021?10?101	?11?1?1100	0?1?111?00	0?0??10021	2011021111	0100???0?1	????????1?	?
Jonkeria	0211102101	1100001110	01101?1200	0101021121	2011?211?0	010?100001	1210121001	1
Estemmenosuchus	0101101?11	1?0?102100	0?101?1211	0101?00021	20???21100	01?01001?1	0210020001	1
Biseridens	?????1?1?0	1101002100	101?1?????	??????0???	?????012?0	0???2?0???	??????????	?
Patranomodon	0110?1?100	1100000100	1111111001	1111021100	1011002210	0011211002	????-?- - 10	0
Suminia	0111111100	11000?2100	111011101?	??11021100	1011102210	0111210102	1?00-?- - 11	0
Gorgonops	1100102100	1100002100	0011101112	1111110010	2111002201	1000110?10	0000100110	?
Lycaenops	1000102100	1100002100	0011101112	1111121120	2111002201	1000110?10	0000100110	0
Cyonosaurus	1100102100	1100002100	0011101112	1111110110	2111002201	1000110?10	00001?0110	0