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On the affinities of *Tetraceratops insignis*, an Early Permian synapsid

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The affinities of the Early Permian synapsid *Tetraceratops insignis* have been reevaluated several times since the early 20th century, being considered as an eothyridid, a spenacodontid, or a therapsid. This controversy continues into the 21st century, with recently raised doubts about the interpretation of *Tetraceratops* as the oldest known therapsid, a hypothesis supported by the only redescription of this fossil in the second half of the 20th century. Our study examines the arguments proposed to refute therapsid affinities, and concludes that *Tetraceratops* indeed is the sister-group of all other known therapsids. The most recently published phylogenetic data matrix that includes *Tetraceratops* fails to confirm its therapsid affinities. However, adding seven characters to that matrix leads to the conclusion that *Tetraceratops* is the basal-most and oldest therapsid. The recent suggestion of a Laurasian origin of therapsids appears poorly supported; too few data are available on the distribution of Permian synapsids to settle this question.

Key words: Therapsida, phylogeny, biogeography, center of origin, range extension, Paleozoic, Pangaea, North America.

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Introduction

Despite a remarkably continuous fossil record, synapsids exhibit a paleontological hiatus during the Middle Permian, a hiatus known as Olson’s gap (Lucas and Heckert 2001; Reisz and Laurin 2002). This gap was used to separate the Permian–Carboniferous synapsids (still often called “pelycosaurs”) from therapsids but more recently, this gap was partly closed by the suggestion that *Tetraceratops insignis*, from the Early Permian, is the oldest known therapsid (Laurin and Reisz 1990, 1996), and by the suggestion that the North American Chickasha Formation, which has yielded several amniote fossils (but not *Tetraceratops*), is Middle Permian (Reisz and Laurin 2001, 2002). Both claims have been disputed; Lucas (2002) argued for an Early Permian age of the Chickasha Formation, whereas Conrad and Sidor (2001) and Liu et al. (2009) have disputed the therapsid affinities of *Tetraceratops*.

Tetraceratops insignis Matthew, 1908 is known only from a partial skull and mandible (Figs. 1, 2), AMNH 4526. It has been successively considered as a spenacodontid (Matthew 1908), an eothyridid (Romer and Price 1940), and a synapsid incertae sedis (Reisz 1986). More recently, *Tetraceratops* has been considered to be the basal-most and oldest therapsid, partly reducing the drastic difference in the synapsid fauna on either side of Olson’s gap (Laurin and Reisz 1990, 1996). This nomenclatural decision reflects both the affinities of *Tetraceratops* (sister-group of all other known therapsids) and a choice in taxon delimitation, which is nec-

essarily subjective. Laurin and Reisz (1996: 100) proposed a branch-based definition of Therapsida: “mammals and all other synapsids that share a more recent common ancestor with them than with spenacodontids”. We retain this conceptualization, but would like to bring it into conformity with the PhyloCode (Cantino and de Queiroz 2010) by proposing the following branch-based definition: Therapsida (converted clade name) is the largest clade that includes *Cynognathus crateronotus* Seeley, 1895 but not *Sphenacodon ferox* Marsh, 1878. This definition respects historical and prevailing usage of the name Therapsida (to the extent possible by the requirement of monophyly), as recommended by the PhyloCode (Cantino and de Queiroz 2010). Thus, it includes all taxa that have generally been considered therapsids (biarmosuchians, anomodonts, dinocephalians, gorgonopsians, therocephalians, and cynodonts) and excludes all synapsids that have traditionally been excluded (caseosaurs, varanopids, ophiacodontids, edaphosaurids, the paraphyletic “haptodontines”, and spenacodontines) under any phylogeny proposed in the last decades (e.g., Reisz 1986; Reisz et al. 1992; Laurin 1993; Sidor and Rubidge 2006).

Doubts have repeatedly been expressed about the therapsid status of *Tetraceratops*. Conrad and Sidor (2001) and Liu et al. (2009) argued that *Tetraceratops* was not a therapsid, although they accepted its synapsid status. Regarding therapsid affinities for *Tetraceratops*, Rubidge and Sidor (2001: 452–453) commented “Although not impossible, the damaged and poorly preserved nature of the single *Tetraceratops* specimen

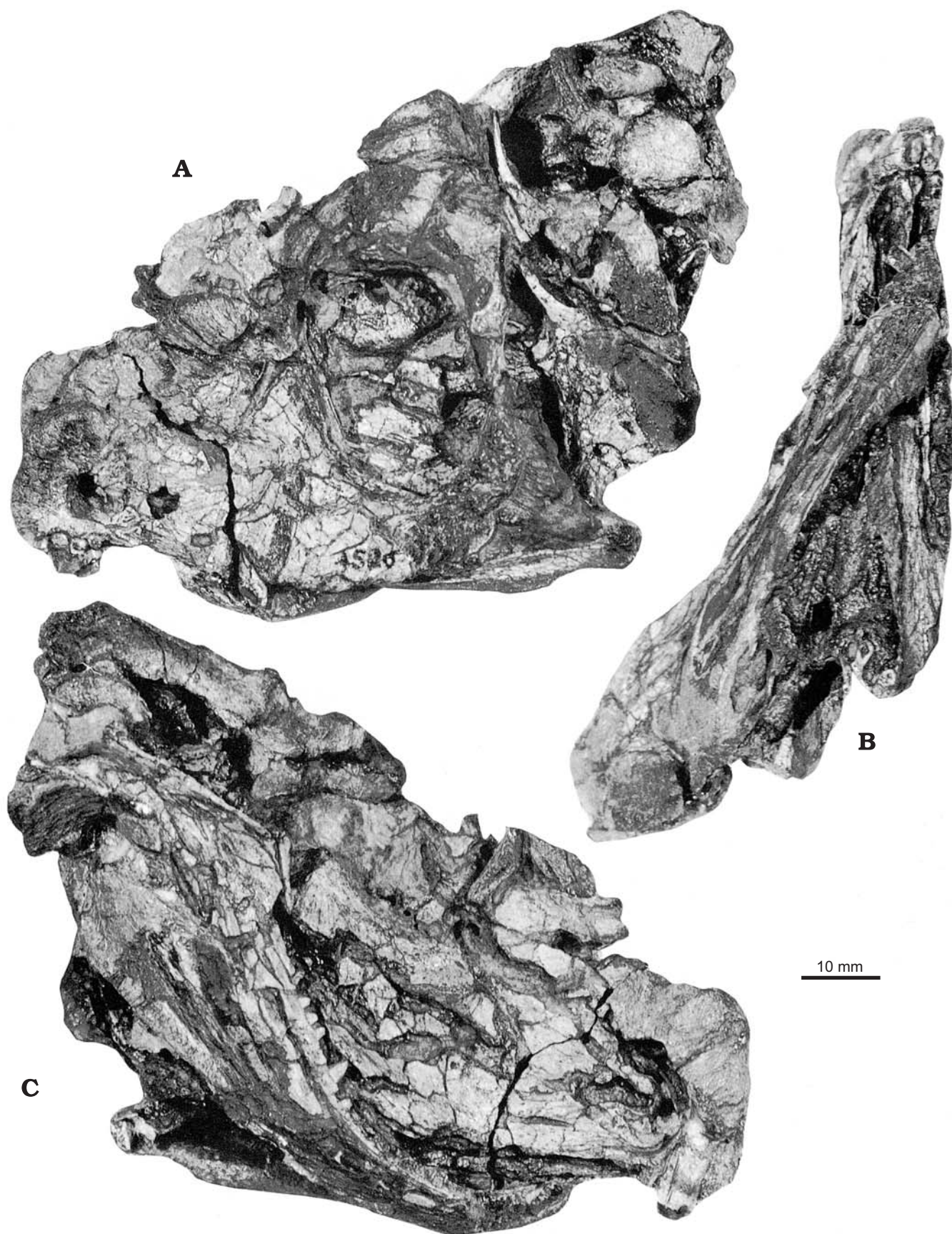


Fig. 1. Picture of the synapsid *Tetraceratops insignis* Matthew, 1908, AMNH 4526 (modified from Laurin and Reisz 1996), holotype (Clear Fork Group: Leonardian, Texas). Left lateral (A), palatal (B), and right lateral (C) views. Reproduced with permission from the Society of Vertebrate Paleontology.

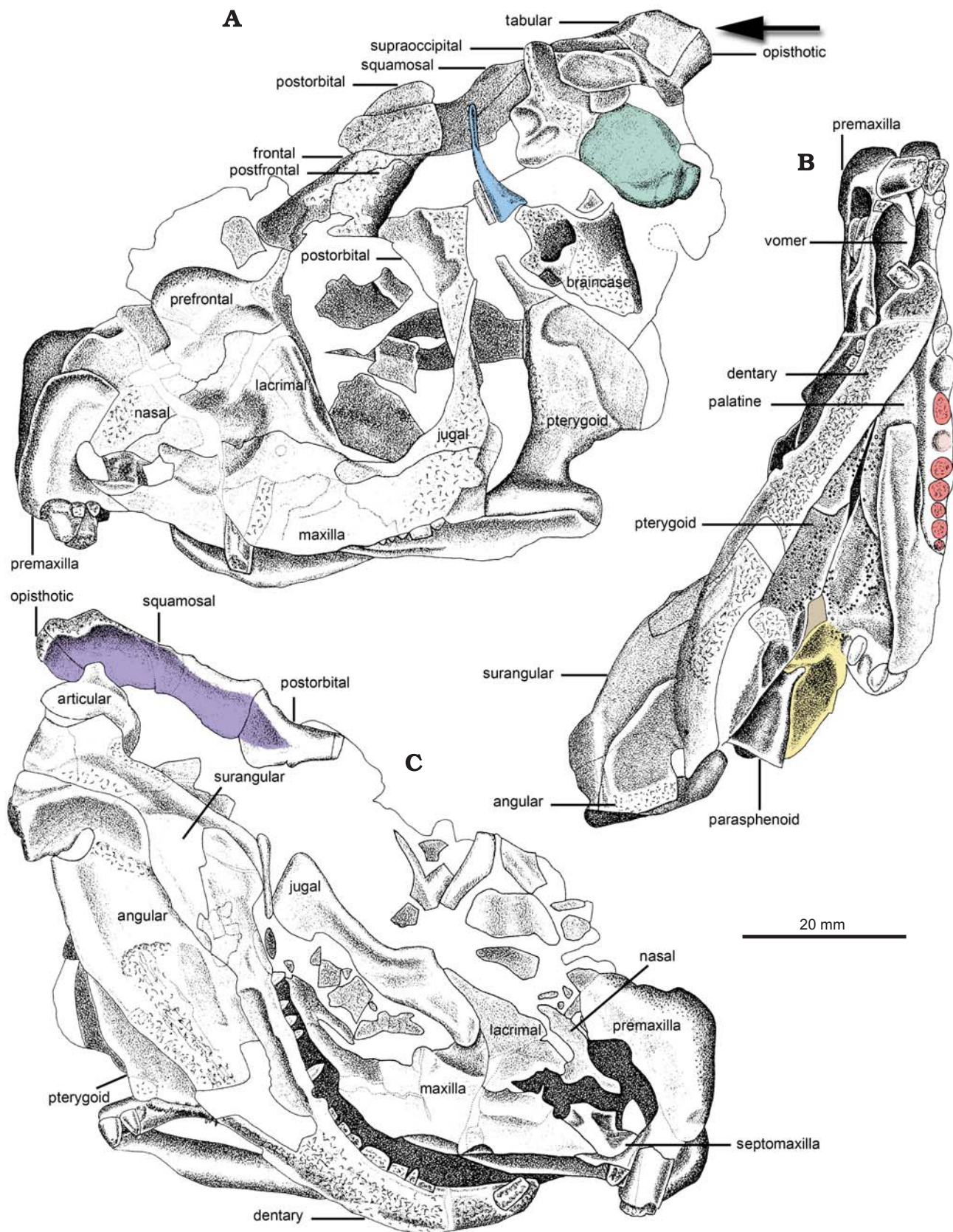


Fig. 2. Drawing of the synapsid *Tetraceratops insignis* Matthew, 1908, holotype (Clear Fork Group: Leonardian, Texas). AMNH 4526 (modified from Laurin and Reisz 1996). Left lateral (A), palatal (B), and right lateral (C) views. The black arrow indicates the suture between braincase and dermal skull. The quadrate is colored in green, epipterygoid in blue, upper postcanines in orange, upper margin of the temporal fenestra in purple, quadrate process of the pterygoid in yellow, and interpterygoid vacuity in brown.

makes a confident assessment of its phylogenetic placement difficult". Nothing can be done about the fragmentary nature of the specimen, and the presence of a single specimen coming from an intensively prospected area suggests that it may be allochthonous, which implies that finding more specimens of *Tetraceratops* will be extremely difficult. However, the statement by Rubidge and Sidor (2001) suggests that a more detailed presentation of the characters used to assess the affinities of *Tetraceratops* would be useful. The fragmentary nature of the specimen is presumably not the only reason for the frequent skepticism about the affinities of *Tetraceratops*, as the even more fragmentary *Raranimus* was recently erected as the basalmost therapsid (Liu et al. 2009). Another factor may be the great geological age of *Tetraceratops* (Clear Fork Group, Leonardian, equivalent to Artinskian; see Wardlaw et al. 2004), which makes it by far the oldest potential therapsid, and the only one in the Early Permian. In the present study, the relationships of *Tetraceratops* are reevaluated using additional characters that were not taken into consideration in the last study of its affinities (Liu et al. 2009). We also examine the alternative anatomical interpretations of the temporal region of *Tetraceratops* proposed by Conrad and Sidor (2001), and their potential phylogenetic significance. An examination of potential synapomorphies with sphenacodontines is also performed.

Institutional abbreviation.—AMNH, American Museum of Natural History, New York, USA.

Material and methods

In order to gain new insights on the affinities of *Tetraceratops*, seven characters were added to the matrix of Liu et al. (2009) that includes 23 taxa (Appendix 1). These characters supported therapsid affinities of *Tetraceratops*, according to Laurin and Reisz (1996); therefore, any assessment of the affinities of that genus should consider them. The coding of characters 8, 12 and 69 in Liu et al. (2009) was also modified (Tables 1, 2). The last character, an enlarged dentary tooth (number 78 in Tables 1, 2), has been added to verify the thesis of the exclusion of *Tetraceratops* from therapsids advocated by Conrad and Sidor (2001). All scorings were performed on the basis of the descriptive literature (Appendix 1), in contrast with previous studies from our lab, in which specimens of at least a few taxa were checked (e.g., Marjanovic and Laurin 2008: 176–177) because the Parisian collections do not include specimens of relevant taxa, and because the most relevant of these, *Tetraceratops*, is far away in New York. This is not problematic for this study because the scoring of most taxa and most characters of our matrix can be readily determined from the literature, and because the second author has detailed personal knowledge of the most relevant taxon, *Tetraceratops*, that he had prepared, drawn, reconstructed, and described in earlier studies (Laurin and Reisz 1990, 1996). He has similar detailed knowledge of the outgroup *Haptodus garnettensis* Currie,

1977 (Laurin 1993) and of one of the Late Permian therapsids, *Lycaenops* (Laurin 1998). Furthermore, the present study focuses on a more detailed presentation of the characters, first given by Laurin and Reisz (1990, 1996), that suggest therapsid affinities of *Tetraceratops*; it does not rely on new data on *Tetraceratops*. Two phylogenetic analyses were then performed (see Supplementary Online Material at http://app.pan.pl/SOM/app56-Amson_Laurin_SOM.pdf) using the matrix of 78 characters and PAUP 4.0b10 (Swofford 2001). The first reflects our anatomical interpretations (justified below) and ordering scheme; the second discards data on *Tetraceratops* that is based on anatomical interpretations that have been criticized in the abstract of Conrad and Sidor (2001), and treats one of our characters as unordered. Both parsimony searches were performed using the branch-and-bound algorithm and a bootstrap analysis (1000 replicates) using a heuristic search (each with 10 random addition sequences). The cladogram was rooted considering *Haptodus garnettensis* as the outgroup. That taxon is named using its binomen because the genus *Haptodus*, as recognized in some previous studies, is probably paraphyletic (Laurin 1993).

The following characters were added or modified:

Character 8: Maxilla: bordered dorsally by lacrimal and septomaxilla (0), reaches nasal dorsally (1) or reaches nasal and prefrontal dorsally (2) (ordered).

The ancestral state of this character, namely a maxilla bordered dorsally by lacrimal and septomaxilla, is found in *Haptodus garnettensis* and *Tetraceratops*, whereas all other taxa included in the matrix show an unknown or derived state of the character (but state 0 is present in more distant relatives, such as edaphosaurids and ophiacodontids, showing that it is the primitive condition). Consequently, this is the only character not supporting inclusion of *Tetraceratops* in Therapsida. Liu et al. (2009) recognized only two states for this character; the present coding recognizes one more relevant state that can potentially exclude *Tetraceratops* from the smallest clade that includes all other therapsids.

Character 12: Adductor musculature originated on lateral surface of postorbital absent (0), present (1), originated on both postorbital and postfrontal (2).

Liu et al. (2009) had coded this character as unknown in *Tetraceratops*, but the specimen clearly displays a concave surface for musculature on the postorbital (Figs. 1, 2B). This appears as a short, vaguely triangular gently concave surface on the posterior half of the postorbital. The lateral surface of the postfrontal is not preserved. Therefore, we have rescored *Tetraceratops* as 1/2 (partial uncertainty).

Character 69: Number of upper postcanines: 12 or more (0) or less than 12 (1) (colored in orange in Figs. 2–4). A reduction in number of the upper postcanines (to fewer than 12 postcanines) is a common feature of therapsids. For instance, in gorgonopsids, the number of upper postcanines generally does not exceed seven (Fig. 3D; Sigogneau 1970). Six postcanine teeth and an empty alveolus are visible (Figs. 1, 2). Moreover, the small size of the last upper postcanine and the length of the lower tooth row led Laurin and Reisz (1996) to

Table 1. Matrix displaying the modified characters (in grey) from Liu et al. (2009) and seven added characters.

Taxon / Character	8	12	69	72	73	74	75	76	77	78
<i>Haptodus</i>	0	0	0	0	0	0	0	0	0	0
<i>Dimetrodon</i>	1	0	0&1	0	0	0	0	0	0	0
<i>Tetraceratops</i>	0	1/2	1	1	1	1	1	1	1	0
<i>Raranimus</i>	2	?	?	?	?	?	?	?	?	?
<i>Biarmosuchus</i>	2	1	1	2	1	2	1	?	1	0
<i>Hipposaurus</i>	2	0	1	2	?	2	1	?	1	0
<i>Herpetoskylax</i>	2	0	1	2	?	?	?	?	1	0
<i>Lycaenodon</i>	2	0	1	?	?	?	?	?	?	0
<i>Lemurosaurus</i>	2	0	1	2	?	1	?	?	1	1
<i>Proburnetia</i>	?	0	1	2	?	2	?	?	1	?
<i>Burnetia</i>	?	0	?	2	1	2	?	?	1	?
<i>Syodon</i>	2	2	1	2	1	2	1	?	?	0
<i>Titanophoneus</i>	2	2	1	2	1	2	1	?	1	0
<i>Stenocybus</i>	2	2	1	?	?	?	?	?	?	0
<i>Styraccephalus</i>	2	1	1	2	?	1	?	?	1	0
<i>Jonkeria</i>	2	1	0	1	1	1	?	1	1	0
<i>Estemmenosuchus</i>	?	?	0	2	0&1	1	?	?	?	0
<i>Biseridens</i>	2	1	1	?	1	?	?	?	1	0
<i>Patranomodon</i>	2	1	?	2	0	1	1	?	1	?
<i>Suminia</i>	2	1	1	1	1	1	1	0	1	0
<i>Gorgonops</i>	2	1	1	2	1	1&2	1	1	1	?
<i>Lycaenops</i>	2	1	1	2	1	1&2	1	1	1	1
<i>Cyonosaurus</i>	2	1	1	2	1	1&2	?	?	1	?

Table 2. Description of states of characters coded in Table 1; characters in grey were modified from Liu et al. (2009).

Character number	Character description
8	Maxilla : bordered dorsally by lacrimal and septomaxilla (0), reaches nasal dorsally (1) or reaches nasal and prefrontal dorsally (2) (ordered).
12	Adductor musculature originates on lateral surface of postorbital absent (0), present (1), originates on both postorbital and postfrontal (2).
69	Number of upper postcanines: 12 or more (0) or less than twelve (1).
72	Pterygoid at level of posterior edge of transverse flange: far from sagittal plane, leaving the interpterygoid vacuity posteriorly opened (0), interpterygoid vacuity closed or constricted posteriorly by median flange (1), or quadrate processes of pterygoid medially appressed (2).
73	Upper margin of temporal fenestra: narrow (0) or broad (1).
74	Interpterygoid vacuity: long (0) or short (1).
75	Quadrate height: greater (0) or lower (1) than half of skull height.
76	Epipterygoid ventral plate: large, part of basicranium (0) or small, excluded from basicranium (1).
77	Braincase: loosely (0) or firmly (1) sutured to the dermal skull.
78	Anterior dentary teeth: include a distinctly enlarged tooth (0) or all of subequal size (1).

infer a maximum of ten postcanines on the maxilla. This character was already present in the coding of Liu et al. (2009) in which *Tetraceratops* was scored as unknown, which seems suboptimal.

Character 72: Pterygoid at the level of the posterior edge of the transverse flange: far from the sagittal plane, thus leaving interpterygoid vacuity posteriorly open (0), close to sagittal plane, posteriorly constricting the interpterygoid vacuity by a medial flange (1), or the quadrate processes are medially

appressed (2) (ordered in the main analysis only, colored in yellow in Figs. 2, 3).

Tetraceratops and some therapsids such as *Suminia* (Rybczynski 2000: fig. 2) and *Jonkeria* (Boonstra 1936) display a medial flange of the pterygoid at the level of the posterior edge of its transverse flange. This results in a posteriorly closed or constricted interpterygoid vacuity. A more derived morphology (farther from the ancestral morphotype of synapsids), a medially appressed quadrate process that closes

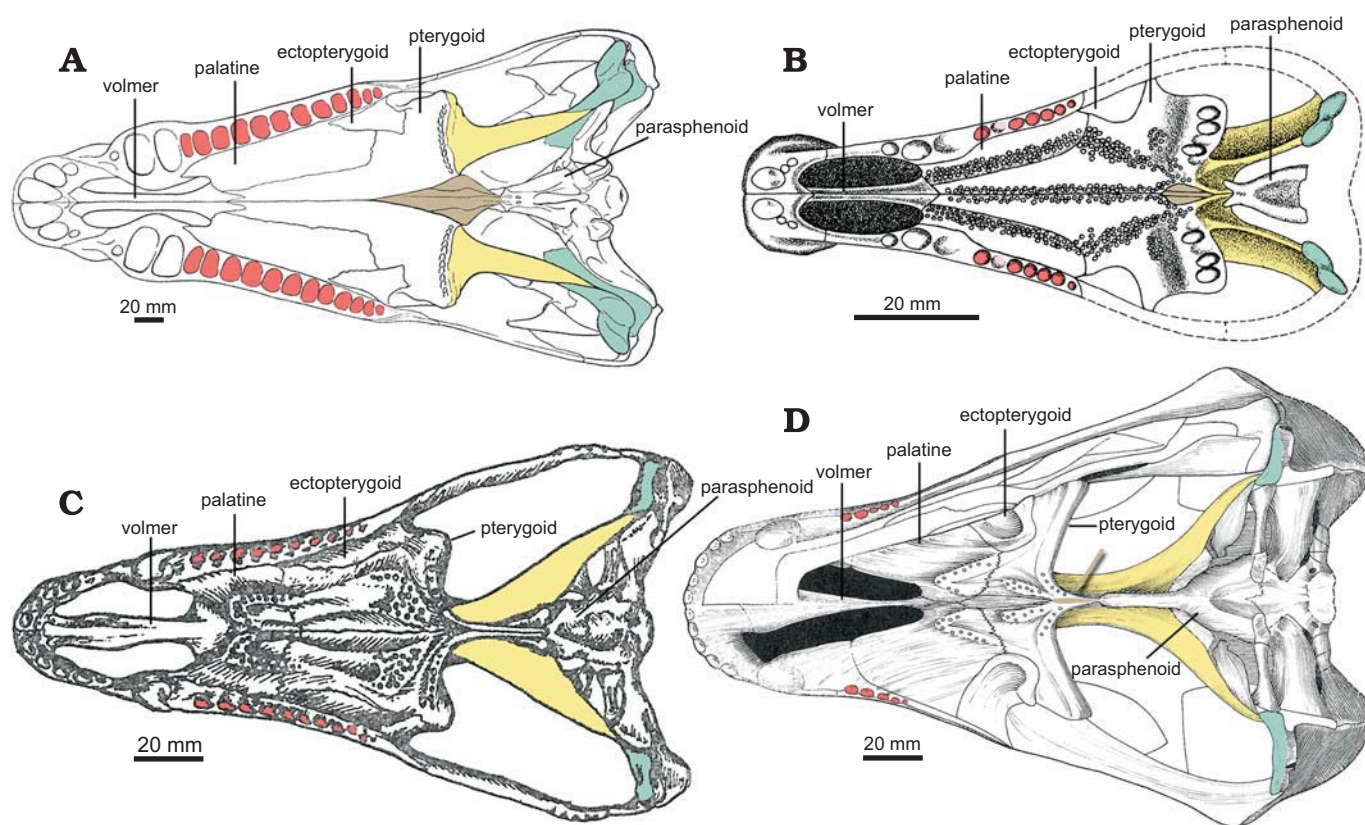


Fig. 3. Reconstructions in palatal view of synapsid skulls. **A.** *Dimetrodon limbatus* Cope, 1877 (modified from Romer and Price 1940). **B.** *Tetraceratops insignis* Matthew, 1908 (modified from Laurin and Reisz 1996). **C.** *Biarmosuchus tener* Tchudinov, 1960 (modified from Ivakhnenko 1999). **D.** *Gorgonops torvus* Owen, 1876 (modified from Sigogneau 1970). The quadrate is colored in green, upper postcanines in orange, quadrate process of the pterygoid in yellow, and interpterygoid vacuity in brown (see arrow in D).

the interpterygoid vacuity posteriorly and makes up a sagittal septum linking the palate and to the braincase, prevails in most therapsids, such as *Gorgonops torvus* Owen, 1876 (Fig. 3D; Sigogneau 1970) or *Biarmosuchus tener* Tchudinov, 1960 (Fig. 3C; Ivakhnenko 1999). In this character, *Jonkeria* seems somewhat intermediate between *Tetraceratops* and *Suminia*, on one hand, and most other therapsids, on the other. In *Suminia*, the flanges do not quite reach the sagittal plane, thus leaving a narrow posterior opening at the posterior edge of the interpterygoid vacuity. In *Tetraceratops*, the flange seems to completely close the vacuity posteriorly (Fig. 3B), although it is possible that this condition results from the medial displacement of the bones; thus, both taxa may resemble each other more closely in this respect than suggested by the previously published cranial reconstructions. In *Jonkeria*, the medial flange has a long sagittal contact that may represent the morphological precursor of state 2, in which the body of the quadrate ramus itself is in the sagittal plane. This apparent morphocline justifies our tentative ordering of this character in the main analysis. No therapsid retains state 0.

Character 73: Upper margin of the temporal fenestra: narrow (0) or broad (1) (colored in purple in Fig. 4).

A broad upper margin of the temporal fenestra is visible

in *Tetraceratops* (Fig. 4C), as in half of the studied therapsids (mostly coded as unknown for the others). In *Tetraceratops*, this broad, concave surface that presumably accommodated the origin of part of the jaw adductor musculature covers the whole preserved lateral surface of the squamosal, with a short, vaguely triangular extension covering the posterior half of the postorbital (Fig. 2B). Among other therapsids, *Syodon efremovi* Orlov, 1940 (Fig. 4D; Orlov 1958) clearly shows a similarly broad upper margin. This synapomorphy may represent a larger surface for the origin of the mandibular muscles and hence, a more developed musculature. On the contrary, *Haptodus garnettensis* (Fig. 4A) and *Dimetrodon* show a narrow upper margin of the temporal fenestra.

Character 74: Interpterygoid vacuity: long, extending well anterior of transverse flange of pterygoid (0), short, barely extending beyond transverse flange of pterygoid (1), or closed (2) (colored in brown in Figs. 2, 3).

A short or closed interpterygoid vacuity is displayed by *Tetraceratops* (Figs. 2C, 3B) and all therapsids studied here (see arrow in Fig. 3D). For instance, *Patranomodon nyaphuli* Rubidge and Hopson, 1990 shows a short interpterygoid vacuity (Rubidge and Hopson 1996), and *Biarmosuchus tener* Tchudinov, 1960 (Fig. 3C; Ivakhnenko 1999) displays a closed vacuity (state 2). On the other hand, *Haptodus* and

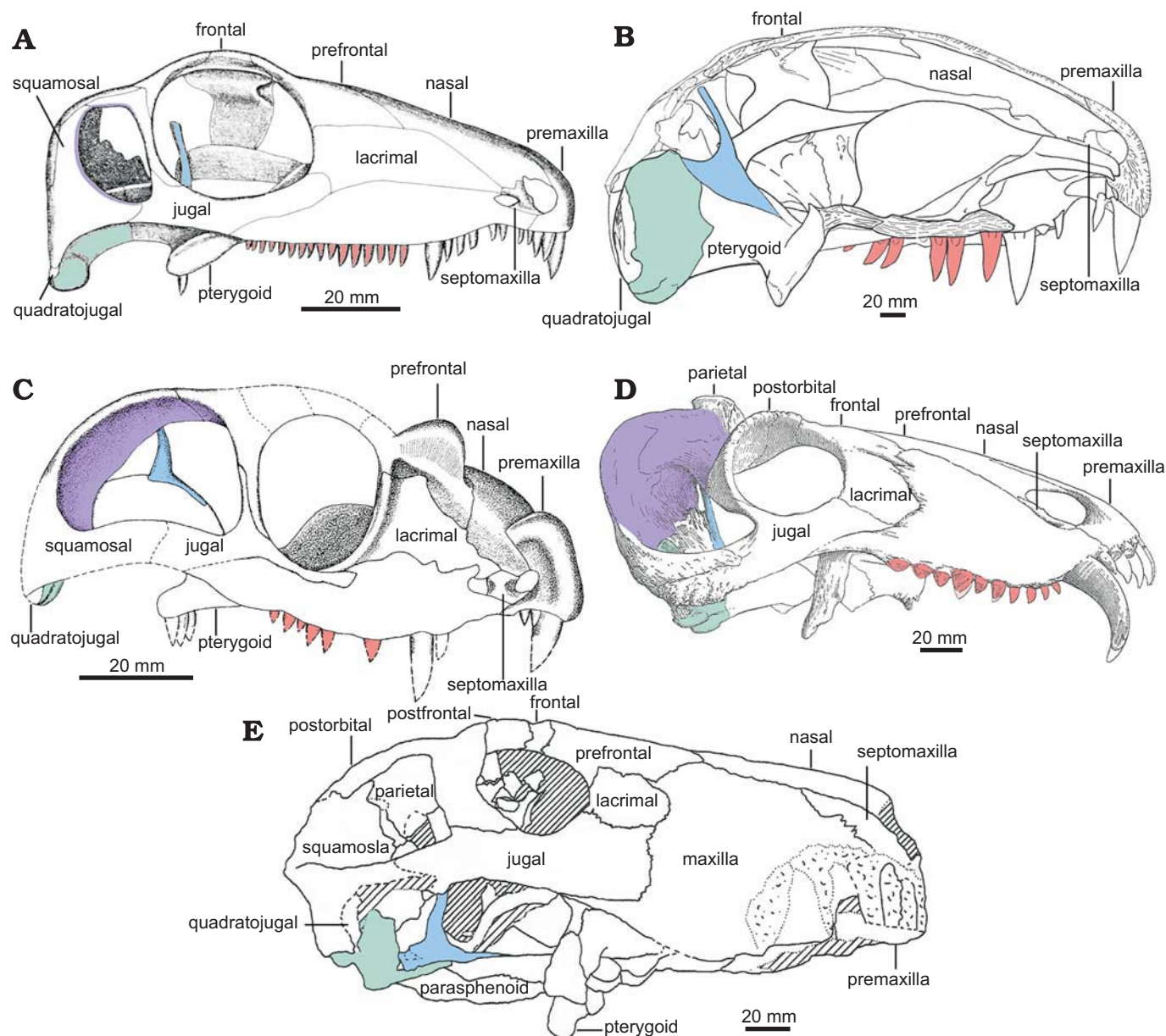


Fig. 4. Reconstructions (A–D) or specimen drawings (E) in lateral view of synapsid skulls. A. *Haptodus garnettensis* Currie, 1977 (modified from Laurin 1993). B. *Dimetrodon limbatus* Cope, 1877, sagittal section (modified from Romer and Price 1940). C. *Tetraceratops insignis* Matthew, 1908 (modified from Laurin and Reisz 1996). D. *Syodon efremovi* Orlov, 1940 (modified from Orlov 1958). E. *Lycaenops angusticeps* (Broom, 1913) UCMP 42701 (modified from Laurin 1998). The quadrate is colored in green, epipterygoid in blue, upper postcanines in orange, and upper margin of the temporal fenestra in purple.

Dimetrodon (Fig. 3A) have a long one that extends anteriorly to the level of the ectopterygoid. This character is not tightly linked with character 72 because it refers to the anterior extent of the vacuity, rather than to its posterior extent.

Character 75: Quadrate height: greater (0) or less (1) than half of the skull height (colored in green in Figs. 2–4).

A quadrate having its height inferior to half of the skull's height is shared by *Tetraceratops* (Figs. 2A, 4C) and therapsids for which an adequate view is available (Fig. 4D, E). Both *Dimetrodon* (Fig. 4B) and *Haptodus* have a tall quadrate.

Character 76: Epipterygoid ventral plate: large, part of the basicranium (0) or small (1) (colored in blue in Figs. 2, 4).

A small epipterygoid ventral plate can be observed in *Tetraceratops* (Figs. 2A, 4C) and the other therapsids when an adequate view is available, as in *Lycaenops angusticeps* (Broom, 1913) (Fig. 4E). The largest ventral plate in the therapsids sampled here is found in *Suminia* (Rybczynski 2000), but despite its distinct expansion, it is substantially smaller than in Permo-Carboniferous synapsids such as *Haptodus* and *Dimetrodon* (Fig. 4A, B), in which the epipterygoid contributes to the mobile basicranial articulation. This character should not be confused with the expansion of the epipterygoid that occurs (mostly in its dorsal part, the columella) in eutheriodonts (Hopson and Barghusen 1986) and

that is especially obvious in cynodonts. This marks the transformation of the epipterygoid into the alisphenoid.

Character 77: Braincase: loosely (0) or firmly (1) sutured to the dermal skull.

The opisthotic and tabular are still sutured to each other in the *Tetraceratops* specimen, despite the fact that the skull is crushed and some fragments are displaced from their original positions. This suture extends the whole length of the slender paroccipital process, and is visible both in anterior and posterior views (Fig. 2A, C). The tabular is also sutured dorsal to the paroccipital process, as shown by a posteromedial view of the large braincase fragment that preserves both bones (Fig. 2A). The identity of both elements is supported by their position on the occiput, by the characteristic three-dimensional shape of the opisthotic (with a long, cylindrical paroccipital process and a complex portion articulating with other braincase elements, anterodorsal to the base of the process), and by the flat, broad shape of the tabular. Thus, the braincase of *Tetraceratops* may be considered as firmly sutured to the dermal skull, an apomorphy shared by all therapsids. In all these taxa, there is a strong, three-dimensional sutural contact that firmly binds the braincase to the dermal skull, resulting in very infrequent disarticulation of the braincase, even in species of small body size, such as *Suminia getmanovi* Ivachnenko, 1994 (Rybczynski 2000: fig. 6), at a skull length of barely 5 cm. The plesiomorphic state for synapsids was already described in *Haptodus* by Laurin (1993); the braincase was loosely attached to the dermal skull at the distal surface of the paroccipital process of the opisthotic, indirectly through the stapes and quadrate, and through the supraoccipital, which articulated against the skull roof. All these contacts are rather loose, even in fairly mature individuals, and may even have involved soft tissue and intervening cartilage. Thus, braincases of Permo-Carboniferous synapsids are often found dislocated from the rest of the skull. This has been shown by Reisz et al. (1992: fig. 5) for *Secodontosaurus* and by Laurin (1993: fig. 6) for *Haptodus garnettensis*. Only in the largest specimens of species reaching a much larger body size than *Tetraceratops* (about 10 cm skull length) do we see a firm attachment develop in some Permo-Carboniferous synapsids, such as in *Edaphosaurus novomexicanus* (Modesto and Reisz 1992: fig. 1), at a skull length of about 15 cm, and in *Sphenacodon ferocior* Romer, 1937, but not in all mature individuals, despite the large size (cranial length exceeding 20 cm) of that species (Eberth 1985: figs. 17, 24).

Character 78: Anterior dentary teeth: include a distinctly enlarged tooth (0) or all of subequal size (1).

This character has been added because it has been argued that it does not support therapsid affinities for *Tetraceratops* (Conrad and Sidor 2001). However, all the taxa studied here show a larger tooth on the anterior part of the mandible (when a proper view is available) except for *Lemurosaurus pricei* Broom, 1949 (Sigogneau 1970) and *Lycaenops augusticeps* (Broom, 1913) (Sigogneau 1970). For example, *Tetraceratops* and *Stenocybus acidantatus* Cheng and Li, 1997 (Cheng and Li 1997) display an enlarged dentary tooth.

No other changes were made to the scoring of the matrix of Liu et al. (2009). For instance, these authors scored *Tetraceratops* as unknown for the presence of a supratemporal, which is correct, as the relevant part of the skull is incompletely preserved. Even though that bone is not preserved, only a small part of the occiput is preserved, and this shows mostly the tabular and opisthotic (Fig. 2A). Liu et al. (2009) also scored *Tetraceratops* as retaining a row of teeth on the transverse flange of the pterygoid (a structure lost in many other therapsids), which is correct.

All the information given above was incorporated into the first parsimony search. For the second search, we rescored *Tetraceratops* as unknown for characters 12, 73, and 77 to test the potential phylogenetic impact of the alternative anatomical interpretations of Conrad and Sidor (2001), even though we consider them unlikely. We also changed the ordering status of character 72 (pterygoid at level of posterior transverse flange) from ordered to unordered.

Results

The phylogenetic analyses show that *Tetraceratops* is the sister-group of all other known therapsids (Fig. 5). In the first analysis (reflecting our anatomical interpretations), eight derived states (in characters 12, 44, and 72–77) are shared by *Tetraceratops* and therapsids (Tables 1, 2 and SOM 1). The node linking *Tetraceratops* to other therapsids has a bootstrap frequency of 95%, the second largest value found by this analysis, and a Bremer index of four. Adding a stratigraphic calibration using Mesquite and its Stratigraphic Tools (Josse et al. 2006, Maddison and Maddison 2009) to the cladogram, and assuming that no taxon was the ancestor of any other, allowed building a time-calibrated tree (Fig. 5). The second analysis, based on the matrix in SOM 2, yields only slightly different results, with an identical topology, but with weaker bootstrap support (83%) and Bremer index (2) supporting the therapsid status of *Tetraceratops*.

Discussion

Our phylogenetic analyses show that *Tetraceratops* is indeed a therapsid. Therapsids share eight apomorphies, characters 12, 44, and 72–77. These were described above, except for character 44, referring to the presence or absence of dentition on the ectopterygoid. Laurin and Reisz (1990) argued that the loss of this dentition was a therapsid apomorphy shared by *Tetraceratops*; this character is not described above because it was accepted by Liu et al. (2009).

Three of the synapomorphies mentioned above (characters 12, 73, and 77) rely on anatomical interpretations that have been disputed. Conrad and Sidor (2001) have claimed that several bones were misinterpreted by Laurin and Reisz (1996); the opisthotic, tabular and postorbital are respec-

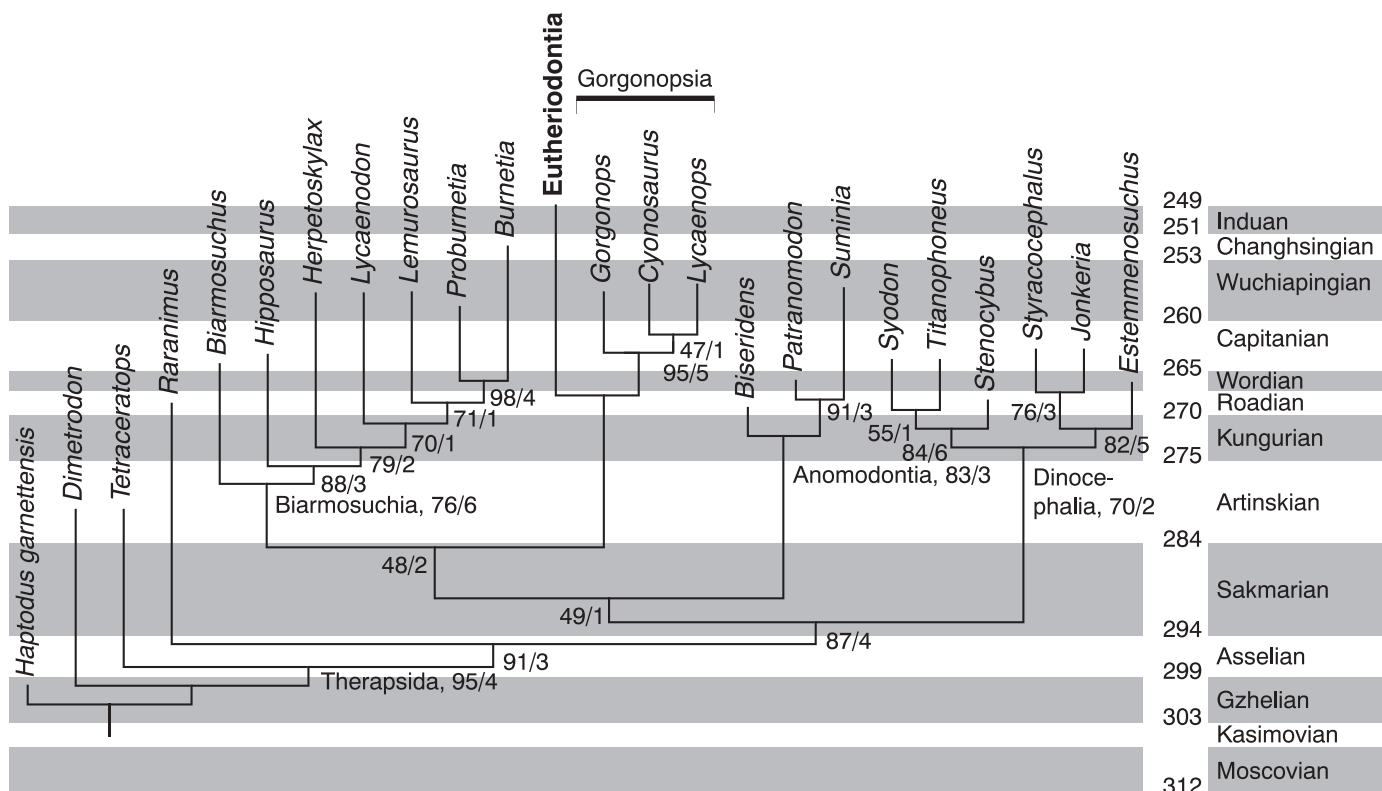


Fig. 5. Time-calibrated tree displaying the relationship between *Haptodus*, *Dimetrodon*, *Tetraceratops*, and 20 other therapsids. The putative position of Eutheriodontia (a taxon that includes Therocephalia and Cynodontia, the latter including Mammalia) was added after the analysis, in the position suggested (for Cynodontia) by Liu et al. (2009). The bootstrap and Bremer support values are also included. The branch lengths are approximate but reflect geological time.

tively reinterpreted as quadratojugal, squamosal and zygomatic process of the jugal. The lateral surface (as exposed) of the fragment in question being concave (Figs. 1, 2), this reinterpretation would imply that these bones have rotated about 180°, bringing the quadratojugal (which is always much smaller than the squamosal) in dorsal position with respect to the squamosal. This interpretation does not seem plausible because this topology is currently unknown in any Permian synapsid (or even amniote). However, rescoring *Tetraceratops* as unknown for these characters does not change the topology, although it lowers bootstrap and Bremer support.

Conrad and Sidor (2001) have also considered that two characters, enlarged dentary tooth and shape of the articular glenoid, support spenacodontid affinities for *Tetraceratops*. The articular glenoid is not frequently pictured in the literature; therefore its phylogenetic implications are difficult to assess. The character “enlarged anterior dentary tooth” was added to the matrix and appeared plesiomorphic for all Sphenacodontia. Hence, this character does not support spenacodontid affinities of *Tetraceratops*.

A short nomenclatural digression is necessary. Sphenacodontia traditionally included at least the paraphyletic “haptodontines” and spenacodontines (Romer and Price 1940: 18–19), and thus formed part of the paraphyletic therapsid stem-group. Reisz et al. (1992: 164) made the group monophyletic by also including therapsids, and proposed the fol-

lowing phylogenetic definition: “*Haptodus*, Sphenacodontidae, Therapsida, and all synapsids that share a more recent common ancestry with them than with edaphosaurids”. The PhyloCode (Cantino and de Queiroz 2010) recommends basing definitions on the core taxa that have generally been included (thus, Therapsida should not be used as a specifier), and it also requires using species or specimens, rather than higher-ranking taxa, as specifiers. Thus, we propose the following emended definition for Sphenacodontia: the largest clade that includes *Haptodus baylei* Gaudry, 1882, *Haptodus garnettensis* Currie, 1977, and *Sphenacodon ferox* Marsh, 1878, but not *Edaphosaurus pogonias* Cope, 1882.

The reflected lamina of the angular of *Tetraceratops* is somewhat problematic. Laurin and Reisz (1996) already noted that its shape was reminiscent of spenacodontines, and Liu et al. (2009) scored its shape as unknown (in their character 55), a decision with which we agree. As noted by Laurin and Reisz (1996), it does not show a dorsal incision as in other Permian therapsids, but its poor preservation precludes detailed comparisons.

Tetraceratops retains an ancestral synapsid character, a lacrimal contacting the external naris. Among all other taxa included in this analysis, only *H. garnettensis* show this feature. This is the only character with a distribution incongruent with a therapsid status of *Tetraceratops*. It suggests either a reversal in the latter, or convergence between spena-

codontines and more recent therapsids. Despite the inclusion of this character that should increase support for the interpretations of Conrad and Sidor (2001) and Liu et al. (2009), the analysis still provides strong support for therapsid affinities of *Tetraceratops*.

Liu et al. (2009) considered the Chinese fossil *Raranimus* as the basal-most therapsid, inferring thereby a Laurasian origin for the latter. *Raranimus* is marginally relevant to this question because China was isolated from Pangaea during the Early Permian (Metcalf 2006); it became part of Pangaea (Laurasia was not distinct from Gondwana in the Permian, according to recent paleogeographical reconstructions) only during the Middle Permian, age of occurrence of the first Chinese amniotes. Hence China probably represents an area of range expansion rather than an area of origin of therapsids.

No certainty exists on the area of origin of therapsids, mainly because of the poor fossil record on this period of synapsid evolution. Our knowledge of Permo-Carboniferous synapsids is almost exclusively restricted to North America and Europe (Reisz 1986), two areas that were located relatively close to the paleoequator (Metcalf 2006: fig. 8b), but the record of continental vertebrates is too poor to conclude that synapsids did not occur in other areas as well. In any case, by the Middle Permian, synapsids appear to have had a nearly global Pangaeian distribution, which hampers determination of the area of origin of therapsids. The recent description of a disputed (Dias-da-Silva et al. 2006) basal synapsid from Permo-Triassic deposits of Uruguay (Piñeiro et al. 2003), and the well-established co-occurrence of varanopids, caseids, and biarmosuchians in the same basin in Russia (Reisz and Berman 2001; Ivakhnenko 2008), and of varanopids, dinocephalians, therocephalians and anomodonts in the same levels in South Africa (Dilkes and Reisz 1996; Reisz and Laurin 2002) underscore this point.

In conclusion, the addition of a few characters to the study of Liu et al. (2009) supports the therapsid status of *Tetraceratops*, even if characters based on disputed anatomical interpretations are excluded. A debate remains on the presence of a gap, called Olson's gap, in the early Middle Permian vertebrate fossil record. Some authors argue that the gap is real (Lucas and Heckert 2001; Lucas 2002, 2004, 2005), others that it is not (Reisz and Laurin 2001, 2002; Lovosky 2005). But in both cases, *Tetraceratops* represents a precursor of the Middle and Late Permian therapsids.

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Appendix 1

Taxa included and the source of data:

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|--|--|
| <i>Haptodus garnettensis</i> (Laurin 1993) | <i>Syodon</i> (Orlov 1958) |
| <i>Dimetrodon</i> (Romer and Price 1940; Berman et al. 2004) | <i>Titanophoneus</i> (Orlov 1958) |
| <i>Tetraceratops insignis</i> (Laurin and Reisz 1990; Laurin and Reisz 1996) | <i>Stenocybus</i> (Cheng and Li 1997) |
| <i>Raranimus dashankouensi</i> (Liu et al. 2009) | <i>Styracocephalus</i> (Rubidge and van den Heever 1997) |
| <i>Biarmosuchus</i> (Chudinov 1960; Ivakhnenko 1999) | <i>Jonkeria</i> (Boonstra 1936) |
| <i>Hipposaurus</i> (Sigogneau 1970) | <i>Estemmosuchus</i> (Chudinov 1960; Ivakhnenko 2000) |
| <i>Herpetoskylax</i> (Sidor and Rubidge 2006) | <i>Biseridens</i> (Li and Cheng 1997; Liu et al. 2010) |
| <i>Lycaenodon</i> (Sigogneau 1970; Sidor 2003) | <i>Patranomodon</i> (Rubidge and Hopson 1996) |
| <i>Lemurosaurus</i> (Sigogneau 1970; Sidor and Welman 2003) | <i>Suminia</i> (Rybczynski 2000) |
| <i>Proburnetia</i> and <i>Proburnetia</i> (Rubidge and Sidor 2002) | <i>Gorgonops</i> (Sigogneau 1970) |