PALÆO VERTEBRATA

The skull of *Tetraceratops insignis* (Synapsida, Sphenacodontia)

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Abstract: The synapsid *Tetraceratops insignis* is known from a single, crushed skull from the lower Permian of Texas. Its unique combination of cranial characters has made it a central figure in discussions of therapsid origins, with previous researchers recognizing *Tetraceratops* as the earliest therapsid. Without a therapsid identity for *Tetraceratops*, the 'mammal-like' Therapsida and their sister taxon, the pelycosaur-grade Sphenacodontidae, would be separated by one of the longest ghost lineages in the tetrapod fossil record. Since its initial publication, however, uncertainty has surrounded the therapsid hypothesis of identity for *Tetraceratops*, based in large part on the poor preservation of the holotype. A thorough re-evaluation of the holotypic skull reveals that previously-proposed therapsid traits cannot be supported, including a rejection of the presence of a supposed adductor shelf in the temporal fenestra. New information on 'pelycosaurian' character variation and relationships indicates that *Tetraceratops* represents a haptodontine-grade or (less likely) sphenacodontid 'pelycosaur'.

Keywords: cranium, pelycosaur, Permian, therapsid origins

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INTRODUCTION

During a time of pioneering research into the systematics of pelycosaur-grade synapsids (Baur & Case, 1899; Case, 1907; Williston, 1912), the taxon *Tetraceratops insignis* was described, based on a single crushed skull from the upper Cisuralian (lower Permian) of Texas (Matthew, 1908). Despite its fragmentary condition, the holotype of *Tetraceratops* is highly diagnostic, and the validity of the taxon has never been questioned. Although its synapsid nature was recognized from the beginning, the precise taxonomic position of *Tetraceratops* has been subject to greater discussion (Romer & Price, 1940; Reisz, 1986). Laurin & Reisz (1990, 1996) provided the first detailed description and reconstruction of *Tetraceratops* and proposed that it represents the oldest known therapsid, filling a long-discussed gap between early Permian pelycosaur-grade synapsids and middle Permian to Mesozoic therapsids (Olson, 1962; Lucas, 2004). In subsequent studies, *Tetraceratops* was repeatedly claimed to be an early therapsid, preceding the main therapsid radiation into the well-defined subclades (Biarmosuchia, Dinocephalia, Anomodontia, Gorgonopsia, Eutheriodontia) that first appear in the middle Permian record (Sidor & Hopson, 1998). Although brief criticisms of the therapsid hypothesis for *Tetraceratops* have appeared in the literature (Conrad & Sidor, 2001; Liu *et al*., 2009), the most recent research on this taxon (Amson & Laurin, 2011) repeatedly supported the previous therapsid hypothesis. The current study presents the results of a careful re-examination of the holotype skull of *Tetraceratops insignis* and a discussion of previous hypotheses of its relationships in light of recent advances in our knowledge of sphenacodontian morphology and evolution (Spindler, 2015, 2016, 2019).

Institutional abbreviations. **AMNH FARB**, Fossil Amphibian, Reptile and Bird collection, American Museum of Natural History (New York, NY); **MCZ**, Museum of Comparative Zoology (Cambridge, MA).

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA Osborn, 1903
SPHENACOMORPHA Ivakhnenko, 2003
SPHENACODONTIA Romer & Price, 1940 (*sensu* Reisz, Berman & Scott, 1992)
Tetraceratops Matthew, 1908
Type and only species. *Tetraceratops insignis* Matthew, 1908

Material. Holotype and only material is AMNH FARB 4526, crushed and flattened skull (Figs. 1, 2).

Type locality and age. Big Wichita River, Baylor County, Texas (Matthew, 1908; Romer & Price, 1940). Amson & Laurin (2011) state that this locality is well-prospected. The specimen originates from the Leonardian of the Clear Fork Group, Arroyo Formation. According to Lucas (2004), this probably falls into the late Artinskian and is no younger than the earliest Kungurian. However, based on the correlations of Lucas (2006), it might be younger, possibly middle Kungurian.

Emended diagnosis. Medium-sized pelycosaur-grade synapsid with boss- or horn-like ornamentation on the premaxillae and prefrontals; shortened facial region; three premaxillary teeth; first premaxillary tooth greatly enlarged; broad septomaxilla; long maxillary diastema; single, tiny precaniniform tooth; two caniniform teeth; lacrimal contributing to septomaxillary foramen; extensive palatal dentition; pterygoid transverse process with four large teeth; shallow dentary symphysis.

General notes

The present description provides additional information and reinterpretation beyond that of previous accounts of *Tetraceratops* (Laurin & Reisz, 1996; Amson & Laurin, 2011). Due to heavy compaction in the skull, the posterior cranium

exhibits very little preserved morphology. Moreover, the specimen has suffered some damage from preparation with a grinding head, which was previously documented in the drawing of Laurin & Reisz (1996: fig. 1). These tool traces affect, for example, a hole in the highest portion of the left maxilla, longitudinal fluting on the palate, damage to the occiput, and the medial tooth position in the transverse flange of the left pterygoid.

The skull of *Tetraceratops* reflects a predatory synapsid with noticeably large orbits, even more pronounced than in haptodontine-grade synapsids and most early therapsids. In overall shape, the skull of *Tetraceratops* is unique among early synapsids, but roughly resembles *Haptodus*, *Cutleria*, or *Biarmosuchus* in some aspects. The holotype is likely to represent a mature individual, based on the bone texture of the skull, development of extensive cranial ornamentation, and a high degree of ossification, for example in the fully ossified articular.

The overall shape (Fig. 3) of the skull of *Tetraceratops* is different from any early tetrapod. It probably represents a specialist of unknown habits, in which certain similarities to other synapsids may be affected by functional aspects more than true synapomorphies under stable trends (as for *Haptodus*, *Pantelosaurus*, *Sphenacodon*, and *Dimetrodon*). The overall robust skull architecture (Laurin & Reisz, 1990) runs somewhat counter to the descriptions of the premaxilla and maxilla below. The mandible is remarkably delicate in its anterior half. The preserved teeth are slender, whereas incomplete tooth bases indicate an unknown degree of heterodonty. The size difference between some neighboring teeth is much more conspicuous than in other early synapsids, possibly reflecting enlarged crushing teeth (but also paralleled by the tipped teeth in e.g. the Permian parareptile *Colobomycter*, MacDougall *et al.*, 2017). Durophagy would appear to be a reasonable, though tentatively stated model for interpretation.

Many of the skull proportions are dependent on the reconstruction utilised. The orbit has an anteriorly-shifted position. As in Caseasauria (including faunivorous forms)

Figure 1. AMNH FARB 4526, holotype of *Tetraceratops insignis*. Stereographs of crushed skull from both lateral aspects, as well as frontal and dorsal views (with distinct premaxillary bulges). Scale bar measures 5 cm.

and derived Edaphosauridae, this condition is achieved by a shortened facial area, not via elongation of the temporal range as seen in many therapsids and probably varanodontine varanopids. Regarding the dislocation of the left jugal, the orbits may have been subcircular in life.

The eponymous skull ornamentation is present on the premaxilla and prefrontal. Further protuberances have been interpreted as present on the angulars (Laurin & Reisz, 1996), which could explain the strange anatomy of the articular region. Craniomandibular excrescences are also frequently present in early therapsids, typically in the orbital and temporal regions (Tchudinov, 1960; Rubidge & van den Heever, 1997; Day *et al*., 2018) but also sometimes on the angular (Kammerer,

2011, 2016) or dentary (Whitney & Sidor, 2016). However, no therapsid exhibits the paired, flange-like premaxillary and prefrontal ornamentation of *Tetraceratops*, and these structures are unlikely to be homologous to those of therapsids (Laurin & Reisz, 1990). The preserved horns are spongiose along their dorsal facets, implying some soft tissue continuation. Their robust morphology also suggests a possible use in combat or a fossorial lifestyle, rather than pure display (comparable to the horns in the Neogene rodent *Ceratogaulus* and possibly the cingulate *Peltephilus*, explained as defense in fossorial forms by Hopkins, 2005, maybe during head exposure in the terminal burrow).
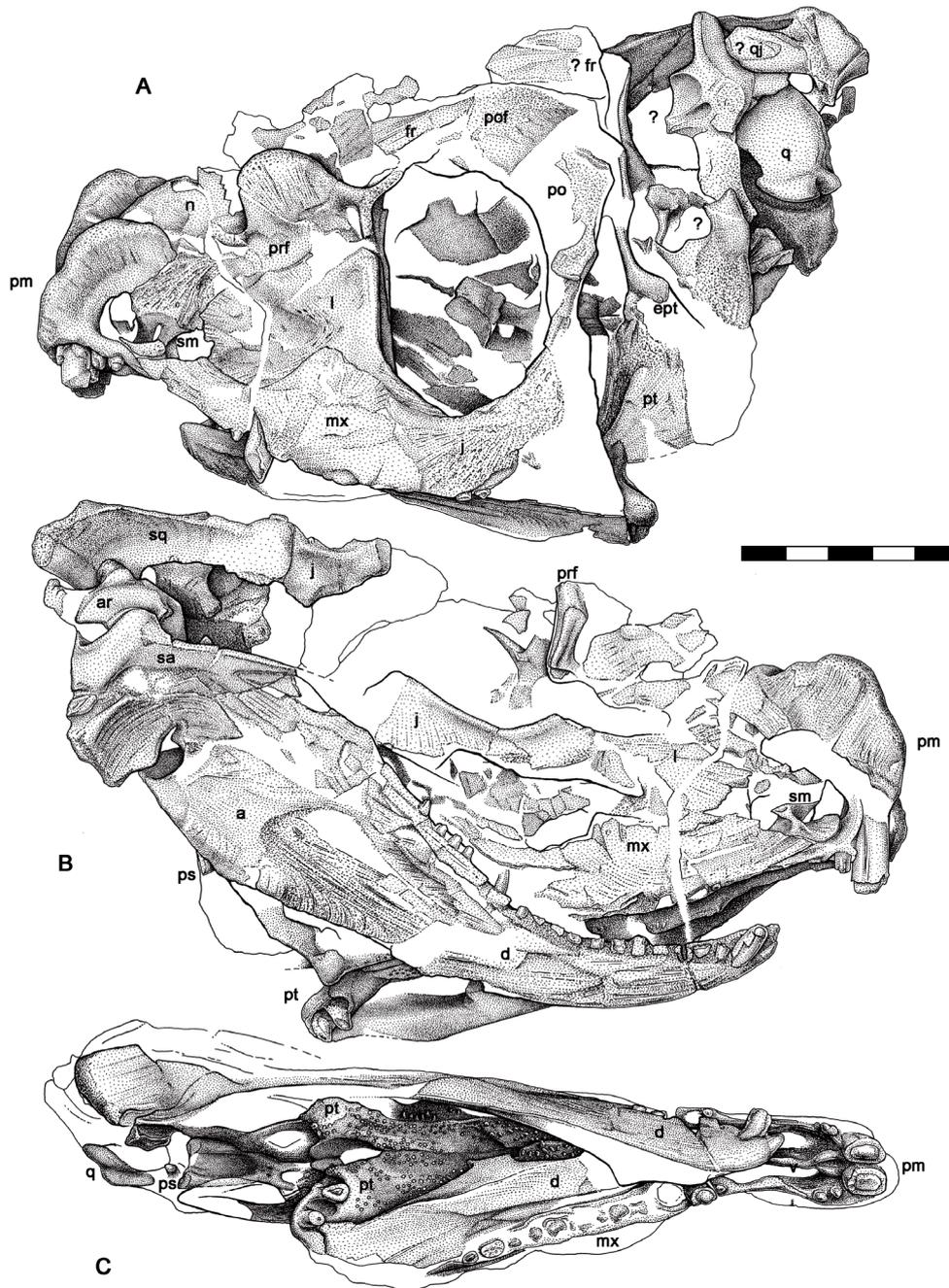

Figure 2. AMNH FARB 4526, holotype of *Tetraceratops insignis*. **A**, skull in left lateral aspect; **B**, right lateral aspect; **C**, ventral view. Abbreviations: a - angular, ar - articular, d - dentary, ept - epipterygoid, fr - frontal, j - jugal, l - lacrimal, mx - maxilla, n - nasal, pm - premaxilla, po - postorbital, pof - postfrontal, prf - prefrontal, ps - parasphenoid, pt - pterygoid, q - quadrate, qj - quadratojugal, sa - surangular, sm - septomaxilla, sq - squamosal, v - vomer. Scale bar measures 5 cm.

The crucial evidence supporting a therapsid identification for *Tetraceratops* comes from Laurin & Reisz's (1990) interpretation of the posterior portion of the skull. Specifically, the therapsid hypothesis hinges on the identification of a temporal adductor shelf in the anterodorsal bar of the squamosal and the adjacent corpus of the postorbital, as suggested by Laurin & Reisz (1990, 1996) and Amson & Laurin (2011). If their identification of the adductor shelf is correct, this would indeed be strong evidence for the therapsid status of *Tetraceratops*, as the presence of this feature is a classic synapomorphy of therapsids (Hopson & Barghusen, 1986), with almost no homoplasy. However, several aspects of this reconstruction are problematic. Firstly, the therapsid adductor shelf correlates with a vertically oriented temporal fenestra in all early representatives, linked to the modified bite musculature found in therapsids, unlike the longitudinally stretched reconstruction of *Tetraceratops* required by Laurin & Reisz's (1990) hypothesis (a longitudinally stretched temporal fenestra occurs in varanodontine 'pelycosaurs' and rather derived therapsid subclades). No functional significance can be reconstructed for the autapomorphic, but fragmentarily known, adductor region of *Tetraceratops*. The synapomorphic re-organization of the definite therapsid adductory apparatus (Laurin & Reisz, 1996; citing Kemp, 1982; Kemp, 2007) is in no way reflected in *Tetraceratops*. Remarkably, this has not been noticed before. Moreover, the impact of the depicted interpretation is amplified by redundant coding (Amson & Laurin, 2011: characters 12 & 73).

A broadened adductor shelf with a squamosal strongly resembling that of *Tetraceratops* (as reconstructed by Laurin & Reisz, 1990, 1996) is also found in the varanopid *Varanodon* (pers. obs.). Further similarities result from the dorsal lobe of the maxilla. Thus, a much lower tree position of *Tetraceratops* is possible a priori (compare Romer & Price, 1940), especially when regarding the widely scattered similarities to certain other synapsids. Nonetheless, several other characters of *Tetraceratops* support a sphenacodontian position, specifically dental morphology as well as the shape of the angular and the postfrontal (see below).

The current study has independently found osteological traits in *Tetraceratops* in accordance with Conrad & Sidor (2001). The enigmatic, bar-like structure in the temporal region is herein reidentified as the zygomatic arch (Fig. 3), with associated re-evaluations for most of the other elements in this region. This identification is supported by the direction of compaction in the fossil: the skull roof is twisted the same way as in the right cheek, which moved dorsally. This matches the dislocation of the right quadrate relative to the parasphenoid. Because taphonomic alteration of the type skull involves extensive crushing, but minimal disarticulation or loss, the position of the bar-like structure is best explained as the displacement of the zygomatic arch by a single shear process during diagenetic compression.

Amson & Laurin (2011) disputed the identifications of Conrad & Sidor (2001), arguing that they would require a rotation of the supposed zygomatic arch about 180° and exposure of the quadratojugal on the external side of the skull in life. These arguments are disputed herein: (1) the identity of the

Figure 3. Reconstruction of the partial skull of *Tetraceratops*, exposing the pterygoid-quadrate sheet in the posterior section. Scale bar measures 5 cm. Miniatures show the previous and corrected positions for the questionable bar in the skull of the holotype AMNH FARB 4526, as red and green, respectively.

quadratojugal is questionable in previous interpretations. The true quadratojugal might be identified in a structure that could have been disarticulated before the torsion (Fig. 2). (2) A strong rotation is indeed possible, since the jugal is broken anyway (like in the nasals of *Cutleria*), and a laterally exposed skull would require a torsion of only 90° for certain elements to be in this orientation during compaction. (3) However, a rotation of the zygomatic arch is not necessary, as the orientation of the posterior jugal fragment is not unambiguous. An untwisted arch would match the ventrally concave condition in basal synapsids, instead of the convex arc in most therapsids.

A critical review of the previous reconstructions of the skull of *Tetraceratops* provides additional reasons to question its therapsid identity. The bar that Amson & Laurin (2011) defended as being a squamosal and part of the postorbital has been added to the skull restoration (Fig. 3). The skull length is known from the mandible and pterygoid. Independent from the problematic orientation of the debated bar, there are two reasons to reject the previous reconstruction by Laurin & Reisz (1996: fig. 3): (1) The bar did not reach the required position of the jaw hinge; (2) the pterygoid and epipterygoid were too high, since the only slightly concave bar would produce a shallow posterior skull roof. This is very unlikely, which is why the bar is artificially flexed in the reconstruction of Amson & Laurin (2011: fig. 4C, and preceding). Nevertheless, a typical therapsid pattern with enlarged temporal fenestra and deep cheek is not possible in the temporal region of *Tetraceratops*.

Comparative description

Dermal skull roof. Compared to other sphenacodontians, the premaxilla is strongly built. Contra Laurin & Reisz (1996), the robust architecture is restricted to the anterior part, where it contributes to the ornamentation. Medially, the premaxillae are shallow and weak. Furthermore, the lateral ramus is delicate, which is not found in any sphenacodontian crownward of *Pantelosaurus*, except in the specialist *Secodontosaurus* and some early dinocephalians. A deep root for the first tooth is uncertain at best, if not impossible. The dorsal ramus of the premaxilla is not elongated.

The maxilla shows a moderate ventral convexity. There is a long diastema that lacks a distinct concavity to form a step towards the premaxilla. This jaw morphology is unique, matching neither the sphenacodontid nor the therapsid morphology. The simple presence of a diastema can no longer be considered diagnostic of Therapsida, as it is also known in haptodontine-grade and edaphosaurid Sphenacomorpha (Spindler, 2015; Lucas *et al*., 2018). Homology with the diastema of therapsids has been questioned by Laurin & Reisz (1990, 1996). The alveolar shelf is no broader than required by the tooth sockets. Contra Laurin & Reisz (1996), the constricted condition at the canine level is not necessarily unaffected by compaction. There is a medial swelling of the tooth-bearing shelf, whereas the presence or absence of an ascending buttress is unknown. Dorsally, the maxilla is shallow in its anterior part. Tracing its suture by textural indications, it exhibits a tall lobe in the posterior region. This ascending process is anteriorly bordered by a concave lacrimal suture, as found in some varanopids and caseasaurians, as well as a pelycosaur-grade sphenacodontian (Spindler, 2019) and few therapsids.

The septomaxilla is short and stout, contrasting the facial exposure in therapsids. It is separated from the lacrimal (contradicting Laurin & Reisz, 1996), a condition which seems highly variable among early synapsids. The medial shelf is greatly enlarged and curved ventrally to meet the footplate. This unique pattern is not found in any synapsid, except for the fragmentary snout tip MCZ 2987 (originally referred to *Cutleria*, rejected by Laurin, 1994), which is currently under re-description. In MCZ 2987, the lacrimal process of the septomaxilla is enlarged, resulting in a facial exposure that is as large as in therapsids, but anatomically different. Together with *Tetraceratops*, it demonstrates the variable character distribution that obscures the clear sequence of character acquisition in therapsid origins. The very large septomaxillary foramen of *Tetraceratops* vaguely resembles that of *Archaeovenator* (Reisz & Dilkes, 2003) and *Varanodon* (Reisz & Laurin, 2004; Campione & Reisz, 2011; Benson, 2012: fig. A2).

Since the time of Romer & Price (1940: pl. 21), there has been consensus about the long lacrimal reaching the narial fenestra. Herein, it is outlined taller than previously thought, based on textural observations under multiple magnifications. The long lacrimal separates the maxilla from the prefrontal, contrasting the sphenacodontoid synapomorphy of a nasal-maxilla contact. The lack of this contact in *Tetraceratops* is discussed as a possible reversal by Amson & Laurin (2011). Such a reversal raises the question of its evolutionary explanation (pathological, random, or adaptive), in order to conform with the onus of proof, as it would represent the unique documentation of the reversal of a strong synapomorphy from a single crushed skull of *Tetraceratops*. As seen in the nasal, the facial part of the skull is shortened, meaning that the geometrical constraints during evolution would not derive a secondarily elongate lacrimal from the sphenacodontoid condition. Considering the long lacrimal of *Tetraceratops*, three scenarios can be proposed within a trend-based phylogenetic model: (1) *Tetraceratops* is excluded from Sphenacodontoidea, (2) Sphenacodontoidea is invalid due to polyphyly, or (3) within Sphenacodontoidea the shortened lacrimal evolved twice.

Because of the uncertainties in the dorsal skull roof, the nasals cannot be conclusively outlined. The left nasal is about as long as the prefrontal. The preserved width of the naso-frontal surface indicates that the skull was broader, with most of the dorsal plane tilted sub-parallel to the left cheek. A medial ridge in the nasal pair (Laurin & Reisz, 1996) cannot be proved to be either anatomical or taphonomic.

As in many members of Sphenacomorpha, the prefrontal bears a pocket-like excavation. Usually, it results from the transversely broad orbital rim, which is present in *Tetraceratops*, and the dorsal roofing of the anterior upper rim of the orbit. The latter is not preserved in the described skull, making it uncertain whether the pocket is homologous with other synapsids or results from the prefrontal protuberance. This bulb-like ornamentation is higher than the lateral exposure of the rest of the prefrontal.

Few fragments can be assigned to the frontals with certainty. What Laurin & Reisz (1996: fig. 1A; not Amson & Laurin, 2011: fig. 2A) labeled as the right postorbital does not match their own interpretation, but may in fact be better identified as a frontal fragment. One broad fragment and its eroded impression indicate a shield-like postfrontal.

Regarding the zygomatic arch interpretation for the right side, the jugal posterior process seems strongly built. The preservation of the jugal in two broken and dislocated pieces is not impossible, especially when compared to the broken nasal complex of *Cutleria* (from a similar host rock). On the left side, Laurin & Reisz (1996) traced a narrow tip of the anterior jugal,

which is suggested by the presence of a pale band. This unusual and functionally questionable condition is rejected for the following reasons: first, the right jugal can be merged based on the texture and outline, producing a broad anterior ramus. The area below the left orbit is eroded, but continuous around the break, which Laurin & Reisz (1996) interpreted as the maxillary suture. Moreover, this area exposes a radial texture, definitely fitting the jugal growth center, but not the maxilla. A pale shelf underneath the eroded plane envelops the posteriormost marginal teeth. Thus, the area does not expose the original bone surface, but the lingual side of the eroded jugal overlying the maxilla. If the maxilla was eroded, it would exhibit tooth roots or alveolar bone. In fact, the jugal relic is raised above the maxillary surface. In conclusion, *Tetraceratops* shows an anteriorly deep jugal. This is found in most sphenacodontids and therapsids, but can vary. In early sphenacomorphs of a similar size to *Tetraceratops*, the jugals are conspicuously shallower. This suggests that *Tetraceratops* was adapted for stronger bite forces. Other early members of Synapsida show deep jugals in a variety of subclades (Ophiacodontidae, Sphenacodontidae, Therapsida), probably linked to increasing body size.

Little can be said about the postorbital. Its ventral bar is broad at the mid-height level of the orbit. It cannot be verified whether or not it is overlapped by the jugal. In the small portion where the contact is not eroded, the postorbital overlaps the slender dorsal splint of the jugal.

The squamosal is long in its ventral portion. Subject to the above discussion of the zygomatic arch, the posterior shield-like expansion of the squamosal cannot be observed. This is perhaps due to poor preservation. If anatomically absent, it would support a therapsid affinity more than a varanopid-like condition.

The quadratojugal cannot be located with certainty. It might be the posterior cap of the zygomatic arch, as suggested by Conrad & Sidor (2001). However, the fragment located anteromedial to the zygomatic arch provides a better match with basal sphenacomorph quadratojugals.

Palate, basicranial articulation, and palatoquadrate complex.
The palate is strongly affected by compaction, casting doubt on the sutural patterns. *Tetraceratops* retains the plesiomorphic condition of numerous palatal denticles that are not restricted to certain lines or clusters as in therapsids. Between these denticles, much of the embedding matrix rock is preserved, blurring the sutures of the corresponding bones.

The description of the vomers given by Laurin & Reisz (1996) is confirmed. Its edentulous ventral surface is taken as a true condition with little doubt, based on the teeth placed very posteriorly in the vomer of *Biseridens* (Liu *et al.*, 2010), one of the rare exceptions among Sphenacodontoidea. The actual range of the choana is hidden, but the continuation of the palatal dentition field (further anterior than revealed in the aspect of Fig. 2C) does not allow for a reconstruction of the therapsid condition, in which the choana terminates far beyond the level of the canines.

The palatines may be contoured by their slight dislocation. As in the anterior pterygoid, scattered denticles are visible. No obvious ectopterygoid could be located (contra Laurin & Reisz, 1990, 1996).

A low vertical blade appears to be present in the anterior pterygoid, which is common for haptodontine-grade sphenacodontians, but not Sphenacodontidae (Sphenacodontoidea?) and *Ianthodon*. The quadrate ramus is

extraordinarily tall (description accepted from Laurin & Reisz, 1996), which also raises doubts regarding the supposedly small quadrate. The transverse flange has a specialized dentition, with four markedly enlarged teeth, which resembles no other synapsid except *Secodontosaurus* (Reisz *et al.*, 1992). For the skull reconstruction (Fig. 3), the position of the pterygoid has been estimated from the coronoid eminence and posterior range of the marginal dentition, assuming a functional linkage to the longitudinal position of the pterygoid transverse flange. Considering the mandible length and the shape of the quadrate, the posterior pterygoid seems incompletely preserved.

Two strongly correlating therapsid characters stated for *Tetraceratops* (Laurin & Reisz, 1990, 1996) require detailed commentary: the closure of the interpterygoid vacuity and the reconfigured basicranial articulation. The first is considered to be indicated by an additional posteromedian flange in the pterygoid that contacts the basipterygoid process as in therapsids (Laurin & Reisz, 1996). In fact, these processes are reduced in therapsids because of the fusion of the basicranial articulation. *Tetraceratops* shows a plesiomorphic para-basisphenoid complex with joint processes (Fig. 2). This character corresponds with the presence of a primarily open interpterygoid vacuity. The re-examination of the material clearly shows that the conditions resemble sphenacodontids much more than any therapsid.

The low and shallow quadrate in therapsids and therefore shallow quadrate flange of the pterygoid co-occurs with a low level for the basicranial articulation. In *Tetraceratops*, the tall quadrate ramus matches the early synapsid pattern. The flanges interpreted as forming a posterior closure of the interpterygoid vacuity (Amson & Laurin, 2011) are set high above the primary palate. As in all Sphenacomorpha, there is no median flange. These sub-vertical blades may contribute to the basicranial articulation. As indicated by the basipterygoid processes of the parasphenoid, there is a distinct bifid articulation, affected by the strong compaction. A fused but reopened vacuity such as that observed in derived Dinocephalia (King, 1988: fig. 3-7) cannot be confirmed. Even though the blades might be offset from the pterygoid quadrate ramus, they ascend dorsally and converge the same way as the quadrate flanges in all basal Sphenacodontia.

The basicranial articulation itself is mentioned as present in *Tetraceratops*, in contrast to all other therapsids, where the joint is fused (Laurin & Reisz, 1990, 1996). The authors also discuss that there may have been a limited amount of movement, whereas the exclusion of the epipterygoid indicated an akinetic condition. This is disputed on the basis of close observations. First, the epipterygoid is not well preserved. Second, it cannot be verified that the basipterygoid processes connect with the pterygoid flanges that are supposed to close the interpterygoid vacuity. In fact, the basipterygoid processes are strongly built, contributing to a real joint. In therapsids, the processes are absent or reduced to sharp splints (Orlov, 1958: pl. 28A). Admittedly, this area shows an atypical morphology, but nothing that indicates a definite therapsid interpretation. There is also diversity in the position of the basicranial articulation. In *Tetraceratops*, it is rather high in the skull, otherwise observed only in *Palaeohatteria* and *Dimetrodon*, but unlike therapsids. The basicranial articulation (or stiff contact) relative to the transverse flange of the pterygoid yields information previously unknown for *Tetraceratops* (character introduced by Reisz *et al.*, 1992). The contact is positioned far posterior to the transverse flange in all known basal representatives of therapsid subclades, as well as in most

sphenacodontids. In the crushed skull of *Tetraceratops* the longitudinal shear during compaction was minimal, indicating that the same plesiomorphic condition is present in all non-sphenacodontoid synapsids.

Another striking feature of therapsids considered for *Tetraceratops* is the epipterygoid, previously interpreted as bearing a small ventral plate that did not contribute to the basicranial articulation (Laurin & Reisz 1990, 1996; Amson & Laurin, 2011: character 76). This condition is known in Gorgonopsia and Eutheriodontia, but not in more basal synapsids. The character is related to various modifications, altogether reflecting conditions of the basicranial articulation. In *Tetraceratops*, the epipterygoid is incompletely known. The exposure of the basicranial articulation facet is hidden, if not in the destroyed area. Neither the shape nor the position opposes the condition found in early Sphenacomorpha. The comparison to the ventrally enlarged epipterygoid in *Dimetrodon* (Amson & Laurin, 2011: fig. 4B) is not representative of the initial sphenacodontoid condition.

One of the rare elements clearly outlined in the damaged skull of *Tetraceratops* is a right quadrate. It reveals a posterior squamosal contact resembling the condition of early synapsids, in which the posterior margin of the cheek is not overturned as in therapsids (and initially in juvenile Palaeohatteriidae, Spindler, 2016). The dorsal process of the quadrate is stated to be smaller than in other basal synapsids (Laurin & Reisz, 1990, 1996). This cannot be discussed as a therapsid synapomorphy independently from the obvious autapomorphic nature of *Tetraceratops*. Furthermore, the size of the quadrate might interfere with size effects of proportional differences in sphenacodontoid subclades. A reduced quadrate is a synapomorphy of Therapsida, not fully independent from the enlargement of the temporal region and changes in the braincase and occiput. If reconstructing the skull, with regard to the multiple deformations and considering that the quadrate is not completely exposed, a coding of *Tetraceratops* equaling therapsids appears less convincing. A smaller quadrate is also found in some Ophiacodontidae (Berman *et al.*, 1995). The quadrate of *Tetraceratops* might be only slightly reduced when compared proportionally to Sphenacodontidae, somewhat resembling the condition in *Cutleria* (Spindler, 2015). The height of the quadrate and posterior flange of the pterygoid are also bound to the level of the basicranial articulation. It is possible that the quadrate was much higher than preserved, as indirectly suggested by the position of the quadrate process of the pterygoid, to which it articulated anteriorly in life. As in the posterior pterygoid, the quadrate seems to reflect the same shortening as in the preorbital region. However, the relative size of the quadrate is hard to estimate, since the relation is affected by various proportional modifications.

Braincase and occiput. Laurin & Reisz (1996) describe the parasphenoid accurately, pointing out its basal sphenacodontian configuration. The trapezoidal plate is somewhat narrower than in haptodontine-grade taxa, but lacks the deep sulcus of sphenacodontids. Identified by the position of the carotid foramina, both basipterygoid processes are preserved. The cultriform process is hidden and obviously dorsal to the parasphenoid plate. Its identification in the left orbit (Laurin & Reisz, 1996) is uncertain.

The position of the parasphenoid (Fig. 2C) is consistent with the pterygoid and epipterygoid, whereas the supposed basioccipital and further elements (Amson & Laurin, 2011: fig. 2A) are strongly disarticulated. The separated arrangement of the supraoccipital and the opisthotic, as proposed by Laurin & Reisz (1996), would require an extraordinary disarticulation.

Also, Laurin & Reisz (1996) listed some therapsid characters in the occipital region, such as a wide tabular, a narrow paroccipital process of the opisthotic, and a firm attachment of the braincase to the cheek. Most of these observations are rejected on the basis of the renewed osteological interpretation. The alternate version of Conrad & Sidor (2001) is not fully accepted, as the quadratojugal (instead of the opisthotic) remains questionable. The occipital region is strongly damaged and affected by preparation artifacts. No definitive identifications can be given, although a seemingly complete inventory may be present.

Mandible. The overall form of the mandible is slender. Around the rather posterior position of the coronoid, the dorsal edge of the mandible rises, but the surangular itself has an almost straight dorsal edge. This geometrical configuration is common among Sphenacodontoidea, but is also seen in *Edaphosaurus*, thus does not specifically resemble *Titanophoneus* (contra Laurin & Reisz, 1996).

Compared to other early sphenacodontians, the dentary is proportionally elongated. Its symphysis is low compared to Sphenacodontoidea, although underestimated in the reconstruction by Laurin & Reisz (1996: fig. 3A). The diagenetically bent dentary illustrates the mode of deformation that affected the specimen. The posterior end of the dentary is not at the dorsal edge of the mandible (Laurin & Reisz, 1996), which is tentatively confirmed.

The angular bears a ventral keel, which seems to be pronounced, as the sculpturing is much deeper than in early sphenacomorphs. However, it remains questionable whether a reflected lamina is present (Amson & Laurin, 2011). No obvious notch is preserved. Regarding this character, *Tetraceratops* appears less derived than *Pantelosaurus*. Posterior to the angular, a strong process is interpreted as another horn-like protuberance by Laurin & Reisz (1996). Both the texture and general orientation exclude it from being the reflected lamina (Conrad & Sidor, 2001). Based on its surface striation, it could also be a surangular process. Particularly in this feature, there is a resemblance to *Pantelosaurus* (Spindler, 2016).

The surangular is strengthened in its posterior portion. A hidden bone fragment underneath the right jugal superficially resembles an additional tooth, but in fact belongs to the surangular. No surangular vertical lamina is present, otherwise commonly found in basal therapsids.

The description and identification of the articular provided by Laurin & Reisz (1996) is tentatively accepted. The articular glenoid forms elongate, oblique troughs in *Tetraceratops*, whereas a screw-shaped hinge is found in other Sphenacodontia, and longitudinal troughs in non-sphenacodontian synapsids.

Marginal dentition. The dentition is comparable to the pattern of reduction and differentiation found in Sphenacodontoidea, but it reveals a specialized, autapomorphic condition. The tooth type is barely observable, since no tip is completely preserved. The curvature of the crown seems unspecialized, neither strongly bent like in sphenacodontids and many therapsids, nor straight like in Caseasauria or *Pantelosaurus*. The basal sections are mostly round, but, because of the compressed bases of a few teeth, the outline is uncertain. One maxillary stump appears to show a rectangular cross section with plicidentine

infolding as in a variety of sphenacodontians (Brink *et al*., 2014), but lacks further evidence and likely instead represents the alveolar bone, considering that its canine-like size would otherwise collide with neighboring tooth positions.

Each premaxilla bears three teeth, of which the first is outstandingly enlarged. Unfortunately, all tips are missing, hampering the functional interpretation as slender fangs, stout breakers, or even rodent incisors (compare MacDougall *et al*., 2017; Lucas *et al*., 2018). Whereas uneven premaxillary teeth are common among early synapsids, therapsids including *Raranimus* evolved an incisiviform region of evenly enlarged premaxillary teeth.

It can be verified that a small precanine is preserved on each side, representing the smallest marginal tooth in *Tetraceratops*. The loss of precanines has been considered as supporting a therapsid affinity of *Tetraceratops* (Laurin & Reisz, 1990). However, the presence of a precanine tooth has been documented since Romer & Price (1940: pl. 21). Precanine reduction occurred in derived Sphenacodontidae.

Tetraceratops retained the double caniniform arrangement of less derived reptiles and synapsids. The posterior socket on the left side, seen as a replacement pit (Laurin & Reisz, 1996) reveals a round basal section. The extrapolation of presumably very long canines (Laurin & Reisz, 1996) is reasonable, but might ignore the possibility of shorter teeth with apical bending zones.

In the postcanine series, eight to nine positions are preserved on the left side. As the most posterior of them has already reached the level of the orbit, this is probably close to the true number.

The right dentary preserves 19 teeth, with three additional positions. There are 17 smaller teeth posterior to the largest one in the symphysial area, with the last one not shown in the drawing (Fig. 2B). In the tip of the dentary, the second tooth is enlarged, probably forming a prominent caniniform, as seen in some sphenacodontids and common in therapsids. Medial to the first tooth, the lingual shelf is raised, not to be confused with an additional tooth.

DISCUSSION OF RELATIONSHIPS

Matthew (1908) considered *Tetraceratops* most comparable to *Dimetrodon* among 'pelycosaurs', but did not explicitly refer it to any particular 'pelycosaurian' family. Early classifications of *Tetraceratops* mostly suggested a sphenacodontid placement, as summarized by Romer & Price (1940; see also Abel, 1919). However, Romer & Price (1940) themselves did not accept that classification, and instead tentatively included *Tetraceratops* among the less derived 'pelycosaurs' as a possible eothyridid. Some of the proposed dental features supporting this link are now thought to have arisen convergently in different early synapsid groups, such as between Caseasauria (Reisz *et al*., 2009; Spindler *et al*. 2016) and Ophiacodontidae (Brinkman & Eberth, 1986; Lucas, 2013), with *Tetraceratops* being potentially another example (Reisz, 1986).

Laurin & Reisz (1990, 1996) were the first to thoroughly re-evaluate the morphology of *Tetraceratops* and include it in a cladistic analysis. They concluded that *Tetraceratops* is the oldest and basalmost known therapsid. However, there are several issues with this conclusion: (1) their classification strongly depends on the osteological interpretation of damaged portions of the crushed skull; (2) because the lacrimal of *Tetraceratops* reaches the naris, a shortened lacrimal

would no longer be a synapomorphy of Sphenacodontoidea. The hypothesis that therapsids evolved directly from a haptodontine-grade form (Kemp, 2006) would be supported by this interpretation, making therapsids and sphenacodontids convergent in many details. However, Sidor & Hopson (1998) questioned this interpretation, and the therapsid status of *Tetraceratops*.

Conrad & Sidor (2001) carried out a new cladistic analysis testing the relationships of *Tetraceratops*, recovering a basal sphenacodontian ('haptodontine') placement based on similar osteological re-identifications as found by the current study. Unfortunately, the full details of their analysis were never published. However, they did mention that *Tetraceratops* lacks many synapomorphies of early therapsids, and even lacks one (unreported) trait uniting "*Haptodus*" *garnettensis* with more crownward synapsids (Conrad & Sidor, 2001). Sidor (2003) figured *Tetraceratops* as the sister taxon to the rest of Therapsida in his analysis of mandibular evolution in synapsids; however, this was a composite phylogeny reflecting the work of Laurin & Reisz (1990, 1996) and not the result of a new cladistic analysis (see also the critical perspective in Rubidge & Sidor, 2001). Kemp (2006) rejected *Tetraceratops* as an informative part of the discussion about stem therapsids, and the taxon has been left out of many recent synapsid phylogenetic analyses.

In their description arguing for a basalmost therapsid position of the new taxon *Raranimus*, Liu *et al*. (2009) plotted *Tetraceratops* as unresolved among Sphenacodontoidea (see also Brink *et al*., 2015). After discussing character histories, Liu *et al*. (2009) tended to exclude *Tetraceratops* from Therapsida. Amson & Laurin (2011) modified the matrix of Liu *et al*. (2009), recovering *Tetraceratops* as the sister taxon to *Raranimus* and other therapsids. However, they largely reiterated the pro-therapsid interpretations of Laurin & Reisz (1990, 1996), adding only a few supporting characters, and did not present a detailed anatomical re-investigation of *Tetraceratops* (interpretations affirmed by 'personal knowledge', Amson & Laurin, 2011: p.304). Furthermore, they did not include additional 'haptodontine' taxa in their analysis, with "*Haptodus*" *garnettensis* treated as an outgroup and only *Dimetrodon* representing a pelycosaur-grade ingroup taxon. This sampling a priori limits the recoverable positions of *Tetraceratops* to either the outgroup of Sphenacodontoidea or within Therapsida, and ignores the possibility that it shares additional characters with other 'pelycosaurs' (i.e., even if it does have shared features with therapsids, it does not test whether those features could be homoplastic).

In order to test the alternative interpretation suggested by Conrad & Sidor (2001), a second analysis was carried out by Amson & Laurin (2011) in which they treated the character codings criticized by the former authors as unknown (?) in *Tetraceratops*. This analysis also recovered *Tetraceratops* as a basal therapsid. However, this approach is methodologically questionable. Rather than treating these character states as unknown, a better test would have been to code them using the interpretations of Conrad & Sidor (2001), including additional changes regarding the tabular or opisthotic. Furthermore, characters 12 and 73 yield redundancies. With this in mind, the reanalysis of Amson & Laurin (2011) cannot be considered a true refutation of the results of Conrad & Sidor (2001).

The most recent analyses including *Tetraceratops* recovered it as a less-derived member of the Sphenacodontidae (Brocklehurst & Brink, 2017; Brocklehurst *et al*., 2018), which to some extent parallels its earliest systematic evaluation (Matthew, 1908). Another, rather divergent, idea suggested a

similarity with the diadectomorph *Tseajaia* (D. Peters, pers. comm. 2015), a detailed rejection of which was provided in a precursor to the current study (Spindler, 2015).

Preliminary cladistics tests were carried out by Spindler (2015), applying a completely revised character list to *Tetraceratops*, a wider spectrum of 'pelycosaurs', and early therapsid subclades scored from their best-known representatives. Although questioned a priori, the monophyletic status of Sphenacodontoidea (Sphenacodontidae plus Therapsida) was confirmed once more. In different versions of the analysis, *Pantelosaurus*, *Tetraceratops* and *Cutleria* plotted at various positions around this node, possibly implying a common origin from a quick radiation. The changing positions of these terminal taxa depend on particular character wording, coding of poorly preserved features, and taxa combinations. *Tetraceratops* appeared near therapsids in preliminary trees, mostly as the sister taxon to Sphenacodontoidea. In some cases, it nested among basal Sphenacodontidae, and rarely more basally than *Ianthodon* (maybe through bias due to a greater quantity of autapomorphies that lower the portion of trend-related characters and thus exclude *Tetraceratops* from a certain sequence of character acquisition). A phylogenetic position on the therapsid branch (closer to mammals than to *Sphenacodon*) was never recovered. A revised analysis in the context of early sphenacodontians is currently being prepared, whereas the present study aims to avoid more preliminary tree hypotheses.

This sister-taxon relationship of Sphenacodontidae and Therapsida is well-supported, forming the node-based Sphenacodontoidea (Reisz *et al*. 1992), and has been supported by all phylogenetic analyses of early synapsids (Reisz, 1980; Hopsen & Barghusen, 1986; Reisz *et al*., 1992; Laurin, 1993; Sidor, 2003; Benson, 2012). This implies that there must have been a Carboniferous origin for therapsids, even though any certain fossil record is lacking (Sidor & Hopson, 1998; Spindler, 2014, 2019). Apparently, the therapsid assignment of *Tetraceratops* was promoted by a nowadays outdated perception of 'Olson's Gap' with a turnover from 'pelycosaurs' to therapsids, instead of an early Permian therapsid ghost lineage (for recent discussion see Lucas & Heckert, 2001; Reisz & Laurin, 2001, 2002; Lucas 2002, 2004; Benton, 2012). The refutation of a therapsid identity for *Tetraceratops* herein returns the therapsid ghost lineage to full length, and suggests that new fossils are required to resolve this gap.

CONCLUSIONS

The presence of supposed therapsid traits in the highly autapomorphic early Permian synapsid *Tetraceratops* are refuted through a reinterpretation of the cranial morphology in this taxon. The new results support a pelycosaur-grade status. *Tetraceratops* has been an important taxon in discussions of therapsid origins as the only record filling the immense temporal and morphological gap between Therapsida and their pelycosaur-grade sister group, the Sphenacodontidae. Current understanding of early synapsid evolution requires a better-fitting morphological link than *Tetraceratops* as no definite therapsid older than the middle Permian has so far been identified.

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